

Methods In Quaternary Ecology #9. Fungi

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Volume 16, Number 3, September 1989

URI: https://id.erudit.org/iderudit/geocan16_3art16

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Publisher(s)

The Geological Association of Canada

ISSN

0315-0941 (print)

1911-4850 (digital)

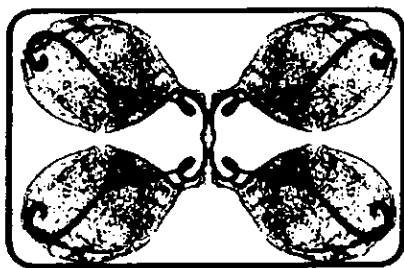
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Cite this article

Pirozynski, K. A. (1989). Methods In Quaternary Ecology #9. Fungi. *Geoscience Canada*, 16(3), 183–189.

Article abstract

Fungi are ubiquitous in Quaternary fossiliferous deposits. Most are incidentally encountered during paleobotanical, including palynological, and paleozoological procedures and are rarely studied. Yet, explicitly paleomycological investigations reveal that fungi have considerable potential to provide data sharpening the focus of biotic and environmental reconstructions hitherto based solely on the more traditional paleontological evidence.



Methods in Quaternary Ecology #9. Fungi

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Summary

Fungi are ubiquitous in Quaternary fossiliferous deposits. Most are incidentally encountered during paleobotanical, including palynological, and paleozoological procedures and are rarely studied. Yet, explicitly paleomycological investigations reveal that fungi have considerable potential to provide data sharpening the focus of biotic and environmental reconstructions hitherto based solely on the more traditional paleontological evidence.

Introduction

Fungi are everywhere. Hyphae and diverse "fruiting" structures bearing spores of many kinds grow in or on living plants and animals or their remains on land and in the water. The spores are in the air, water and soil. Dispersed spores and other components, sometimes still associated with specific substrates, occur in, or find their way to, sites where conditions favour preservation. The special circumstances are anoxic sedimentation or, more rarely, burial in volcanic ash, freezing and desiccation. Vast amounts of fungal material, chiefly dispersed spores, accumulate in aquatic sediments (Muller, 1959; Saad and Sani, 1967; Jarzen and Elsik, 1986). Cross *et al.* (1966) calculated that one gram of dried sediment from the Gulf of California contained up to 22,500 fungal spores, exceeding even the superabundant pine pollen. The spores have already "survived" physical and biological degradation as well as processing in the laboratory. The occurrence of fungi in older sediments, therefore, was to be expected. Indeed, Wolf (1967b) estimated that 1 mL of Holocene sediment cores from East African lakes contained up to 60,000 fungal spores. In Holocene peat bogs of northern Europe and southeastern United States, fungi outnumber algal and animal remains (Van Geel, 1972, 1978; TeStrake, 1979). In a late Wis-

consinan Oklahoma blue clay swamp containing a mammoth skeleton, "fungal spores far outnumber ... all other palynological fossils" (Wilson, 1966). Yet, in that study, fungi were not considered further; in most other palynological studies they are not even mentioned. Fossil fungi are deemed too difficult to interpret and identify or even distinguish from living inhabitants of a given site (Traverse and Ginsburg, 1966). The identification and interpretation of Quaternary fungi, like other fossils, pivots on the familiarity with the living. Few mycologists, however, showed interest in fossil fungi.

Quaternary fungi: what and where?

