

Fossil remains of the mycorrhizal fungal *Glomus fasciculatum* complex in postglacial lake sediments from Maine¹

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Specimens of the vesicular–arbuscular mycorrhizal fungal *Glomus fasciculatum* complex have been identified from lake sediment cores from Gould Pond (central Maine) and Upper South Branch Pond (north central Maine). The fungus became established with tundra vegetation on newly developing soils soon after the melting of Wisconsin ice. This is the first record of such an occurrence for North America. The earliest specimens from Gould Pond were deposited in sediment dated at about 13 000 years old and those at Upper South Branch Pond between about 12 500 and 11 000 years old. This is at least 1000 years prior to the arrival of trees in those areas. Sedimentologic and biologic evidence indicates soil instability and relatively high soil erosion rates from the watersheds during the late-glacial period. Thus erosion probably accounts for the abundance of *Glomus* in late-glacial sediments. The reduced abundance of the fungus in Holocene sediments is attributed to a decrease in the rate of soil erosion after the establishment of trees.

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En examinant des carottes de sédiments lacustres provenant de Gould Pond (Maine central) et du Upper South Branch Pond (Maine centre-nord), les auteurs ont identifié des spécimens du complexe *Glomus fasciculatum*, champignons formant des endomycorhizes à vésicules et arbuscules. Les champignons s'est établi avec la végétation de toundra sur les sols en formation, peu après la disparition des glaces du Wisconsin. Il s'agit de la première mention d'une telle présence en Amérique du nord. Les spécimens les plus anciens à Gould Pond ont été déposés dans le sédiment il y a environ 13 000 ans, et ceux de Upper South Branch Pond, entre 12 500 et 11 000 ans. Ceci était au moins 1000 ans avant l'arrivée des arbres dans ces régions. Les données sédimentologiques et biologiques indiquent la présence d'une instabilité du sol et d'une érosion du sol relativement importante dans ces bassins hydrographiques pendant la fin de la période glaciaire. Ainsi il est probable que l'abondance des *Glomus* dans les sédiments tardi-glaciaires soit liée à l'érosion. La diminution dans l'abondance du champignon dans les sédiments de l'holocène est attribuée à une diminution dans le taux d'érosion du sol lié à l'apparition des arbres.

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Introduction

The symbiotic relationships between plants and mycorrhizal fungi are now recognized to be important to the health and productivity of many plant taxa. Under certain conditions mycorrhizae may enhance growth (Gerdemann 1968), protect the host plant from pathogens (Marx 1972), or both. Vesicular–arbuscular (VA) mycorrhizae (endomycorrhizae) of genera such as *Glomus* are found in association with a great variety of cultivated plants and plants of natural forest communities. These relationships are undoubtedly not recent in origin (Butler 1939; Malloch et al. 1980; Wagner and Taylor 1981). However, there is little evidence that indicates how quickly mycorrhizal plants became established in developing postglacial soils which initially consisted of barren glacial deposits, open to colonization by many forms of biota.

Lake sediments usually contain fossils that provide detailed

evidence about the past characteristics of the lake water, vegetation and soils of the watershed, and the interactions of vegetation and environment. We have been examining lake sediments of Upper South Branch Pond (hereafter called USBP), located at 46°5' N by 68°54' W in north central Maine, and Gould Pond, 44°44' N by 69°19' W in central Maine (Fig. 1), to deduce the characteristics of the vegetation and abiotic environment surrounding the lakes in former times.

The sediments of both lakes contain fossil fungal hyphae and, although fungal hyphae and spores are commonly found in lake and wetland sediments (see for example, Bradbury 1978; Birks 1981; Tolonen 1983), late-glacial and postglacial fossil mycorrhizal fungi from North American sediments are rarely identified and reported (for European reports see van Geel 1978; van Geel et al. 1980). Such reports from North America have been limited to localities in Alberta (Butler 1939), Minnesota (Rosendahl 1943), North Carolina (Wolf 1969), and New York (Miller 1973). We report here on the occurrence of specimens of the vesicular–arbuscular fungus, *Glomus fasciculatum* (Thaxter sensu Gerdemann) Gerdemann and Trappe complex, in ancient sediments from the two localities in Maine.

