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INTERPRETING ASPECTS OF PLANT RARITY

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PLEISTOCENE AND HOLOCENE FLORAS OF  
NEW ENGLAND AS A FRAMEWORK FOR  
INTERPRETING ASPECTS OF PLANT RARITY

NORTON G. MILLER

ABSTRACT

The times of arrival from southern sources and the rates and directions of migration are now known for many species of forest trees in New England. This information has made possible the reconstruction of generalized vegetation types for the period 14,000 to 9000 yr. B.P., as has been done recently by R. Davis and G. Jacobson for Vermont, New Hampshire, and Maine. The regional pattern, which has been based mainly on studies of fossil pollen from wind-pollinated trees, includes a diverse and biogeographically interesting flora of bryophytes, herbs, and shrubs that only recently is becoming defined through studies of plant macrofossils. The most thoroughly investigated sites, Tom Swamp (Massachusetts), Columbia Bridge (Vermont), and Upper South Branch Pond (Maine) have produced late-glacial floras with numerous calcicoles, some of which are rare or lacking in the present New England flora. Fossils of arctic-alpine species are also present at these sites, which are all at low elevations. A prominent calcicole element exists in the late-glacial fossil record regardless of whether the extant flora near a site contains such plants. This pattern is evident for both seed plants and bryophytes. For areas with acidic soils, the loss of calcicoles is correlated with the late-Pleistocene arrival of spruce (as documented by increases in macrofossils) at 12,800 yr. B.P. in southern New England, and some 2300 radiocarbon years later in north-central Maine. Leaching, humus or litter accumulation, and other aspects of soil genesis may have been responsible for the loss, but what caused the pattern is poorly understood. As viewed on a continental scale and over thousands of years, the elimination of calcicoles has left fragmented ranges and rare occurrences in eastern North America of boreal or northern plants that otherwise are today widespread to the west.

**Key Words:** Arctic-alpine plants, biogeography, calcicoles, late-Pleistocene floras, New England, paleoecology, plant macrofossils, plant rarity

INTRODUCTION

The New England flora assembled from diverse sources during and after late-Pleistocene deglaciation. The margin of the continental ice sheet had reached a terminal position south of Cape Cod 18,000 radiocarbon years Before Present (yr. B.P.), and by ca. 12,000 yr. B.P. the margin was located in the St. Lawrence River Valley (Dyke and Prest, 1987). Studies of fossil pollen throughout this region (M. Davis, 1983; R. Davis and Jacobson, 1985), show that successive immigrations of populations of various tree species took place during the late Pleistocene and Ho-

locene after an initial period in which trees were sparse or absent and plant communities consisted of mosses, herbs, and shrubs. An analysis of 47 radiocarbon-dated pollen or plant macrofossil records from northern New England and adjacent Canada showed tundra, woodland, and forest vegetational phases extending one after another across northern New England between 14,000 and 9000 yr. B.P. (R. Davis and Jacobson, 1985). Poplar, spruce, paper birch, jack pine, balsam fir, tamarack, ironwood-ash-elm, oak, maple, white pine, and hemlock arrived in that order and spread in time-transgressive migrations generally northward across this region, with, however, some local differences in sequence and timing due to elevation and other factors.

Much of the late-Quaternary paleobotanical record of New England consists of changing percentages and accumulation rates of pollen from various wind-pollinated forest trees, which are only a small subset of the total flora. Alternative or supplementary sources of information about the history of this flora, although little explored at present, are from seeds, fruits, leaves, and other vegetative structures (plant macrofossils; Birks, 1980) occurring dispersed in lake, peatland, and alluvial sediments (Anderson et al., 1986; Pierce and Tiffney, 1986). Because plant macrofossils are less apt than pollen to be transported over long distances, they are a sample of the vegetation that once existed near the site of recovery. This circumstance, coupled with the greater potential of identification to species than can be achieved for many common pollen types, makes macrofossils highly useful biogeographically.

In this paper I summarize my and other recent studies of late Quaternary plant macrofossils from sites in New England. I use these data to explore connections between late Pleistocene and contemporary floras and to provide a temporal setting for the development of three related patterns of plant rarity, namely arctic-alpine species, northern calcicoles, and the "western" North American element in the flora of New England and nearby areas. My approach is floristic and involves the relationship between where certain species now occur in New England and where they were in the past in this region, as well as the factors or events that can be correlated with changes in distribution. Studies of both vascular plant and bryophyte fossils are included, the latter primarily as a source of information about the edaphic character of late-glacial terrestrial environments.