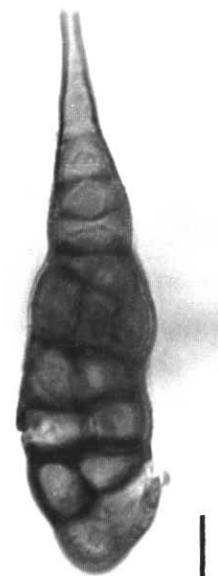
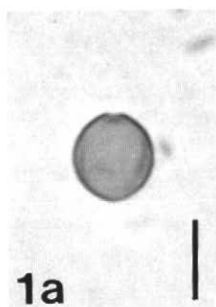
Fungal spores (Figure 1a-d) are "seeds" adapted for dispersal by air, water or animals, and for withstanding physical and biological adversities during the sometimes extended periods of conditions inimical to growth. Their more striking analogy, however, is to pollen which they resemble in size, structure and composition, and in being encountered by palynologists. The analogy to pollen extends further: a sample may be skewed toward species adapted for abiotic dispersal, especially by air; air-dispersed spores may be more robust, for example to resist desiccation, and consequently could be selectively transported, preserved and re-worked to further increase sample bias. The details of the site may be obscured because airborne spores can traverse vast distances, and the direction of travel may not be polarized by biological and ecological traits of parent organisms. In addition, the information content of an individual sample may be grossly distorted if it originally included spore-bearing organs containing, as they sometimes do, hundreds of thousands of individual propagules. The preservation itself depends on rapid burial in an anoxic, usually aquatic milieu, most frequently washed-in sediment, which necessarily involves allochthonous elements from a potentially wide range of habitats, including airborne components (Jacobson and Bradshaw, 1981). Clearly the spectre of a large margin of error weakens interpretations of isolated samples, but is reduced if studies extend to assemblages from different horizons and sites. Palynological methods designed to minimize interpretative errors largely apply to fungal spores, if for no other reason than that there is little else available to students of dispersed paleofungi. Some peculiarities of fungi, however, are already apparent and need to be accommodated. For example, Muller (1959) claimed that estuarine circulation tends to precipitate the relatively smaller fungal spores in bottom sediments closer to shore than pollen, much of which is carried seaward. Hydrodynamic properties of spores of terrestrial fungi have not been investigated in relation to sedimentation. Unlike most pollen, a significant portion of an assemblage may be derived from autoch-

thonous populations of fungi both in water and in the soil. Some will be anachronistic contaminants derived from sediment- or soil-dwelling fungi or from intrusive mycorrhizae (Traverse and Ginsburg, 1966; Elsik, 1986; Pirozynski and Dalpé, 1989). Non-melanized spores or cells are less likely to become fossilized, or to withstand laboratory extraction, than their melanized counterparts. However, the near absence of unpigmented spores in palynologically processed samples may be also partly due to the darkening of walls during acetolysis (Wolf, 1966). Finally, it should be noted that although mycological studies of East African lake-sediments (Wolf, 1967a, 1969) revealed some correspondence between spore content and vegetation, inexplicably some horizons are mycologically sterile. Furthermore, the spore content can decline with depth of sediment for no apparent reason, or fungi mysteriously disappear from refrigerated samples (Wolf, 1969).

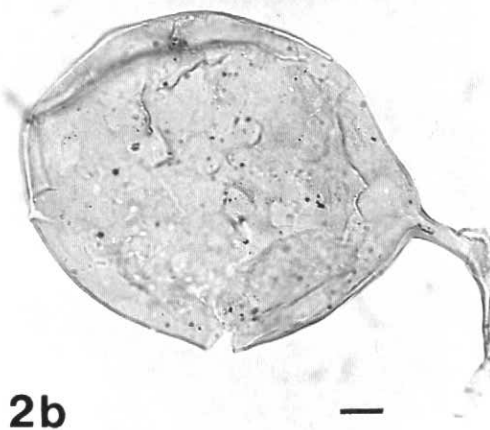
There will, of course, always be the risk of misdetermination of isolated spores or their confusion with similar, but unrelated, objects. Particular care is called for when interpreting one-celled spores, even when they are judged to be distinctive, because, this economical format has been arrived at independently by very different organisms (Pirozynski, 1976). Hence ascospores of *Xylariaceae* resemble some plant microspores (e.g., those of *Isoetes*), and some conidia and sordariaceous ascospores can be confused with cysts of the *Chrysophyceae* (Duff and Smol, 1988) or cyanobacteria (Van Geel, 1986).