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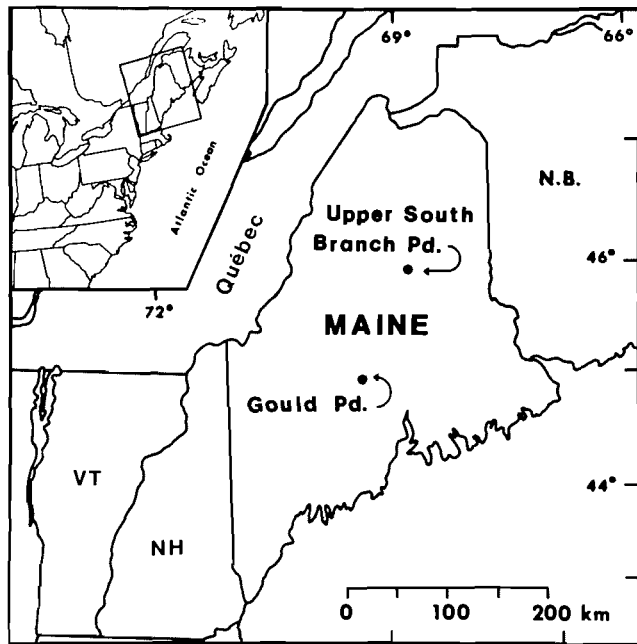


FIG. 1. Locations of Upper South Branch Pond (Pd.) and Gould Pond, ME.

Methods

Sediment cores were collected with a modified Livingstone piston coring apparatus (Livingstone 1955). Subsamples of the sediment cores used for macrofossil analysis were first disaggregated in dilute KOH solution (USBP) or in distilled water (Gould Pond). The slurry was then washed gently through a series of sieves and collected on a 180 μm mesh sieve. Until examined, the macrofossils were stored in either a Formalin solution (USBP) or ethyl alcohol (Gould Pond). Specimens of the fungus selected for photography were then mounted in 70% alcohol.

Results

Specimens of the fossil fungus from either six (USBP) or seven (Gould Pond) levels were examined. The specimens included both chlamydospores and hyphae (Figs. 2 and 3). Chlamydospores occurred in loose aggregations or in small, compact clusters of 4 to 27. The chlamydospores are subglobose to globose, with diameters of 52×67 to $100 \times 125 \mu\text{m}$. Two separate walls are evident in these specimens. The outer thick wall is smooth, has adhering debris, occasionally appears irregularly pitted, and is yellow-brown in color. The inner membranous wall is thinner and lighter in color. The hyphal attachment is ca. 7 μm in diameter, with a wall near the chlamydospore attachment ca. 4 μm thick and yellow-brown in color.

A difference in interpretation of *G. fasciculatum* exists among taxonomic specialists of the Endogonaceae (Gerdemann and Trappe 1974; Trappe 1982; S. Berch, personal communication). The fungus from the two Maine locations has been identified as belonging to the *G. fasciculatum* group (J. Trappe, personal communication; Trappe 1982). It is possible that more than one species is involved. Because of this uncertainty, we have used the term "*Glomus fasciculatum* complex."

The fossil *Glomus fasciculatum* complex material from Gould Pond was recovered from sediment deposited between ca. 13 000 years BP and ca. 10 900 years BP. The USBP samples came from sediment deposited between ca. 12 500 and ca. 10 200 years BP. Nonarboreal pollen types, such as wil-

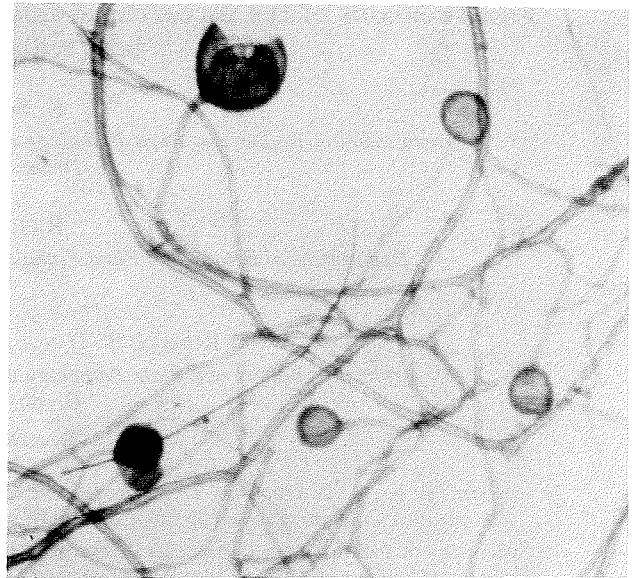


FIG. 2. Fossil members of the *Glomus fasciculatum* complex, Upper South Branch Pond, ME, lake sediment. Chlamydospores and hyphae. Ca. 142 $\times$.

