

Fossil ascomycetes in Quaternary deposits

by

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Abstract: Remains of various ascomycetes, mainly ascospores, have been detected during palynological studies of lake sediments, peat deposits and samples from archaeological sites. Many taxa can be identified to genus or species level of extant taxa. Ascospore remains may sometimes give indications about the palaeohabitat: for instance, *Amphisphaerella dispersella* suggests the presence of *Populus* in the vicinity. Among the identified fungi are several species of the Sordariales, which are valuable dung indicators in archaeological sites. Coprophilous fungi also characterise samples from the Pleistocene mammoth steppe.

Key words: fossil, palaeoecology, palynology, ascomycetes, ascospores, identification, Sordariales, Holocene, Pleistocene.

Introduction

The fossil record of fungi extends back to the Palaeozoic (Pirozynski 1976). Spores are often conserved, less often other carbonized tissues, like ascoma walls, may also be preserved. Palynologists often describe fossil fungi in genera separate from modern day taxa. Even when a similarity with recent genera is detected, the fossils are often described in separate genera, the names generally derived from the name of modern-day genera but modified by a suffix, usually *-ites*, e.g. *Pleosporites*, *Pleosporonites*. In addition, fossil fungi (typically dispersed spores) are given terminological names denoting form-genera.

Obviously not much is known about the ecological requirements of extinct fossil fungi. If fossil fungal remains can be identified with currently existing genera or even species, they become much more useful for the reconstruction of the past ecological conditions. However, there is only a meagre documentation available in the literature and this results in unsuccessful identifications during microfossil analyses. In the past 35 years the first author has paid special attention to fossil fungal remains in Quaternary (Eemian, Weichselian and Holocene) deposits, in most cases from northwest European sites, but also from deposits of the last ice age in the northern Siberian permafrost area (Aptroot & van Geel in press, Brinkkemper et al. 1987, Buurman et al. 1995, van Geel 1978, 1986, 2001, Mol et al. 2003, van Geel & Andersen 1988, van Geel et al. 1981, 1983 a, b, 1986, 1989, 1995, 2003, Pals et al. 1980, Ralska-Jasiewiczowa & van Geel 1992, Willemsen et al. 1996, see also Kuhry 1997, and Innes & Blackford, 2003).

Several hundreds of different fungal 'types' have been reported up to now, mostly rather scattered in non-mycological literature, often archeological or palynological studies. Among the material encountered are many ascomycete remains, often ascospores, but also ascomata and hyphopodia. Many taxa can be identified to modern day genera, and some even to currently existing species. The present contribution gives a survey of a selection of ascomycete taxa, with some additions and changes of identification according to the classification of modern fungi. For each 'type' an illustration and a short indication of the type of deposit and palaeo-environmental indicator value are given.

Materials and methods

The recorded fungal remains were found in pollen samples that had been treated according to the pollen preparation method described by van Geel (2001). Records were made during the analysis of microfossils (pollen and other palynomorphs) in microscope slides, but fungal remains (for example small fruitbodies) were also found during macrofossil (>150 μm) analysis. Macrofossil samples were boiled for 5 min in 5% KOH and sieved. The presence of fruitbodies in macrofossil samples is indicative of the strictly local occurrence of the fungus, because these fruitbodies will not have been transported potentially long distances by wind.

Descriptions of selected taxa

cf. **Actinopeltis** sp. (Plate I, 1a and 1b; van Geel 1978: Type 8C)

Detached fruitbodies of *Actinopeltis* were found in samples of *Sphagnum* raised bogs. In a slide of Holocene material from the Breungesheiner Heide, Germany, numerous fruitbodies were present on a *Sphagnum* leaf. *Actinopeltis* is known from ferns, but the fossil records indicate that *Sphagnum* species may also act as host plant. A final identification to species level is impossible in the absence of ascospores in the fossil remains.

Amphisphaerella dispersella (Nyl.) O.Eriksson (Plate I, 2; van Geel et al. 1981: Type 310)

Ascospores of this species, with the characteristic meridional germ pores, were found in early Holocene deposits in the Netherlands, from where it was reported (van Geel

et al. 1981) under the synonymous name *A. amphisphaerioides* (Sacc. & Speg.) Kirschst.

It is known to be saprobic on *Populus*, and its fossil occurrence (Bos et al. 2005, van Geel et al. 1981) corresponds with records of *Populus tremula* pollen (which is often difficult to identify with certainty), thus corroborating the evidence that *Populus* was present in close vicinity of the site.