The same juxtaposition of circumstances that leads to concentration and preservation of dispersed spores also applies to other microscopic parts of fungi, although predictably most vegetative or reproductive organs are more prone to decay and, consequently, are less likely to become fossilized (Van Geel, 1978). Those that do, comprise some distinctive hyphae and their modifications as hyphopodia, appressoria, terminal or intercalary swelling or "chlamydospores", conidiophores, bristle-like setae, bulbil-like sclerotia, and many kinds of conceptacular fructifications or their more unusual components (Pirozynski *et al.*, 1984) (Figure 2a-d). Pitfalls of convergent evolution, too, await their identification and interpretation. Hence some shield-shaped fruit-bodies (thyriothecia) of leaf-dwelling microthyriaceous and micropeltaceous fungi (Pirozynski, 1978) not only resemble thalli of co-inhabiting green algae (e.g., *Phycopeltis*), but can also be confused with those of aquatic encrusting *Ulve*la. Some "thyriothecia" identified in the Arabian Sea sediments up to 45 km offshore India (Ratan and Chandra, 1982) may be algae, and some shield-shaped thalli attributed to the algae (Hansen, 1980) may be fungi.

A superior source of the more delicate vegetative and reproductive expressions of



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fungi are plant macrofossils. In addition, fossilized macrofungi are occasionally collected by students of plant or animal macrofossils. Together with fungi associated with animal remains, including dung, they represent an important, but largely untapped, paleoecological resource.

Methods of sampling and laboratory extraction

Most Quaternary fungi are preserved as empty cells without permineralization or petrification (Wolf, 1966, 1967a,b, 1969; Vishnu-Mittre, 1975). As noted earlier, most are encountered in paleontological samples processed for a different purpose. Dispersed spores in sediment cores or sections of peat are disclosed by palynological acetolysis following the removal of mineral matrices with appropriate acids (HCl, HF and rarely, HNO₃) (Wolf, 1967b; Pals *et al.*, 1980; MacDonald, 1988). A refinement of this procedure in processing gyttja, substitutes HF with bromoform-alcohol mixture (Van Geel *et al.*, 1983). A simple aqueous suspension of sediment is not satisfactory (Wolf, 1966), but repeated decanting to remove sand eventually concentrates the spores sufficiently to allow direct mounting of the residue in Canada balsam on microscope slides (Wolf, 1969). A similar problem of low concentration and, consequently, insufficient sample size from any one horizon in a depositional sequence, may apply to airborne palynomorphs trapped in perennial snow or ice. Cores are removed by thermal drills, melted, and the meltwater laboriously filtered through micropore acetate filters under rigorous contamination-proof conditions prior to acetolysis or direct mounting of the residue (Licht-Federovich, 1975a,b). Although the resulting pollen spectra are of some value in interpreting broad climatic changes, fungal spores are too infrequent

and the types recovered too widespread to justify the effort.

Some fungal fructifications, chiefly shield-shaped thyrthothecia, are sometimes left intact or almost intact in palynologically processed concentrates (Eriksson, 1978), but they invariably lack spores. Other kinds of fruit-bodies occasionally with spores, and sclerotia accompany macrofossil samples of fruits, seeds or insects, obtained by screening or boiling of sieved-out sediment or peat in 5% KOH for 5 to 10 minutes (Van Geel *et al.*, 1981).

Fossil leaves and, to a lesser extent, wood are the best sources of complete fructifications of fungi. Those embedded in leaf tissues are prepared by peeling off leaves from the matrix and immersing them for two to five days in 5-10% KOH. Cleared leaves are washed in distilled water and can be mounted directly on slides in standard mounting media (Doi and Amano, 1982). Follicolous fungi growing and fruiting on leaf tissues are revealed by clearing the leaves in 5% KOH, washing, dehydrating in a series of alcohols, fixing in xylene and mounting in synthetic resin. This procedure was successfully applied to Eocene fungi (Dilcher, 1965). However, for at least some Quaternary follicolous fungi, the acetate peel technique, which is the standard method of preparing living material (Ellis, 1950), could be employed to advantage. A novel application of the peel technique was to lift fungal spores from archeological potsherds (Stewart and Robertson, 1968). The preparation of Quaternary fungi contained in leaves, or in wood that is not permineralized, can be done by normal mycological procedures of microtome sectioning, or squashing or teasing in standard laboratory reagents (Romans *et al.*, 1966; De Vries, 1966). This certainly applies to fruit bodies of larger basidiomycetes, usually bracket fungi and puff-balls that sometimes still contain spores (Chaney and Mason, 1936).