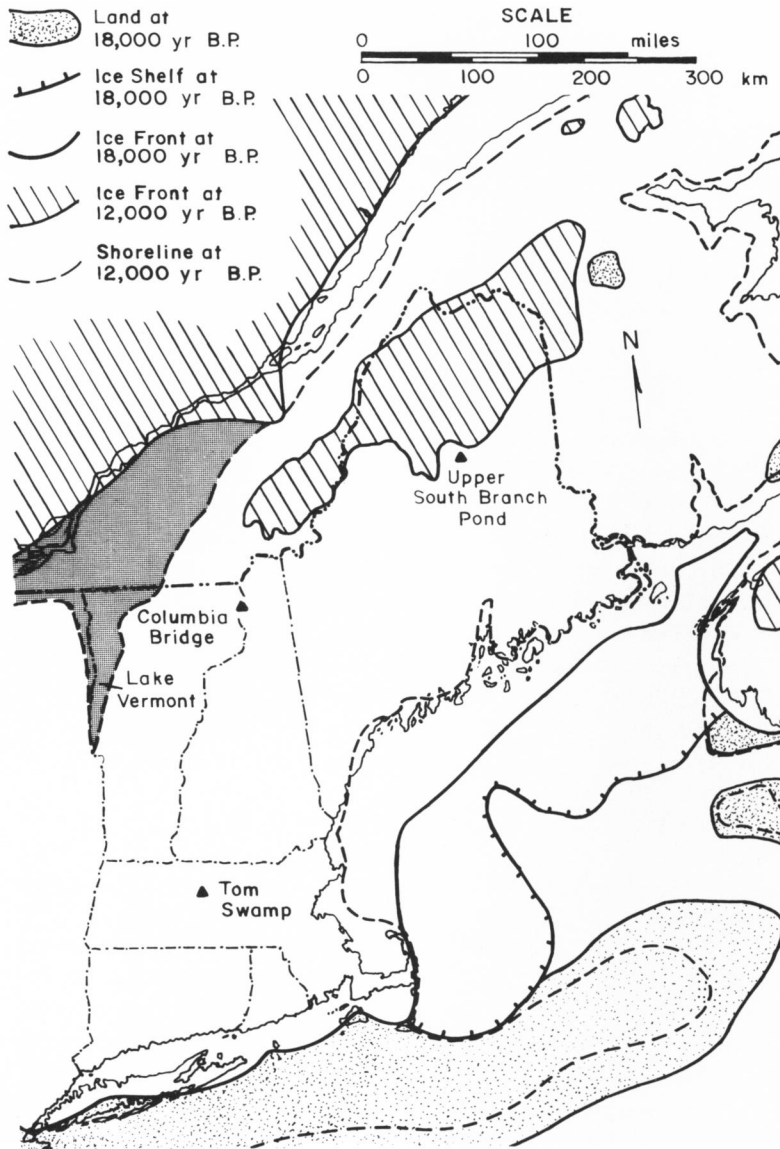


Figure 1. Map of New England and adjacent areas showing position of ice margins and other landscape features at 18,000 and 12,000 yr. B.P. (after Dyke and Prest, 1987). Triangles indicate location of sites discussed in the text.

## SITE DESCRIPTIONS AND METHODOLOGY

Studies at Tom Swamp (Massachusetts), Columbia Bridge (Vermont), and Upper South Branch Pond (Maine) have produced large and diverse late-Pleistocene plant macrofossil assemblages. Other studies of macrofossils in New England (Argus and Davis, 1962; Tolonen and Tolonen, 1984) provide supporting data. The small number of sites from which published records are available does not imply that plant macrofossils are uncommon in New England Pleistocene and Holocene deposits, but indicates instead that most Quaternary paleoecological studies in the region have focused on pollen.

The fossil floras described here are from distant parts of New England (Figure 1), and their depositional settings also differ in a number of ways (Table 1). The Columbia Bridge flora (Miller and Thompson, 1979) was the first late-glacial macrofossil assemblage in New England to be studied in detail using modern techniques. Because it included numerous calcicoles, reflecting perhaps the local presence of calcareous bedrock and glacial drift, study sites for comparison were sought in areas of acidic bedrock. Those selected were Upper South Branch Pond (Anderson et al., 1986) and Tom Swamp (M. Davis, 1958; Gaudreau, 1986) on which related paleoecological studies had been undertaken by other investigators. The three sites have been thoroughly radiocarbon dated, and stratigraphic pollen data are available for all of them.

Plant macrofossil stratigraphies have been published for Upper South Branch Pond (late Pleistocene and Holocene vascular plants and mosses; Anderson et al., 1986) and Tom Swamp (late Pleistocene bryophytes; Miller, 1987a). Presented here are stratigraphic data for vascular plant macrofossils recovered from the late Pleistocene and early Holocene sediments at Tom Swamp. In contrast to the other two records, the Columbia Bridge plant macrofossils (Miller and Thompson, 1979; Miller, 1987b) appear to have been deposited during a short period of time. Because their distribution did not change in any obvious pattern within the sampled stratigraphic interval, the fossils are treated as a single assemblage.

The macrofossils came from sediments collected either with a piston corer operated from the peatland or lake surface (Tom Swamp, Upper South Branch Pond) or by digging by hand at an

Table 1. Site characteristics of late-Quaternary plant macrofossil floras in New England.

Character	Tom Swamp <sup>1</sup>	Columbia Bridge <sup>2</sup>	Upper South Branch Pond <sup>3</sup>
Location	42°31'N, 72°13'W; Worcester Co., MA	44°51'N, 71°33'W; Essex Co., VT	46°5'N, 68°54'W; Piscataquis Co., ME
Elevation	232 m	301 m	300 m
Present setting	250-ha peatland	outcrop of laminated sand, silt, and clay of proglacial (?) lake of unknown size	34-ha lake
Bedrock geology	aluminous mica and quartzose schists, aluminous phyllite	quartz-muscovite phyllite and schist, calcareous mica schist, quartzose and micaceous crystalline limestone	rhyolite
Age	12,830 ± 120 yr. B.P. 11,580 ± 110 yr. B.P. 10,080 ± 100 yr. B.P.	11,390 ± 115 yr. B.P. 11,540 ± 110 yr. B.P.	11 dates, 10,965 ± 230 to 230 ± 70 yr. B.P.