Anthostomella cf. **fuegiana** Speg. (Plate I, 3 a, b; van Geel 1978: Type 4)

Ascospores and fruitbodies (detached from host plant; recorded in macrofossil samples) are of regular occurrence in raised bog deposits in northwest Europe (van Geel 1978). In some cases the clypeus of the fruitbody was found in connection with a monocotyledonous host epidermis.

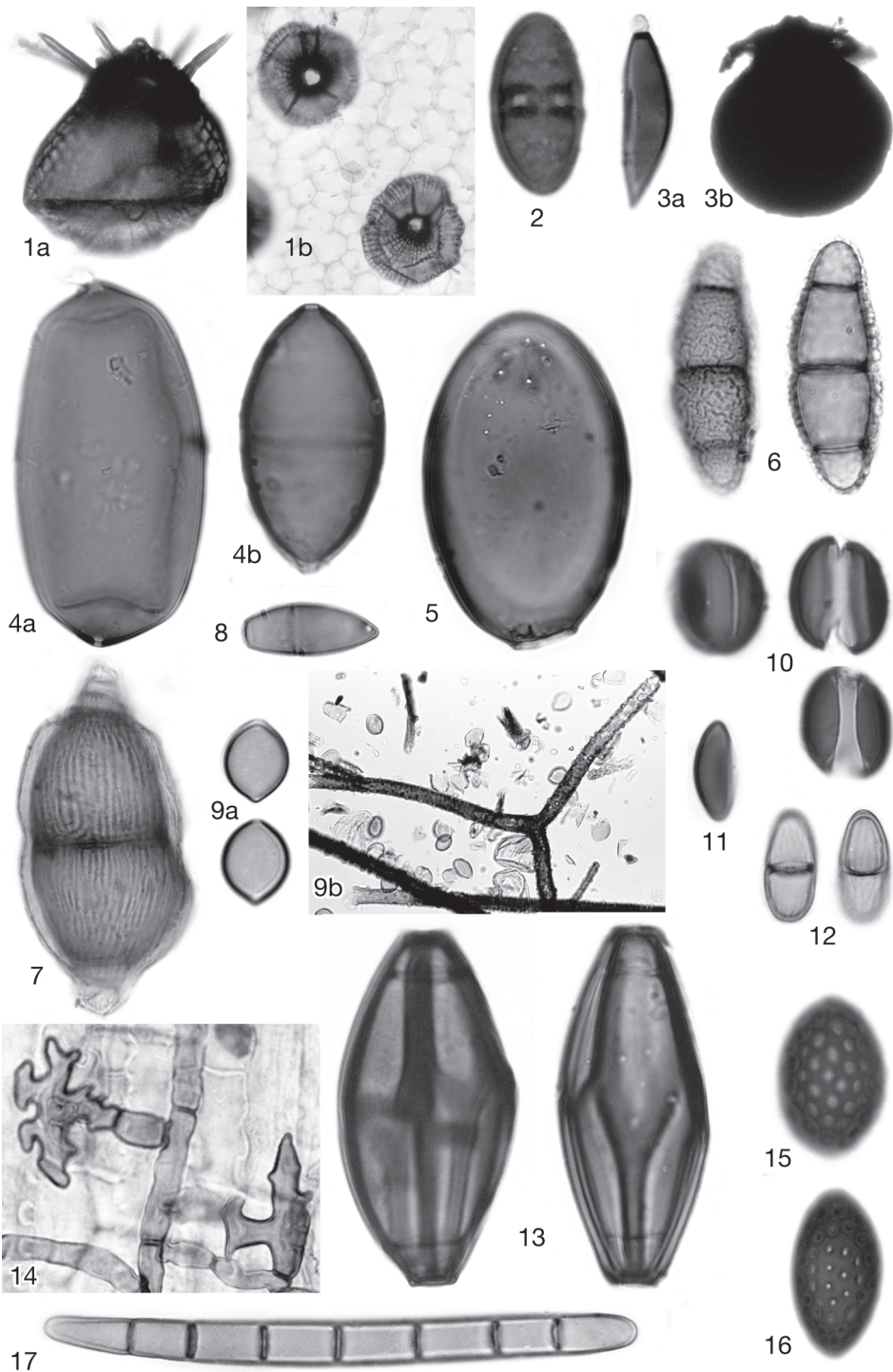
Anthostomella fuegiana grows on *Cladium mariscus*, *Luzula sylvatica*, *Rostkovia grandiflora* and *Eriophorum vaginatum* (Francis 1975). The presence of the fossil fruitbodies indicates that it grew *in situ* in raised bog vegetation. Amongst the host plants, *Eriophorum vaginatum* is the only likely host. In several raised bog studies where *A. fuegiana* was recorded, there is no good correlation between the occurrence of the fungus and the remains of *Eriophorum vaginatum*. Apparently the absence of the fungus does not necessarily imply the absence of the host plant. The identification remains somewhat uncertain, as the large cells of the ascospores of the fossil remains are somewhat shorter (18-25 μm) than those of recent material (26.5-35.5 μm), while they have the same width (5-7 μm). However, no other recent species has similar spores (Lu & Hyde 2000).