Interpretation

Fungi and Physical Environment

Climate. A late glacial stony clay-gyttja from Saskatchewan yielded fragments of *Carex* bearing telia of the rust fungus *Puccinia caricina* (De Vries, 1966). The fungus is heteroecious, with *Ribes* as the alternate host. The inferred requirement for *Ribes*, coupled with the knowledge that *P. caricina* has a narrower tolerance of harsh climate than the potential host, indicated to De Vries (1966) climatic amelioration of the site at the time of deposition of the specimens. Similarly, Pirozynski *et al.* (1984) interpreted the presence of *Thecaphora deformans* spores (Figure 1d) in dung from a ground squirrel's nest in Yukon, some 12,000 years B.P., as indicating a climate more temperate than at present, because modern distribution of this smut of *Astragalus* is farther south. A more extreme climatic shift was implied by Prasad

and Ramesh (1984) who found a distinctive conidium of *Circinoconis* in a Holocene peat bog in Tripura, NW India. The fungus is no longer extant on the subcontinent: the sole representative, *C. paradoxa*, occurs in Malaya and Indonesia.

Fungi may also offer clues to more specific climatic factors. For example, Quaternary occurrences of *Sporormiella*, like the present-day saprotrophic species, appear to correlate with aridity. Certain peat bog fungi are in strongly humified horizons that are presumed to have been formed during drier phases. The occurrence of others correlates more strongly with wetter phases (Van Geel, 1972, 1986; Van der Wiel, 1982). Van Geel *et al.* (1981) also sought correlation between the occurrence of specific kinds of fungal spores in peat and temperature regimes and fluctuations, as did Vishnu-Mittre (1975) in East Anglian fens. The latter found evidence of fungi that no longer live in England, but occur farther south in Europe. The disappearance of some may be linked with the extinction of specific host plants, but the discontinuity of others is more satisfactorily explained by climatic cooling.

Hydrology. Freshwater, brackish and marine habitats are occupied by different fungi that can leave a tell-tale record of salinity (Pirozynski *et al.*, 1988). Thus, mycological data contributed to the tracing of stages in the evolution of a tidal flat (Bakker and Van Smeerdijk, 1982) or a brackish lake (Pals *et al.*, 1980) into a swamp and, eventually a bog; of a rising water table and replacement of carr by open water (Van der Wiel, 1982); and of periodic freshwater inundation of fens (Vishnu-Mittre, 1975). Fungal remains may have considerable potential in paleolimnological reconstructions concerned with currents, rate of flow, pH and seasonal drying out (Sherwood-Pike, 1988).

Soils. The role of saprophytic organisms, including fungi, in ontogeny and characterization of soils and peats has been recognized (Anderson, 1984). However, attempts to implicate fungi in Quaternary pedology failed (Vishnu-Mittre, 1975), though there remains an indirect link between some soil-borne fungi and certain types of vegetation (Van Geel, 1978). The mycorrhizal fungi, especially, can play an important role in characterization of soils.

Fire. Several kinds of fungi are known pioneer colonizers of burnt sites, either as saprotrophs or as mycorrhizal symbionts. Distinctive ascospores of *Gelasinospora* and *Neurospora* are often associated with charcoal or burnt *Molinia*, and their stratigraphy has been widely used in tracing periodic burning of peat bogs (Van Geel, 1978, 1986; Bakker and Van Smeerdijk, 1982; Garneau, 1987).

Fungi and Plants

Microfungi. Unlike Wolf (1966, 1967a,b, 1969), who found little evidence that fungi in East African lake-sediments are derived

(Figures 1–3 opposite page)

Figure 1 (A) ascospore of *Chaetomium* simile; (B) indetermined ascospore; (C) conidium of *Alternaria* sp.; (D) Spore ball of *Thecaphora deformans*. (A) (C) and (D) from dung of Arctic ground squirrel (Pirozynski *et al.*, 1984), (B) from clay balls accompanying the "Hillsborough mastodon" (Pirozynski *et al.*, 1988). (All 1000 ×).