<sup>1</sup> Miller, 1987a, this paper.<sup>2</sup> Miller and Thompson, 1979.<sup>3</sup> Anderson et al., 1986.

outcrop (Columbia Bridge). The fossils were concentrated by flushing fine-grained sediment particles through a 250 or 500  $\mu\text{m}$  sieve after the samples had been disaggregated in tap water, warm 10% KOH, or warm 5%  $\text{Na}_2\text{CO}_3$ . Plant fossils removed from the residues under low-power magnification were identified by comparing them with a reference collection derived from critically determined herbarium specimens. It was sometimes necessary to use special techniques (scanning electron microscopy, anatomical sections, removing the outer layers of seeds and fruits) to attain acceptable comparisons. The geographic scope of the reference collection proved to be an important consideration because the fossils sometimes represented species unknown in the present New England flora.

The designation "cf.," as used in this paper, indicates some uncertainty about an identification. In these cases the fossils were good matches for reference specimens, but other species in the same genus shared some features with the fossil. In a few cases, all species of a genus had similar seeds, and identifications beyond genus were not possible.

LATE-PLEISTOCENE PLANT-MACROFOSSIL AND PRESENT  
FLORAS OF NEW ENGLAND COMPARED

### Tracheophytes

Sediments at Tom Swamp (TS), Columbia Bridge (CB), and Upper South Branch Pond (USBP) produced fossils of 36 different vascular plants, 28 of which were identified firmly to species, six to cf. species determinations, and two to genus only (Table 2). Eight of the 34 species are not known as members of the present flora of New England (Fernald, 1950; Seymour, 1982). However, most of these occur in areas adjacent to the Gulf of St. Lawrence, especially on the Gaspé Peninsula, Québec. The single exception is *Saxifraga* cf. *flagellaris* Willd.<sup>1</sup>, a circumarctic species found also as a disjunct in the mountains of the western United States and in Asia (Hultén and Fries, 1986, map 1019). It is represented by subsp. *platysepala* (Trautv.) Porsild in the Canadian Arctic Archipelago and northern and northeastern Greenland. Seeds re-

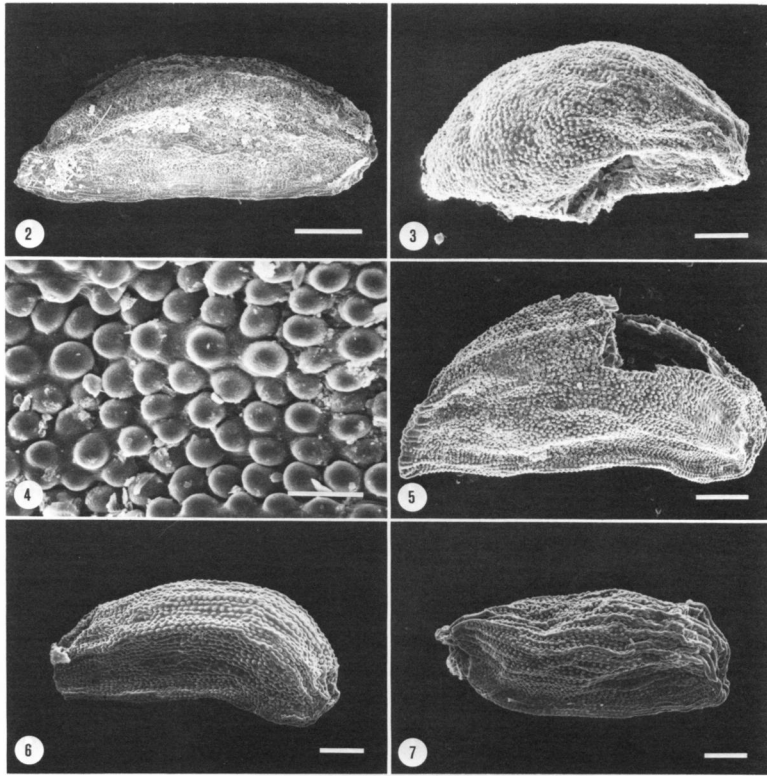
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<sup>1</sup> Vascular plant names are mostly those in Fernald (1950). If different, or if a species is not present in the *Gray's Manual* range, authorship is supplied.

Table 2. Late-Pleistocene tracheophytes of New England based on plant macrofossils. Asterisks (\*) denote species that are not present members of the New England flora.