Apiosordaria verruculosa (C.N.Jensen) Arx & W.Gams (Plate II, 31; van Geel et al. 1983a: Type 169)

Ascospores were recorded (as *Zopfiella* type) by van Geel et al. (1983a) in a late Holocene pool deposit near Bronze Age settlements in the Netherlands. The spores probably became incorporated in the gyttja by translocation of material from unundated spots where dung, dead wood or some other organic substrate was present. Buurman et al. (1995) recorded the same ascospore type (in combination with various other ascospores of Sordariales) in a Bronze Age watering place in the same area. Van Geel et al. (2003) recorded it (as *Tripterospora* sp.) among a range of ascospore types of coprophilous taxa in soil samples from a Roman Period settlement in the Netherlands. In combination with other botanical and zoological data, the fungal record of that site pointed to a high density of domesticated herbivores. The species is mainly known from soil isolations, but also, e.g. from rabbit dung (Domsch et al. 1980).

Arnium spp. (Plate I, 4a and 4b; van Geel et al. 2003: Types 261 & 262)

In soil samples from a Roman Period settlement site in the Netherlands, van Geel et al. (2003) recorded a variety of ascospores of coprophilous species, among which spores resembling those of various *Arnium* species. In combination with other botanical and zoological data, the fungal record pointed to a high density of domesticated herbivores.



Bombardioidea sp. (Plate I, 5; Bos et al. in press: Type 575)

This ascospore type is of regular occurrence in early Holocene deposits in the Netherlands (Bos et al. 2005). It is characterised by several germ pores located near one pole. It differs from all known species in the genus by its dimensions and might be an example of an extinct species. All *Bombardioidea* species are dung-inhabiting, often restricted to *Alces alces*. Elk may well have been the producer of the substrate for *Bombardioidea* during the early Holocene.

Bysothecium circinans Fuckel (Plate I, 6; van Geel 1978: Type 16)

The species is a saprobe or weak parasite on woody substrates and also was observed on *Medicago sativa* (Boise 1983). Fossil ascospores were observed in Holocene peat deposits formed under meso- to oligotrophic conditions, but the fungus avoids relatively wet phases of peat growth (van Geel 1978, van Geel et al. 1981). Ascospores of *B. circinans* were also observed in Colombian Quaternary deposits. The ascospore ornamentation is sometimes (but not always) well developed in fossil conditions.

Caryospora callicarpa (Currey) Nitschke (Plate I, 7)

Ascospores with a characteristic shape and ornamentation referable to this species were abundant in caulking material (mostly consisting of mosses) from a medieval vessel excavated in the Netherlands, but apparently built in the 10th century in Germany (Cappers et al. 2000). *Caryospora callicarpa* is known from decaying wood of different trees, and reported from Europe and North America.

Cercophora sp. (Plate I, 8; van Geel 1978: Type 112)

The fossil record of the ascospores in relation to other, archaeological site information (Buurman et al. 1995, van Geel et al. 1981, 1983a, 2003, Witte & van Geel 1985) indicates that the presence of *Cercophora* often can be used as an indication for (extra) animal dung in the surroundings of the sample site. According to Lundqvist (1972), *Cercophora* species are coprophilous or occur on decaying wood, on culms and on other herbaceous stems and leaves. According to the variation in ascospore size, several species are probably present.