Figure 2 (A) appressorium (1000 ×); (B) chlamydospore of *Glomus* sp. (500 ×); (C) portion of fructification (ascoma) wall (1000 ×); (D) ascomatal appendage of *Chaetomium simile* (500 ×). (A) and (B) from clay balls accompanying the "Hillsborough mastodon" (Pirozynski *et al.*, 1988), (C) and (D) from dung of Arctic ground squirrel (Pirozynski *et al.*, 1984).

Figure 3 *Fomes fomentarius* (A) complete and (B) cross-section of fruit-body (from DAOM 199110) (one-half natural size).

from and, consequently, represent local vegetation, Van Geel and collaborators (Van Geel, 1978, 1986; Van Geel *et al.*, 1981, 1983, 1986) were more successful in documenting such links. In fairness, Van Geel assessed the significance of fungal spores in the broader context of assemblages that included plant and animal macrofossils, pollen and algae, whereas Wolf tried to rely on fungal spores alone. He did, however, note that "it seems reasonable to assume that eventually spore analyses and pollen analyses may both be used in interpreting floristic changes" (Wolf, 1967a). Today, there is evidence that some fungal spores better differentiate local vegetation than pollen. Some of this evidence comes from studies of assemblages of fungal spores in modern soils, that more effectively discriminate ground-cover communities than the co-occurring assemblages of pollen (Kurmánn, 1985). This may be also true of fossils. Elsik (1986) found abundant spores with a skeleton of a giant ground sloth in Texas. The mycological data, combined with pollen data, permitted reconstruction suggestive of a low-lying coastal grassland interspersed with open woodland and traversed by bayous. The evidence for the grassland and the bayous came mainly from the fungi. Elsewhere, a comparative study of *Ustilina deusta* in Quaternary deposits indicated that the ascospores of this weak parasite of broad-leaved forest trees are far less easily transported than the pollen of the hosts (Van Geel and Andersen, 1988).

Vishnu-Mittre (1975) and Van Geel (1978) claimed that most spores in peat originated either from fungi growing on plants or near bogs or from saprotrophic fungi growing in peat. In subsequent contributions (Van Geel, 1986; Van Geel *et al.*, 1981, 1983, 1986; Pals *et al.*, 1980; Bakker and Van Smeerdijk, 1982; Kuhry, 1985), specific fungi or fungal spores were linked with specific plants or plant communities. Additional examples are *Thecaphora deformans* whose spores (Figure 1d), found in an arctic ground squirrel's nest, identified *Astragalus* in the diet and, consequently, in the foraging territory of the animal (Pirozynski *et al.*, 1984), and *Puccinia caricina* which, even if not found on identifiable leaves of *Carex* would have indicated the presence of this plant — as well as that of the alternate host, *Ribes* — in the ecosystem (De Vries, 1966).

Appressoria or hyphopodia of *Gaeumannomyces*, *Buergenerula* and *Clasterosporium* (Figure 2a), the last frequently accompanied by conidia, commonly found in coastal sediments, identify palustrine monocots (Pirozynski *et al.*, 1988) and, consequently, a palustrine stage in terrestrial succession (Cowley and Colquhoun, 1966).

Macrofungi. Of considerable interest, and as yet untapped potential in identifying woody plants and their condition at the time of burial, are bracket fungi which are often remarkably well preserved, sometimes even

with spores (Chaney and Mason, 1936). The purportedly Quaternary finds of *Fomes* (Andrews and Lenz, 1947; Galbreath, 1947; Rosendahl, 1948) and *Ganoderma* (Bondarcev, 1960) are assignable to modern *F. applanatus*, *F. fomentarius* and *F. pinicola* (Mason, 1934; Chaney and Mason, 1936; Buchwald, 1970, 1971) and *G. lucidum* (Chaney and Mason, 1936). Their age has been inferred from stratigraphic correlations, except when attached to trees in a buried forest.