Species	Tom Swamp	Columbia Bridge	Upper South Branch Pond
<i>Selaginella selaginoides</i>	•	+	•
<i>Woodsia ilvensis</i>	•	+	•
<i>Juniperus communis</i>	•	+	•
<i>Potamogeton filiformis</i>	•	+	•
<i>P. pusillus</i>	•	+	•
<i>Eriophorum alpinum</i>	+	•	•
* <i>Carex bipartita</i>	•	+	•
<i>C. aquatilis</i>	•	+	•
* <i>Salix vestita</i>	•	+	•
<i>S. herbacea</i>	+	+	+
<i>S. cf. uva-ursi</i>	+	+	+
<i>S. cf. argyrocarpa</i>	•	+	•
<i>Populus balsamifera</i>	•	+	•
<i>Betula cf. glandulosa</i>	•	+	•
<i>Oxyria digyna</i>	•	+	•
<i>Polygonum ramosissimum</i> cf. var. <i>prolificum</i> Small	•	+	•
* <i>Arenaria cf. dawsonensis</i>	•	+	•
<i>Silene acaulis</i>	+	+	•
<i>Ranunculus cymbalaria</i>	•	+	•
<i>Draba</i> sp.	+	+	•
* <i>Saxifraga cf. flagellaris</i>	+	•	•
<i>S. aizoides</i>	•	+	•
<i>S. paniculata</i>	•	+	•
* <i>Parnassia cf. kotzebuei</i>	•	+	•
<i>Sibbaldia procumbens</i>	•	+	•
* <i>Dryas integrifolia</i>	+	+	+
* <i>D. drummondii</i>	•	+	•
<i>Rubus chamaemorus</i>	•	•	+
* <i>Elaeagnus commutata</i>	•	+	•
<i>Shepherdia canadensis</i>	•	+	•
<i>Ledum groenlandicum</i>	•	+	•
<i>Rhododendron lapponicum</i>	•	+	•
<i>Harrimanella hypnoides</i>	+	•	•
<i>Arctostaphylos uva-ursi</i>	•	+	•
<i>Vaccinium uliginosum</i> var. <i>alpinum</i>	+	+	+
<i>Gentianopsis</i> sp.	•	+	•