Chaetomium sp. (Plate I, 9a and 9b; van Geel 1978: Type 7A)

Ascospores and fruitbodies were observed in peat deposits. Perithecial hairs (essential for identification of species) were not preserved on the ascomata, but sometimes

Plate I. 1a, b: *Actinopeltis* sp., fruitbodies $\times 500$ and $\times 200$. 2: *Amphisphaerella dispersella*, ascospore ($\times 1000$). 3a, b: *Anthostomella* cf. *fuegiana*, ascospore (3a: $\times 1000$) and fruitbody (3b: $\times 100$). 4a, b: *Arnium* sp., ascospores (4a: $\times 750$; 4b: $\times 1000$). 5: *Bombardioidea* sp., ascospore ($\times 750$). 6: *Bysothecium circinans*, ascospore ($\times 1000$). 7: *Caryospora callicarpa*, ascospore ($\times 750$). 8: *Cercophora* sp., ascospore ($\times 1000$). 9 a: *Chaetomium* sp., ascospores ($\times 1000$) and perithecial hairs (9b) with ascospores ($\times 250$). 10: *Coniochaeta ligniaria*, ascospores ($\times 1000$). 11: *Coniochaeta xylariispora*, ascospore ($\times 1000$). 12: *Didymosphaeria massarioides*, ascospore ($\times 1000$). 13: *Diporotheca rhizophila*, ascospores ($\times 1000$). 14: *Clasterosporium caricinum*, mycelium with hiphopodia ($\times 750$). 15: *Gelasinospora* cf. *retispora*, ascospore ($\times 1000$). 16: *Gelasinospora* sp., ascospore ($\times 1000$). 17: *Geoglossum sphagnophilum*, ascospore ($\times 1000$).

separate. *Chaetomium* species are cellulose-decomposing fungi occurring on e.g. plant remains, fibre, wall paper and dung. Van Geel et al. (1989) recorded many spores of *Chaetomium* in a layer representing the initial stage of a sedge fen (Lateglacial deposit Usselo). Apart from the occurrence in natural habitats, *Chaetomium* spores also appeared to be linked to archaeological sites (Buurman et al. 1995, van Geel et al. 2003): in settlements in the past extra dung, damp straw, cloths, leather and other suitable substrates have probably been available. According to the variation in ascospore shape, several species are involved. According to their shape and dimensions, the spores illustrated in Fig. 9a may well originate from the common and ubiquitous species *Chaetomium globosum* Kunze.

Clasterosporium caricinum (Fr. : Fr.) E.G.Simmons (Plate I, 14; Pals et al. 1980: Type 126)

Fossil remnants usually interpreted as hyphopodia of *Gaeumannomyces* cf. *caricis* are of regular occurrence in pollen slides. They may however be re-identified as *Clasterosporium caricinum* (Fr. : Fr.) E.G.Simmons. A comparison of the record of these fossils with macro-fossils and the Cyperaceae pollen curve in a Holocene deposit was made by Pals et al. (1980). The hyphopodial material appeared where *Carex paniculata* and *C. pseudocyperus* started the filling-in of a lake; their co-occurrence with local *Carex* species in the core was obvious. Van Geel et al. (1983a) observed and illustrated the fossils (as hyphopodia of *Gaeumannomyces*) still in organic contact with *Carex* epidermis. The link between the fossils and *Carex* species has interesting implications for the palynological analysis of, e.g., Lateglacial material (van Geel et al. 1989). Since Cyperaceae are usually included in the pollen sum (used as a basis for calculations of pollen percentages) in Lateglacial deposits, the answer to the question whether Cyperaceae constituted an element of the local vegetation is a crucial piece of information. The local presence, respectively absence, of *Carex* species becomes evident from the analysis of the fossil hyphopodia.

Coniochaeta ligniaria (Grev.) Cooke (Plate I, 10; van Geel et al. 1983a: Type 172)

According to Munk (1957), *C. ligniaria* is common on dung and wood. The ascospores were recorded in a late Holocene peat deposit dominated by *Thelypteris palustris* (van Geel et al. 1983a) but they were also of regular occurrence in soil surface samples from a Roman Period settlement site with strong evidence for a high population density of domesticated animals (van Geel et al. 2003).

Coniochaeta xylariispora (Ellis & Everh.) Cooke (Plate I, 11; van Geel 1978: Type 6)

Ascospores and fruitbodies were observed in raised bog peat of Holocene (van Geel 1978) and Eemian (last interglacial) age (van Geel et al. 1995).