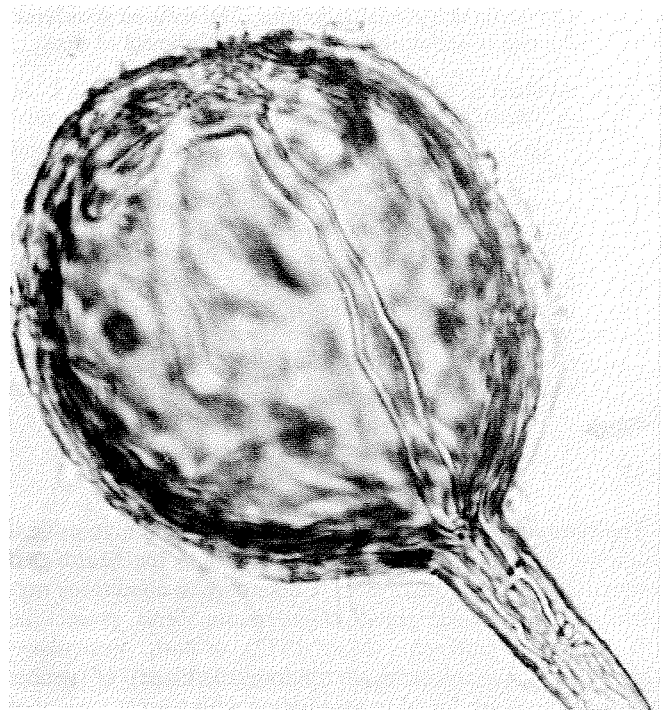


FIG. 3. Fossil member of the *Glomus fasciculatum* complex, Upper South Branch Pond, ME, lake sediment. Chlamydospore enlargement. Ca. 700 $\times$.

lows (*Salix* spp.), sedges (Cyperaceae), grasses (Gramineae), and other herbs, attained maximum postglacial values during these time periods (Anderson and Davis 1980; Anderson et al. 1982). *Vaccinium uliginosum* and *Dryas integrifolia* plant macrofossils are found in many of the same sediment subsamples as the fungus, as well as contiguous subsamples. Macrofossils of arboreal species, beginning with spruce (*Picea*), are found in sediment deposited after ca. 10 800 years BP at Gould Pond and ca. 10 400 years BP at USBP. Tree remains dominated the

macrofossil assemblages throughout the Holocene. *Glomus fasciculatum* complex specimens are found only at widely spaced intervals (ca. 9000, 7700, 6500, 4000, and 100 years BP) in USBP Holocene sediments and are not found in Holocene sediments from Gould Pond.

Discussion

Fossil mycorrhizal fungi recovered from late-Quaternary sediments were first reported by Butler (1939) as species of *Rhizophagus* Dang. from glaciolacustrine and peaty sediments ("muskeg") near Edmonton, Alta., Canada. Later, Rosendahl (1943) described two slightly differing species from Minnesota (Bronson, Jackson, and Moorhead sites): *Rhizophagites butleri* Rosendahl (vesicles light brown, 75×79 to $103 \times 124 \mu\text{m}$) and *R. minnesotensis* Rosendahl (vesicles dark brown, 42×46 to $58 \times 61 \mu\text{m}$). Wolf (1969) recovered *Endogone* (*Rhizophagus*) in peaty lake sediment from New Bern, NC. Miller (1973) described *Rhizophagites butleri* from glacial Lake Iroquois sediments in Lockport, NY. Later, Gerdemann and Trappe (1974) placed *R. butleri* in synonymy with *Glomus fasciculatum*.