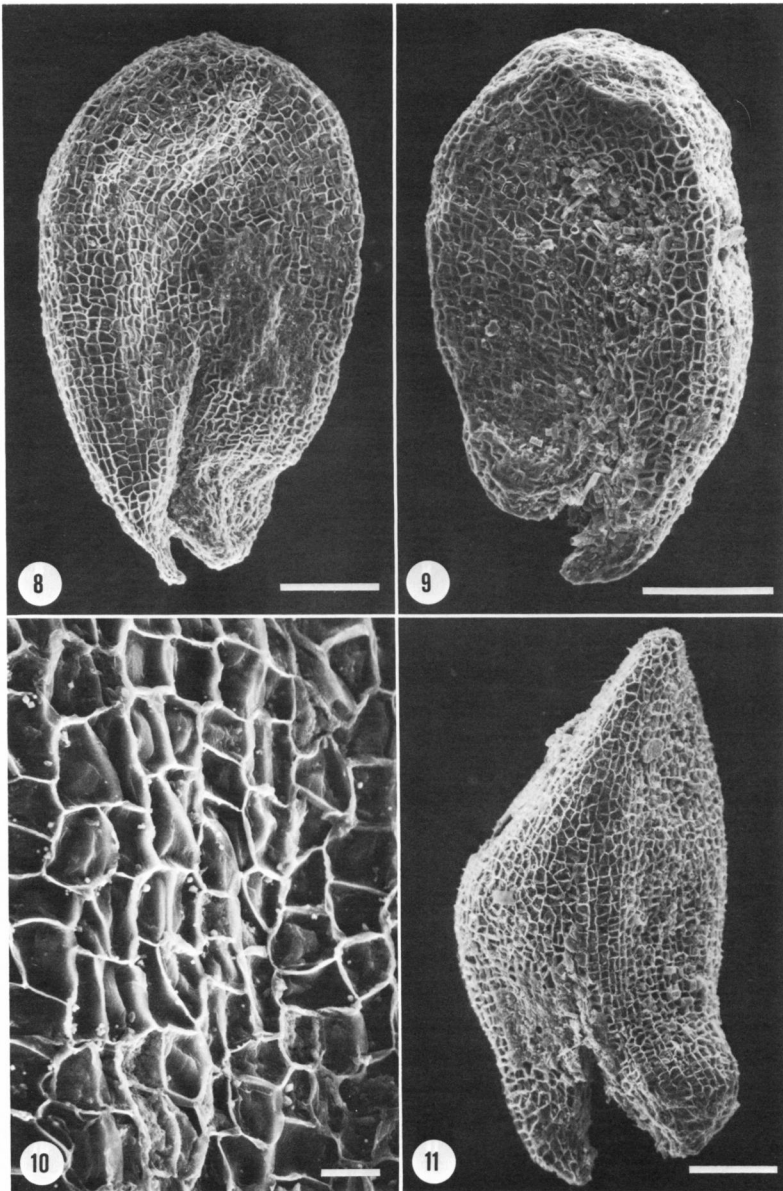




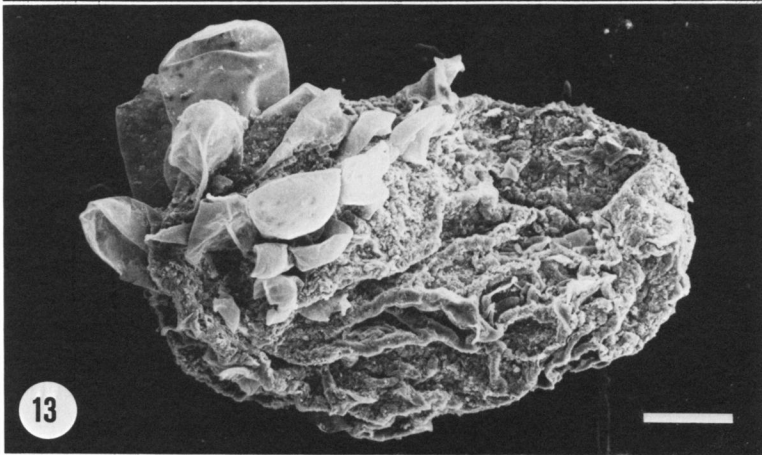
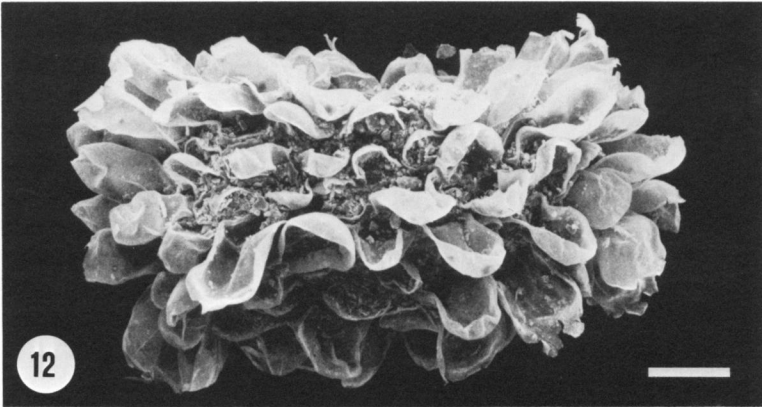
Figures 2–7. Seeds of *Saxifraga*. 2–5. *S. cf. flagellaris*, late-Pleistocene fossils from Tom Swamp, Massachusetts. 4. Papillose surface of seed (Figure 2) enlarged. 6. *S. flagellaris* (Canada, N.W.T., e. slope of Richardson Mts., 68°N, 136°W, Porsild 6828, 15–17 Aug. 1933 (H)). 7. *S. cespitosa* (Canada, Québec, Richmond Gulf, e. coast of Hudson Bay, Abbe *et al.*, 1 Aug. 1939 (GH)). Scale bars: 2, 3, 5, 6, 7 = 100  $\mu\text{m}$ ; 4 = 10  $\mu\text{m}$ .

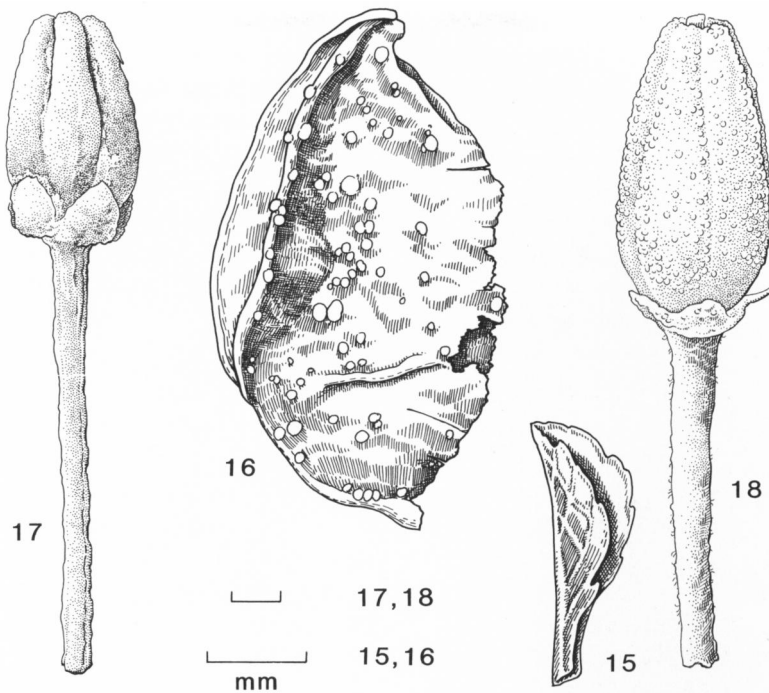
ferred to *S. flagellaris* were recovered from TS (Figures 2–5), and while they agreed well with reference specimens in size and general surface microstructure, the density of seed-coat papillae did not match convincingly (cf. Figures 2, 3, 5 with 6). Another saxifrage with papillose seeds, *S. cespitosa*, offered a less satisfactory comparison (Figure 7), and I can find no other acceptable candidates in the North American flora or in Kaplan's exhaustive studies (1981) of seeds of *Saxifraga*.

I have been unable to identify beyond genus probable seeds



Figures 8–11. Late-Pleistocene seeds of *Draba*-type from Tom Swamp, Massachusetts. 10. Enlargement of surface (Figure 8), outer periclinal cell walls absent. Scale bars: 8, 9, 11 = 100  $\mu\text{m}$ ; 10 = 10  $\mu\text{m}$ .