Didymosphaeria massarioides Sacc. & Brunaud (Plate I, 12; van Geel 1978: Type 85)

Ascospores were recorded (but not yet identified) in Holocene raised bog peat in low frequencies (van Geel 1978). The shape and ornamentation is typical of this species (Aptroot 1995).

Diporothea rhizophila C.Gordon & C.Shaw (Plate I, 13; van Geel et al. 1986: Type 143)

Fossil ascospores were recorded by van der Wiel (1982), at that time as the unidentified fungal spore 'Type 143'. This kind of ascospores occurs regularly in Holocene deposits formed in eutrophic to mesotrophic conditions. A.E.Caseldine (pers. comm. 1979) observed the spores in peat deposits of the Somerset levels where they occurred throughout the profile, which varied from a woody peat to a *Phragmites-Cladium* peat. *Diporothea* spores are rare in the Lateglacial deposits at Usselo (van Geel et al. 1989). They were also recorded in an Eemian lake deposit (van Geel et al. 1986).

Based on fruitbodies still containing ascospores from a sub-recent *Thelypteris* peat deposit in the Netherlands, the Type 143 fungus could be identified (van Geel et al. 1986). We may expect a host-parasite relationship for this representative of the Diporotheaceae. Gordon et al. (1961) mentioned roots of *Solanum* species as a substrate. However, curve matching (comparing frequency curves of the spores with curves of possible host plants) in the above-mentioned sub-recent *Thelypteris* deposit might point to *Thelypteris* as a host plant, but such a relationship is not mentioned in the mycological literature. Van Geel et al. (2003) recorded ascospores and fruitbodies of *D. rhizophila* in soil samples from a Roman Period settlement site in the Netherlands.

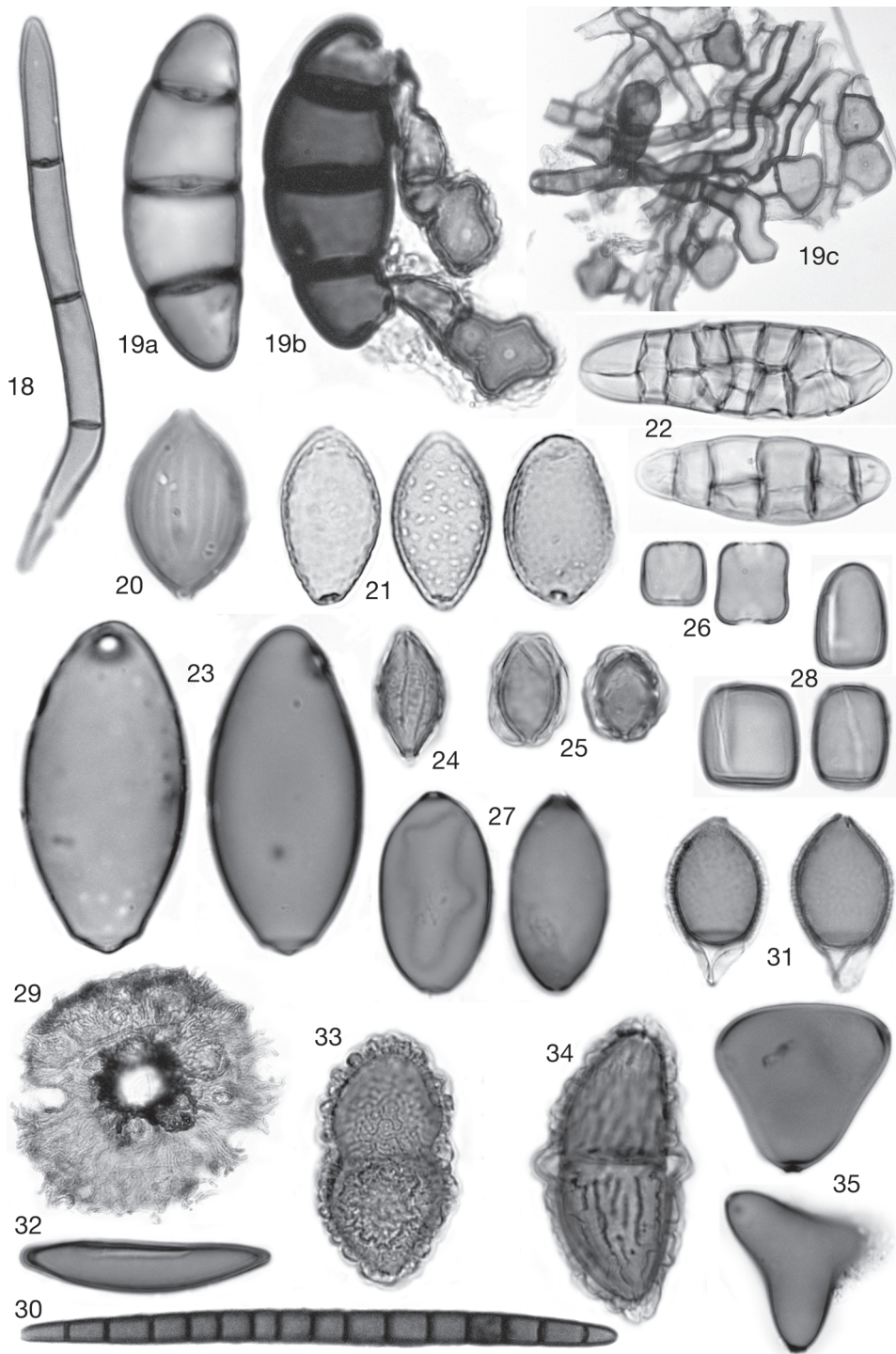
In a review paper about the fossil record and paleoecological potential of freshwater fungi, Sherwood-Pike (1988) illustrated the Tertiary fossil spore genus *Striadiporites* which represents ascospores of *Diporothea*.