Here I record another detached specimen of *Fomes fomentarius* (Figure 3a) found by C.R. Harington and R. Johnson on 13 August 1979, washed out from frozen "muck" (dark organic silt) at Gay Gulch, Eldorado Creek, Dawson (Loc. 45), Yukon Territory, Canada (DAOM 199110), and having a radio-carbon age of 5030 ± 70 years B.P. (Beta 28764). The usual boreal host of *F. fomentarius* is *Betula*. This can be verified because even detached basidiomata often incorporate fragments of host bark. The date marks the onset of cooling that ended the Hypsithermal, but the transition is not inferred from this particular find: both *F. fomentarius* and *Betula* are still extant in the area. The curvature of the adnate side of the fructification indicates that the supporting trunk or limb was about 8 cm in diameter (Figure 3a); darker bands seen in cross-section (Figure 3b), like annual growth rings, reveal a seven-year association with a particular tree (*cf.* Andrews, 1948).

Mycorrhiza

Different kinds of fungi involved in vesicular-arbuscular, ericoid and ectomycorrhizae identify different communities of plants and should record their succession.

Mycorrhizal fungi should not be expected in meso- and oligotrophic peat because wet conditions select for non-mycorrhizal plants, *Sphagnum* and aquatic or semi-aquatic angiosperms, including sedges and rushes. Sclerotia of *Cenococcum* were once claimed to be abundant and ubiquitous in all kinds of peat (*cf.* Vishnu-Mittre, 1975, and refs. therein), but this is an oversimplification. Vishnu-Mittre (1975) noted that *Cenococcum* was more abundant in wood peat than in raised peat bogs, and Van Geel (1978) did not find sclerotia in wet peats except when accompanying intrusive roots from surface vegetation. Contamination from living mycorrhizae may have contributed to the former generalization. Another contributing factor is that sclerotia are hollow, they float and are apparently dispersed by seasonal inundations (Malloch *et al.*, 1987). This complication notwithstanding, even in raised peat bogs it has been possible to correlate the occurrence of *Cenococcum* with drier conditions (Van Geel, 1978) during which bogs may be invaded by mycorrhizal plants. Indeed, abundant sclerotia in *Sphagnum* bogs mark a transition to *Alnus* carr (Van Geel *et al.*, 1981), and they become charac-

teristic of alder peat (Vishnu-Mittre, 1975). *Cenococcum graniforme* is frequently mycorrhizal with alders pioneering bog colonization.

Intrusive roots or root fragments of the Ericaceae growing on peat are characteristically packed with hyphae of mycorrhizal fungi. However, the sometimes implied or claimed (Garneau, 1987) association of the Ericaceae with *Cenococcum* is enigmatic inasmuch as this fungus is not known to form "ericoid" mycorrhiza (such as characterizes peat bog Ericaceae) though it may form "arbutoid" mycorrhiza with, for example, *Arctostaphylos*. The hyphae and chlamydospores accompanying *Calluna vulgaris* (Van Geel, 1978; "type 10"; Kuhry, 1985) cannot be considered in the light of present knowledge as belonging to *Cenococcum* or even as being mycorrhizal.

The establishment of ectomycorrhizal *Alnus*, *Betula*, *Picea*, *Pinus*, etc. cannot be determined from the more usual and often specific fungal symbionts, because their fruit-bodies (mushrooms) and spores are delicate and ephemeral. However, symbiosis alters, to some extent, the anatomy and morphology of roots, and there are grounds for predicting that fragments of mycorrhizae will eventually provide clues to the identity of both plants and the fungi involved. It has already been possible to identify "short roots" of *Pinus sylvestris* in Quaternary peat (Van Geel *et al.*, 1981).