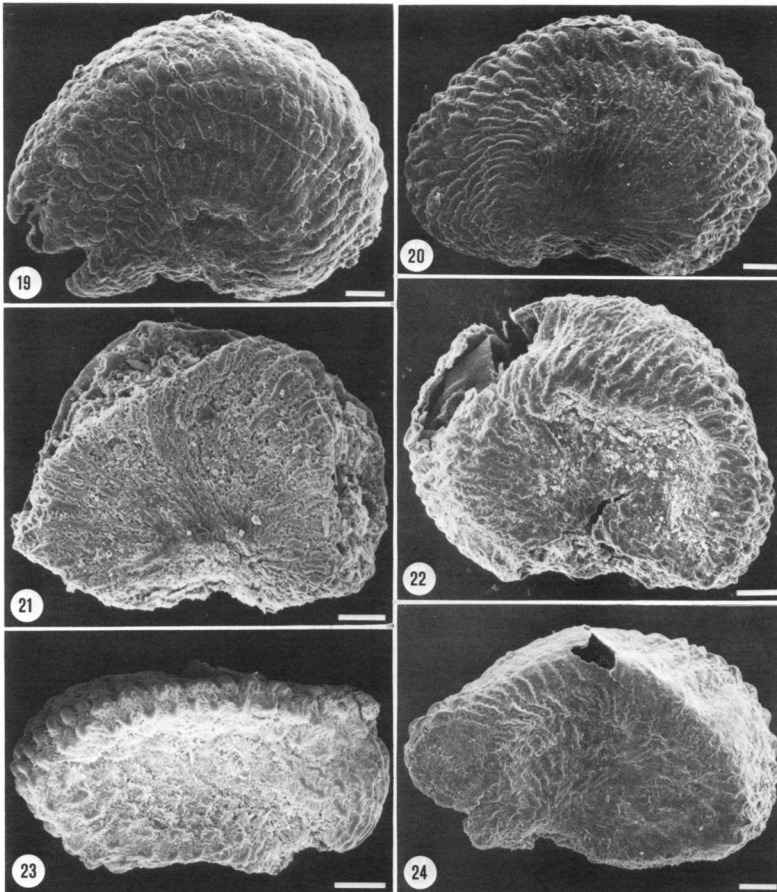


Figures 15–18. Plant macrofossils from the Columbia Bridge Site, Vermont, and a comparative specimen. 15. Juvenile leaf of *Salix herbacea* (fossil). 16. Eroded capsule of *Draba* sp. (fossil), replum visible at left; the numerous round structures are fungal fruiting bodies. 17, 18. Capsules of *Rhododendron lapponicum*. 17. Fossil. 18. From herbarium specimen (Canada, w. Newfoundland, North Arm, Bay of Islands, Long & Fogg 356, 4 Sept. 1926 (GH)).

and a fruit of *Draba* (TS, Figures 8–11; CB, Figure 16), a seed of *Gentianopsis* (CB, Figure 12), achenes of *Potentilla* sp. (TS, CB, USBP), seeds of *Arenaria* and Cruciferae and fruits of Gramineae (TS, USBP), achenes of Compositae (TS, CB), seeds of *Juncus*, fruits of *Ranunculus* subg. *Batrachium* and *Carex* spp., and a needle of *Juniperus* (TS), stem fragments of *Equisetum*, recep-

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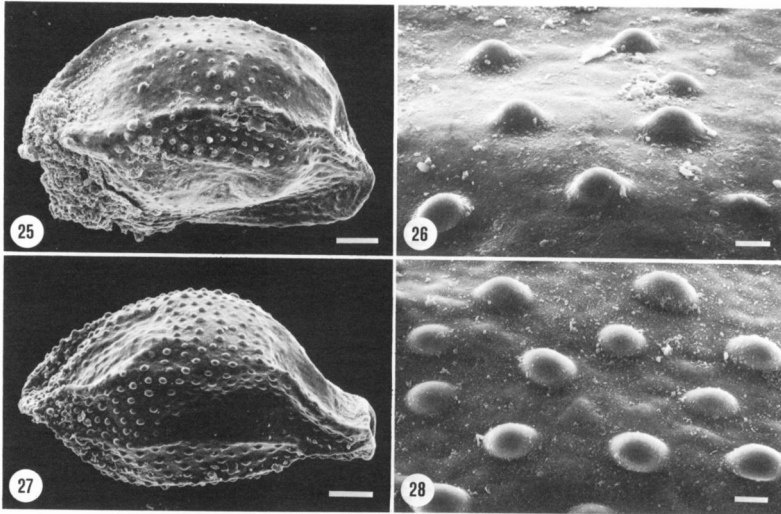
Figures 12–14. Seeds of *Gentianopsis*. 12. Fossil seed from Columbia Bridge Site, Vermont. 13. Fossil seed from Brampton Esker Site, Ontario, described in Terasmae and Matthews (1980). 14. Seed of *Gentianopsis procera* (Canada, Québec, Baie-des-Chaleurs, Rivière Bonaventure, Marie-Victorin 44573, 15 Aug. 1931 (GH)). Scale bars = 100  $\mu$ m.



Figures 19–24. Seeds of *Silene acaulis*. 19, 20. From herbarium specimen (Canada, Québec, Wakeham Bay, Hudson Strait, *Malte 126956*, 24 July 1933 (GH)). 21–23. Late-Pleistocene fossils from Tom Swamp, Massachusetts. 24. Late-Pleistocene fossil from Columbia Bridge Site, Vermont. Scale bars = 100  $\mu\text{m}$ .

tacles of *Geum* (CB), and fruits of Cyperaceae (USBP). Only a few needles or needle or cone fragments of *Picea* were associated with these fossils at TS and CB.