Gelasinospora cf. retispora Cain (Plate I, 15; van Geel 1978: Type 2)

In the fossil record of peat deposits (van Geel 1978, van Geel et al. 1989) the curve of ascospores of *G. cf. retispora* often more or less parallels the curve of *Gelasinospora* sp. (Type 1), which apparently prefers dry conditions and layers with charred material. *G. retispora* (as a recent taxon) has been isolated from a wide range of substrates (Domsch et al. 1980). Based on a phylogenetic reconstruction using molecular methods (García et al. 2004), all species of the genus *Gelasinospora* have recently been included in the genus *Neurospora*, and the relevant combinations made. However, for practical reasons, the present spore is still called *Gelasinospora* here, as its ornamentation differs considerably from that of *Neurospora* s.s.

Gelasinospora sp. (Plate I, 16; van Geel 1978: Type 1)

Studies of Holocene peat deposits have revealed that maxima in the frequency curves of *Gelasinospora* sp. occur in highly decomposed peat, formed under relatively dry, oligotrophic conditions. Often these layers contain charred plant remains (see e.g., Kuhry 1997). The indicator value of the ascospores in Lateglacial peat deposit in the eastern Netherlands (van Geel et al. 1989) are consistent with the above-mentioned conditions in Holocene deposits. According to Lundqvist (1972), *Gelasinospora* species are mainly fimicolous, but they may also be carbonicolous or lignicolous. See also final comment under the previous entry.



Geoglossum sphagnophilum Ehrenb. (Plate I, 17; van Geel 1978: Type 77A)

In the literature (Favre 1948, Maas Geesteranus 1964), *G. sphagnophilum* is reported to grow among *Sphagnum*, and indeed *Sphagnum* remains were present in all samples containing ascospores of *S. sphagnophilum* from the Holocene raised bog Engbertsdijksveen (van Geel 1978), but the curve of the fossil ascospores yields additional information. The spores were encountered in the lower part (age: Atlantic and Subboreal) of the Engbertsdijksveen section, especially in the upper layer of hummock vegetation, just before (wet) *Scheuchzeria palustris* overgrowing phases. Spores were also recorded in a layer characterised by *Scheuchzeria palustris*, *Oxycoccus palustris* and *Andromeda polifolia*. In *Sphagnum rubellum* peat, the ascospores were encountered in low frequencies only. *G. sphagnophilum* was absent in the *Sphagnum imbricatum* peat of Subatlantic age. The change in climatic conditions that caused the growth of *S. imbricatum* (cooler, more oceanic climate) may have been unfavourable for *G. sphagnophilum*. Van Geel et al. (1981) recorded ascospores of *G. sphagnophilum* in early Holocene *Sphagnum* peat formed under mesotrophic conditions. There are no recent records of *G. sphagnophilum* in the Netherlands.

Lasiosphaeria caudata (Fuckel) Sacc. (Plate II, 18; van Geel 1978: Type 63A)

Ascospores were recorded with low frequencies in Holocene raised bog deposits. Also some fruitbodies were found (van Geel 1978).