Vesicular-arbuscular mycorrhizal (VAM) fungi are rarely found in peat, presumably because VAM plants are rare in *Sphagnum* bogs. But although VAM fungi have not been recorded in studies of northern European peats (Van Geel, 1978, 1986; Van Geel *et al.*, 1981, 1983, 1986; Vishnu-Mittre, 1975; Pals *et al.*, 1980; Bakker and Van Smeerdijk, 1982; Kuhry, 1985), it would not be prudent to extrapolate because the probability of contamination from intrusive mycorrhizae, animals or sediments is very real: the vast majority of plants form VAM, especially with the ubiquitous *Glomus* (Figure 2b). Thus *Glomus* (= *Rhizophagites*) was found in a glacial bog in Alberta (Butler, 1939); in a well core section indicative of a spruce-tamarack bog in Minnesota (Rosendahl, 1943, 1948); in post-glacial marine silt and silty clay in Prince Edward Island (Terasmae, 1958); in forest soil horizon in Oklahoma (Wilson, 1965); in lacustrine marl sediment in North Carolina (Wolf, 1969); in glacial lake sediment in New York (Miller, 1973); in lake-sediment cores identifying post-glacial pioneer tundra vegetation in Maine (Anderson *et al.*, 1948; *Glomus fasciculatum* complex); in gyttja and silty clay in Ontario (Berch and Warner, 1985; *G. fasciculatum*); and in *Scirpus* – *Cladium* peat and silty clay also in Ontario (Berch and Warner, 1985; *G. deserticola*). In deposits representing swamps, non-mycorrhizal *Scirpus* – *Cladium* or ectomycorrhizal spruce-tamarack, VAM fungi are likely to be allochthonous. The effectiveness of the

physical transport of *Glomus* is apparent in Terasmae's (1958) sample in which chytrid spores occur with marine diatoms. Pirozynski *et al.* (1988) found *Glomus* and the closely related *Sclerocystis* among spores of fungi that may have been ingested with herbage by a late Pleistocene American mastodon. Dispersal of VAM spores "by gut" appears to be widespread in nature and is both "horizontal", by widely foraging mammals and birds, and "vertical", by earthworms and burrowing mammals (Pirozynski and Malloch, 1988). All these observations cumulatively call for caution in extrapolating even broad vegetational changes from sporadic occurrences of VAM fungi.

Plant Decline and Extinction

The dramatic decline of the American chestnut and elm caused by parasitic fungi during this century has justifiably led to suggestions that similar declines recorded in paleopalynological profiles could have also been caused by epidemics of pathogenic fungi. Particular attention has been focussed on the decline of elm in Europe (Moore, 1985) and of hemlock in North America (Davis, 1981; Allison *et al.*, 1986) about 5000 years B.P. Both claims rely on indirect evidence from (a) comparative analysis of pollen profiles accompanying the recent decline of chestnut and elm and of the ensuing compensatory succession, and (b) elimination of other potential physical and biological causes, notably climatic shift and human impact. Judging from the morphology and ecology of the fungi responsible for the recent extinctions, the probability of finding direct paleomycological evidence for the Holocene outbreaks seems remote. Even when a known parasite has left a record of distinctive spores, e.g., *Ustilina deusta*, the relative abundance of which correlates with the occupation of the site by more or less susceptible trees, the floristic changes are more likely to have resulted from climatic shifts than from disease, however seductive the biological explanation may be (Van Geel *et al.*, 1986; Van Geel and Andersen, 1988).

Fungi and Animals

Fungi parasitic on arthropods are known from Tertiary ambers. Quaternary cases may be equally common, but remain to be diagnosed. Fungi pathogenic to vertebrates are less likely to outlast non-skeletal remains, but, theoretically, should persist on infected mummified animals. Not to be confused are anachronistic biodegraders such as found on the mummy of Rameses II (Mouchacca, 1978). The best documented fossil associations are non-pathogenic and involve fungi of stored food or faeces inside burrows of sedentary animals or in digested food within carcasses, skeletons or in dung (Figures 1 and 2).

Stomachs and skeletons. If "palaeofaeces are pearls beyond price" (Hillman, 1986), it is because the stomachs and guts

of mummified animals, including man, or their presumed contents preserved within skeletal rib cages, have provided direct evidence of the dietary habits and, consequently, of the immediate physical and biotic environment of the consumer. Microscopic fungi are rarely included in the analyses (perhaps partly because modern *Homo sapiens* "supermarketalis" is an atypical, barren control) despite a precedent set by Weber (1915) who listed sclerotia of *Cenococcum graniforme* and spores of *Uredo* and *Uromyces* among 70 plants identified in the diet of the "Borna mammoth". A largely mycological investigation of clay balls associated with the skeleton of the "Hillsborough mastodon" from New Brunswick attempted to redress the balance (Pirozynski *et al.*, 1988). The sample yielded 137 kinds of fungi which cumulatively suggested an enterogastric environment despite a large volume of the accompanying clay. Many were identified as coprophilous; others represented brackish or even marine habitats, exotic to the inferred site of deposition. A suggestion that tidal clay may have been ingested to provide salt is underscored by an independent claim of the importance of salt in a mastodon's diet and the effect of its availability on the distribution and, ultimately, the demise of this animal in North America (Holman *et al.*, 1988).