The present geographical affinities of the plants listed in Table 2 are varied. Some belong to the arctic-alpine element (e.g., *Salix herbacea* (Figure 15), *S. cf. uva-ursi*, *Oxyria digyna*, *Silene acaulis* (Figures 21–24), *Saxifraga aizoides*, *S. cf. flagellaris* (Figures 2–



Figures 25–28. Seeds of *Saxifraga paniculata*. 25. Late-Pleistocene fossil from the Columbia Bridge Site, Vermont. 26. Papillose surface of fossil (Figure 25) enlarged. 27, 28. Comparative SEM micrographs, seed from herbarium specimen (Canada, Ontario, Thunder Bay District, mouth of Black River, Schreiber, *Hosie et al.* 2129, 21 July 1937 (GH)). Scale bars: 25, 27 = 100  $\mu\text{m}$ ; 26, 28 = 10  $\mu\text{m}$ .

5), *S. paniculata* Mill. (*S. aizoon*) (Figures 25, 26), *Sibbaldia procumbens*, *Rhododendron lapponicum* (Figure 17), *Harrimannella hypnoides* (L.) Coville, *Vaccinium uliginosum* var. *alpinum*) and are restricted to present to high-elevation stations in New England or to a few edaphically and microclimatically favorable habitats elsewhere in this region. Others (e.g., *Selaginella selaginoides*, *Eriophorum alpinum* L., *Salix* cf. *argyrocarpa*, *Populus balsamifera*, *Shepherdia canadensis*, *Ledum groenlandicum*, *Arctostaphylos uva-ursi*) are boreal, subarctic, or subalpine in distribution. A third group has a similar northern distribution, but the ranges of the individual species are fragmented into western and eastern North American segments. Examples include *Salix vestita*, *Parnassia* cf. *kotzebuei*, *Dryas drummondii*, and *Elaeagnus commutata*, none of which is presently native to New England.

### Bryophytes

Associated with fossils of species listed in Table 2 were plant fragments of 66 species of mosses (Miller, 1987a), and nine ad-

Table 3. New England late-Pleistocene moss floras (from Miller, 1987a).

Site	No. Species	% in		% in		% Calicoles		% Calicoles	
		Local	Regional	Local	Regional	in Local	in Regional	Flora	Flora
		Flora	Flora	Flora	Flora	Flora	Flora	Flora	Flora
Tom Swamp	32	41	75	47	20	60			
Columbia Bridge	45	82	82	71	75	75			
Upper South Branch Pond	24	38	75	38	0	22			

ditional species have been recorded at other sites in New England and nearby Quebec (Mott et al., 1981; Tolonen and Tolonen, 1984). Most of these mosses are presently distributed widely within boreal and subarctic North America, although some have more restricted arctic or arctic-alpine ranges. For a few, the fossils represent occurrences 600–3000 km south of present stations, which are mostly in arctic Canada (Miller, 1987b).

The sizes and some general floristic characteristics of the late Pleistocene moss assemblages at TS, CB, and USBP are summarized in Table 3. In common with moss assemblages of similar age elsewhere in glaciated eastern and northern North America (Miller, 1987a), the three assemblages contain many species that are members of the present local (i.e., within 100 km or less of the sites) or regional (i.e., state) floras. As has been pointed out elsewhere (Miller, 1984), this distribution may indicate that the moss flora of glaciated North America was derived in large part from populations that grew in close association with the fluctuating ice margins rather than from distant sources, for example the southeastern United States.

#### PALEOECOLOGY

The three late Pleistocene floras are similar ecologically and consist of mixtures of calcicole and calcifuge species. Edaphic characteristics of New England plants, in particular the correlation between species occurrence and calcareous rock or soil, have been extensively discussed in the pages of *Rhodora*, especially in a paper by Fernald (1907), the autecological investigations of Wherry (1920), and more recent studies. The terms calcicole and calcifuge are used here in the sense of these and other authors as a plant growing on substrata rich in calcium salts or a plant intolerant of calcareous substrata, respectively.

The discovery of fossils of *Dryas integrifolia* and other calcicoles in the oldest sediments of TS and USBP was unexpected because at these sites the local bedrock and soils are acidic. The fossil moss assemblages from TS and USBP (Miller, 1987a) also contained calcicoles, and these fossils indicate the former occurrence of xeric to mesic calcareous rock or soil near both sites and of calcareous (minerotrophic) fens or flushes near TS. The CB fossil flora (both tracheophytes and mosses), which is from an area of calcareous bedrock, was dominated by calcicoles. While this as-





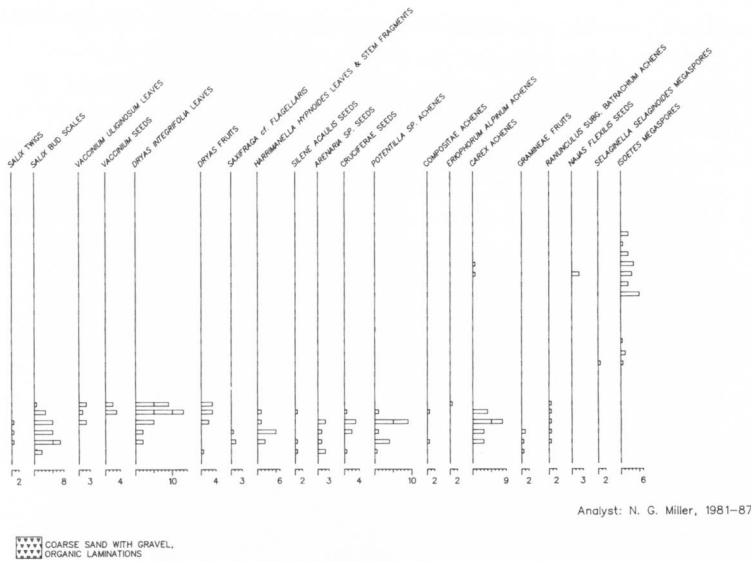


Figure 29. Continued.

calcareous bedrock in a region dominated by acidic soil or rock, and the bryoflora of the Nashoba outcrops includes calcicoles that are otherwise rare or absent in southeastern New England (Mishler and Miller, 1983).