Munk (1957) found *L. caudata* on decaying wood of *Picea*. This tree was not yet present in northwest Europe during the period studied by van Geel (1978). The presence of fruitbodies in the peat samples strongly suggests that *L. caudata* occurred *in situ* in the (treeless) bog vegetation. The macrofossil study did not yield any indication of the substrate of the fungus. Recently we studied (unpublished report) a late Holocene raised bog core from Lille Vildmose (Denmark). *Picea* was planted in the surroundings of the bog in historical time. The rise of *Picea* pollen coincided with the appearance and a sudden rise of the spore frequency of *L. caudata*, presumably indicating a host-parasite relationship.

Meliola ellisii Roumeg. (Plate II, 19a-c; van Geel 1978: Type 14)

Ascospores, mycelium and fruitbodies regularly occur in raised bog peat (van Geel 1978). Often the fossil fruitbodies still contain ascospores. Sometimes the observed ascospores had germinated before fossilisation.

Plate II. 18: *Lasiosphaeria caudata*, ascospore (× 1000). 19 a-c: *Meliola ellisii*, 19a. ascospore (× 1000); 19b. germinating ascospore (× 1000); 19c. mycelium (× 500). 20: *Neurospora crassa*, ascospore (× 1000). 21: cf. *Persiciospora* sp., ascospores (× 1000). 22: *Pleospora* sp., ascospores (× 1000). 23: *Podospora* sp, ascospores (× 1000). 24: *Pteridiosperma* sp., ascospore (× 1000). 25: *Rhytidospora* cf. *tetraspora*, ascospores (× 1000). 26: cf. *Scopinella barbata*, ascospores (× 1000). 27: *Sordaria* sp., ascospores (× 1000). 28: *Sporormiella* sp., part-spores (× 1000). 29: *Stomiopeltis* sp., fruitbody (× 300). 30: *Trichoglossum hirsutum*, ascospore (× 750). 31: *Apiosordaria verruculosa*, ascospores (× 1000). 32: *Ustilina deusta*, ascospore (× 1000). 33: *Valsaria* cf. *variospora*, ascospore (× 1000). 34: *Valsaria* sp., ascospore (× 1000). 35: *Zopfiella lundqvistii*, ascospores (× 1000).

Meliolaceae are obligate and rather oligophagous parasites on green plants (Hansford 1961). *Meliola ellisii* (synonym *M. niessleana* G.Winter) is the only species of *Meliola* in Britain, where it is associated with *Vaccinium vitis-idaea* (Dennis 1968). Eriksson (1974) found *M. ellisii* on several species of *Vaccinium* in Fennoscandia, and it is known from several other Ericaceae genera (but not *Calluna*) elsewhere. Van Geel (1978) showed with curve matching in the record of the Holocene raised bog Engbertsdijksveen, that fossil ascospores, mycelium and fruitbodies correspond with the *Calluna vulgaris* records (*Meliola* being indicative of stands of *Calluna* in the immediate surroundings of the sample site). Fossil mycelium and even fruitbodies were found still in organic contact with fossil *Calluna* leaves and stems. *Meliola ellisii*, or a closely allied species (or a physiological race slightly different from the recent ones) was probably a common parasite on *Calluna vulgaris* in raised bogs during the Atlantic to Subatlantic period. Van Geel et al. (1995) also found the relationship between *Calluna vulgaris* and *Meliola ellisii* in a late Eemian/early Weichselian raised bog deposit. If still growing on *Calluna*, *Meliola ellisii* has been overlooked on this plant. Hansford (1961, 1963) did not describe a single *Meliola* species from *Calluna vulgaris* in his monograph of the Meliolineae. Fossil remains of Meliolaceae of Eocene age were found by Köck (1939), Dilcher (1965) and Selkirk (1975). Recently we studied a Holocene peat deposit from an intermediate ombrotrophic bog in northern-England, for micro- and macrofossils and discovered the hyperparasite *Isthmospora spinosa* together with its host *Meliola ellisii* (van Geel et al. in press).