Although none of the above specimens was found conclusively in organic connection with other plant materials, information on associated fossil plants is available for all specimens. Only the Alberta specimens remain undated. *Picea-Larix* bog remains (Bronson and Jackson sites) and boreal forest litter deposits (Moorhead site) are associated with the Minnesota fungi (Rosendahl 1948). Radiocarbon dates on these materials have been reported as follows: Bronson site, greater than 36 000 years BP (Flint and Rubin 1955); Moorhead site, 9930 ± 280 years BP (Wright and Rubin 1956). On stratigraphic grounds, the Jackson, MN, material is no less than 13 700 years old (Denton and Hughes 1981). The Lockport, NY, fungus, dated at about 12 000 years BP, was associated with plants from a wide variety of habitats, and the vegetation was interpreted as being similar to boreal forest. No associated plants were reported for the ca. 24 000 year old North Carolina materials (Wolf 1969), but D. A. Livingstone (personal communication) suggested a forest association there also.

Members of the *Glomus fasciculatum* complex are known to occur naturally with a wide variety of plant species characteristic of temperate and boreal forest ecosystems (Gerdemann and Trappe 1974); as mentioned above, the fossil specimens in the previous studies were found in association with plants characteristic of such environments. Unnamed VA endomycorrhizae have also been reported from modern tundra soils near Barrow, AK (Miller and Laursen 1978). These authors found an association with several members of the Ranunculaceae, Gramineae, Cyperaceae, and *Saxifraga* and with at least one moss, *Pogonatum*. However, the occurrence of members of the *G. fasciculatum* complex in the lowest sections of the two Maine cores is significant because it is the first known occurrence of the fungus deposited with late-glacial tundra plant assemblages from North America. Pollen and macrofossils from sediment levels containing the fungus, and from adjacent core intervals, suggest that during this period of tundra around Gould Pond and USBP, sedges (Cyperaceae) and grasses (Gramineae) were common along with, at USBP, *Oxyria digyna* (L.) Hill and *Arenaria rossii* Richards. (Anderson and Davis 1980; Anderson et al. 1982). *Saxifraga* pollen was recovered from Gould Pond sediments (R. S. Anderson, unpublished data). The most common dwarf shrubs included *Dryas integrifolia* M. Vahl, *Salix* spp. (*S. herbacea* L. and

S. uva-ursi Pursh at USBP), *Vaccinium* cf. *uliginosum* and *V. cf. vitis-idaea*. *Pogonatum alpinum* (Hedw.) Rohl. grew around USBP, along with at least two species of arctic-alpine mosses, *Didymodon asperifolius* (Mitt.) Crum, Steere and Anders. and *Aulacomnium turgidum* (Wahl.) Schwaegr. (N. Miller, personal communication). No macrofossils of trees were found in sediments deposited during the tundra period. From macrofossil evidence, spruce did not grow around Gould Pond until ca. 10 800 years BP and USBP until ca. 10 400 years BP. The fungi were present in soils for at least 1000 years before the arrival of tree species.

The only sporadic occurrence of specimens of the *Glomus fasciculatum* complex in posttundra sediments of USBP and the absence of the fungus in posttundra sediments of Gould Pond are best explained by the stabilization of soils and subsequent decrease in erosion around the lakes, following the establishment of arboreal species. The lake sediments deposited during the tundra period contain higher percentages of inorganic matter derived from the terrestrial environment, indicating that soils were probably less stable during the tundra period than in later times. The 41 samples of late-glacial tundra sediments at USBP average 97.4% inorganic matter, whereas the 153 samples of Holocene sediments average 78.0% inorganic matter. At Gould Pond, the 19 samples of late-glacial tundra sediments average 97.2% inorganic matter, while the 45 samples of Holocene sediments average 77.3% inorganic matter. A link between establishment of trees and a decrease in deposition of inorganic matter has also been suggested for Mirror Lake, NH, by Davis and Ford (1982), who found that the postglacial arrival of *Picea* in the region coincided with a precipitous decline in rates of inorganic accumulation within the basin.

In addition to sedimentary indicators of landscape instability, early successional mosses that colonize bare rock (*Grimmia* sp., *Arctoa-Kiaeria* sp., *Andreaea rothii* Web. & Mohr) and mineral soil (*Ceratodon purpureus* (Hedw.) Brid., *Pogonatum alpinum* (Hedw.) Rohl., *Polytrichum* sp.) are common at USBP (N. Miller, personal communication). These species occur as fossil only in the sediments deposited during the tundra period. Based on pollen evidence, Spear (1981) suggested that periglacial frost activity on the White Mountains of New Hampshire during the late-glacial period contributed to landscape instability. This would have provided continuously fresh mineral surfaces near the lakes. The periglacial frost hypothesis is strengthened if relict periglacial features are found within the area.

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