The three late-Pleistocene floras described here indicate that calcareous soils and base-rich wetlands or seeps occurred widely in New England during late-glacial time regardless of whether the fossils were from sites in areas of calcareous or acidic rock or drift. This evidence suggests that calcicoles were once present in many areas where they are now rare or lacking.

The reason for the loss of calcicoles is not known completely. At TS, fragments of arctic-alpine plants (Figure 29) and of calcicole mosses (Miller, 1987a) ceased being deposited at ca. 12,830 ± 120 yr. B.P. with the onset of the regular occurrence of spruce macrofossils and an increase in the percentage of spruce pollen in the stratigraphic record. These changes correlated with an increasing amount of autochthonous organic matter (gyttja) in the sediment and a corresponding reduction in the deposition of inorganic sediment, suggesting that the arrival of spruce somehow

rapidly altered the ground-layer vegetation, possibly through onset of humus accumulation, shading, or other kinds of competitive interactions. The soil may also have become leached of carbonates and certain cations (e.g.,  $\text{Ca}^{2+}$ ) at this time.

To the north at USBP, parallel stratigraphic changes occurred about 2300 radiocarbon years later. There, the disappearance of calcicoles and arctic-alpine tracheophytes from the record also correlated with the arrival of spruce (based on macrofossil evidence) and with the onset of gyttja deposition. The moss record at USBP documents the transition from late-glacial conditions with fossils of calcicoles to postglacial (Holocene) conditions with fossils of only calcifuge species of mosses.

What are the implications of these temporal and spatial changes for an improved understanding of historical aspects of plant rarity in the New England flora? Arctic-alpine, arctic, subarctic-subalpine, and certain western North American species, including a number of calcicoles, now occur in New England in limited areas of climatically and edaphically suitable habitat. This geographic restriction is in contrast to their occurrence in the late Pleistocene when many of them grew at low elevation sites south of their present range limits. For example, of the 28 species native to New England listed in Table 2, 15 have been designated as rare or endangered in this region by Crow et al. (1981). The loss of these plants from areas of New England that now have acidic soils seems to have occurred at the time of late Pleistocene spruce immigration, which took place time-transgressively in a generally northward direction. I suggest that some species, particularly the calcicoles, may have survived as changing populations through the Holocene at or near stations where they now can be found. At these localities, soil conditions remained appropriate for pioneer species, and competition from trees and shrubs was reduced or absent. However, whether such populations are in fact relicts requires direct evidence, such as that provided by a continuous fossil record beginning in the late Pleistocene. A record of this sort is not now available for any rare species in the New England flora.

The elimination of calcicoles from parts of New England and nearby regions produced fragmented ranges of species that are more widespread in western North America (Miller and Thompson, 1979). This process has left a biogeographical legacy that

may prove important in untangling the taxonomy of difficult species complexes, especially those containing calcicoles. One of these is the genus *Gentianopsis* Ma, which has been studied by Iltis (1965). A seed of *Gentianopsis* was recovered from the Columbia Bridge deposit. Although seeds of species of *Gentianopsis* are similar, the fossil can be referred with some confidence to the *G. procera* (Holm) Ma species-complex, based on the preference of plants of this complex for calcareous soil. The other principal species in eastern North America, *G. crinita* (Froel.) Ma, favors acidic sites.

Iltis (1965) proposed that *Gentianopsis procera* underwent post-glacial migration into glaciated eastern North America from a Pleistocene refugium in western North America south of the glacial boundary. However, the fossil record of *Gentianopsis*, which consists of the Columbia Bridge seed and another seed (Figure 13) from late Pleistocene sediments near Brampton, Ontario, establishes that species of *Gentianopsis* grew on recently deglaciated surfaces. This genus and other “western” elements in the flora of eastern North America, such as *Dryas drummondii* and *Elaeagnus commutata*, appear to have been widely established in the East during the late Pleistocene. Although these species now occur mostly in glaciated parts of western North America, they may have been frequent at this time across the continent north of the limit of glaciation when glacier retreat generated appropriate habitats for some few thousand years before the arrival of spruce and other trees. Given the cyclic nature of Pleistocene glacial advances and withdrawals, it is possible that some of these “western” elements may prove to have extensive interstadial histories in eastern North America as well.

The preceding is presented as a framework in which to investigate further some historical aspects of plant rarity in New England. The data reviewed are pertinent especially to arctic-alpine species and northern calcicoles. The history of these elements, as presently understood, may not apply to all calcicoles or to all arctic-alpine species in the New England flora because some species in these categories may have reached New England in the Holocene. Existing data, however, are insufficient to know whether this has indeed happened. Biogeographical problems such as these should be investigated on a case-by-case basis, employing the fossil record whenever possible.

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