Dung. Dung has long been recognized as an important source of data on food, feeding and, consequently, on the immediate environment of the consumer. Recent literature pertaining to Quaternary North America include Spaulding and Martin (1979), Davis *et al.* (1984) and Mead *et al.* (1984, 1986a,b). An explicitly mycological investigation of fecal pellets found inside a ground squirrel's nest in the Canadian arctic (Pirozynski *et al.*, 1984) yielded accidental contaminants from air or arthropods, fungi incidentally ingested with plants and often betraying their identity, and specialists which are either adapted for dispersal by ingestion (enterophiles) or are both dispersed "by gut" and utilize dung as the normal growth substrate (coprophiles). The coprophiles frequently offer clues to the identity of the consumers as well as their diets, and are thus important in the interpretation of "dispersed" dung. The pioneering attempts by Davis (1976) and Davis *et al.* (1977, 1984) in western North America and by Pals *et al.* (1980), Van Geel *et al.* (1981, 1983) and Witte and Van Geel (1985) in northern Europe attributed the increased abundance of coprophilous fungi in lake sediments and peat to the invasion of, or introduction to, the sites of large grazing herbivores. The concomitant disturbance is independently verifiable by the elevated counts of pollen of weeds and, in historic times, by the appearance of pathogenic fungi characteristic of agroecosystems. Davis (1976, 1987) singled out *Sporormiella* as quantifying grazing pressure both before the megafaunal extinction in the Pleistocene and

after the introduction of grazing livestock in the Holocene. He noted that, although not all heavily grazed sites studied in the western USA yielded *Sporormiella*, all *Sporormiella* sites show signs of abundant grazers. In contrast, Pirozynski *et al.* (1988) did not find *Sporormiella* among 175 spores associated with the skeleton of an American mastodon in Atlantic Canada, though admittedly the fungus may be more characteristic of grasslands and grazers. Nor has *Sporormiella* been found in northern European peats, even in horizons indicating relatively dry conditions that opened these sites to large herbivores (Van Geel *et al.*, 1981). Saprotrophic, non-coprophilous species of *Sporormiella* are particularly abundant in arid regions of North America (D.W. Malloch, pers. comm.) suggesting that the distribution of the coprophilous elements too may correlate more strongly with dry environments.

Fungi and Man

Since time immemorial, fungi have served as man's food and medicine, contributed to rituals, provided escape from reality, competed for crops, and became "domesticated" by adapting to man's habits as a sedentary social hoarder of food. But although fungi are sporadically mentioned in archeological literatures (e.g., Sharma, 1976) only very rarely did they invite a more detailed study. Among exceptions are fungi, including sclerotia of psychoactive ergot, in paleofaeces of "bog people" (Hillman, 1986; Scaife, 1986 and refs. therein) and of a Peruvian mummy (Vreeland and Korf, 1978). Potsherds excavated in Iraq yielded spores of fungi characteristic of grasses which, as Stewart and Robertson (1968) inferred, came from chaff and manure used for tamping in making clay pots. But, in addition, spores of fungi pathogenic to cultivated grain crops provided indirect evidence of the kind of cereals planted, and of the problems encountered in their cultivation. Dried puffballs in pre-Hadrianic and Roman sites in Great Britain were thought (Watling and Seaward, 1976) to have served as haemostatic agents or as tinder.

Conclusion

The few examples of paleomycological approaches to Quaternary studies reviewed above, indicate that fungi can substantially contribute to the accuracy and completeness of Quaternary paleoenvironmental reconstructions, but at present this potential of fungi is underutilized and hampered by often real, but mostly imagined, difficulties in identification of the fossils.

Acknowledgements

I thank Dr. C.R. Harington for making the specimen of *Fomes fomentarius* from Yukon Territory available for study and for helpful comments on the manuscript, and R.G. Day and K. Shepherd for the photographs.

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