Neurospora crassa Shear & B.Dodge (Plate II, 20; van Geel 1978: Type 55C)

Ascospores were observed in a layer of charred *Molinia* remains in the Holocene peat deposit of Engbertsdijksveen (van Geel 1978). More evidence for *Neurospora* ascospores as local fire indicators was given by Bakker & van Smeerdijk (1982). Shear & Dodge (1927) and Dennis (1968) mention the occurrence of the anamorph of *Neurospora* on vegetable matter, developing often after it has been charred by fire. The ascospores do not germinate under ordinary cultural conditions but grow readily after having been subjected to moist heat at 65-70°C for a few minutes (Shear & Dodge 1927). Conceivably, the conditions in the burnt *Molinia* layer at Engbertsdijksveen were comparable with the artificially created conditions favourable for ascospore germination. Based on literature and the observations of the fossil ascospores in charred peat layers, it can be concluded that *Neurospora crassa* is an indicator of local fires. However, it is also evident that often *Neurospora crassa* ascospores are absent in the charred layers that represent former fires in fens and bogs.

cf. **Persiciospora** sp. (Plate II, 21; Pals et al. 1980: Type 124)

Ascospores with a characteristic ornamentation probably referable to this genus (Cannon & Hawksworth 1982) but differing by the presence of only one germ pore are common in mesotrophic peat deposits (Pals et al. 1980). The spores were also found in the fill of a Bronze Age water pit (Buurman et al. 1995).

Pleospora sp. (Plate II, 22; van Geel 1978: Type 3B)

Ascospores and fruitbodies were observed in ombrotrophic peat formed under relatively dry conditions (van Geel 1978). The ascospores belong to various different species of the genus. Species of *Pleospora* occur typically on dead plant remains. Various spore types, indicating a range of species, have been found in the fossil record, including the ubiquitous *P. herbarum* (Pers. : Fr.) Rabenh., which has been recorded on plant remains in mammoth dung (Aptroot & van Geel in press).

Podospora sp. (Plate II, 23; van Geel et al. 1981: Type 368)

Ascospores are often recorded in samples with an archaeological context (van Geel et al. 1981, 1983b, 2003, Buurman et al. 1995). A relation with the presence of man or domesticated animals (providing dung as a substrate; Lundqvist 1972) seems probable. Observations of ascospores of *Podospora* were also made in deposits containing remains of *Mammuthus* in the Netherlands and in Siberia (Aptroot & van Geel in press, Cappers et al. 1993), in Norwegian *Calluna-Sphagnum* peat deposits with palynological evidence for grazing (project P.E.Kaland; unpublished record), and in Holocene deposits from Mexico (Almeida-Lenero et al. 2005).

Pteridiosperma sp. (Plate II, 24)

Ascospores with their characteristic ornamentation were repeatedly found in the infill of a Bronze Age watering place (Buurman et al. 1995). All species of this genus are dung-inhabiting.

Rhytidospora cf. **tetraspora** R.S.Jeng & Cain (Plate II, 25; van Geel et al. 1983a: Type 171)

Ascospores with a characteristic ornamentation probably referable to this species (Jeng & Cain 1977) were repeatedly found in the infill of a Bronze Age watering place (Buurman et al. 1995). The number of ascospores per ascus, reported to be a valid character in this genus, could of course not be assessed, leaving some doubt about the species identification. All known species of this genus are dung-inhabiting.

cf. **Scopinella barbata** (Pers.) Lév. ex Sacc. (Plate II, 26; van Geel et al. 1981: Type 343)

According to Hawksworth (1975), *Scopinella barbata* occurs on fallen leaves of *Quercus*, *Castanea*, *Potentilla* and *Rhododendron* species.

Ascospores were recorded in *Drepanocladus* peat of Preboreal age in the Netherlands (van Geel et al. 1981). W.O. van der Knaap (pers. comm. 1989) recorded similar spores in late Holocene samples from King George Island (Antarctica). There only the two native vascular plants of Antarctica occur, viz. *Deschampsia antarctica* (Poaceae) and *Colobanthus quitensis* (Caryophyllaceae), which grow in combination with *Polytrichum alpinum* and *Drepanocladus uncinatus*. The local occurrence of *Drepanocladus* at both sites may indicate ecological preferences, but at the present state of knowledge this is speculation only.

Sordaria sp. (Plate II, 27; van Geel et al. 2003)

Ascospores of coprophilous *Sordaria* species, including ones indistinguishable from recent *S. fimicola* (Rob.) Ces. & De Not. and *S. humana* (Fuckel) G.Winter are common in samples from archaeological sites (Bakker & van Smeerdijk 1982, Buurman et al. 1995, Willemsen et al. 1996, Witte & van Geel 1985, van Geel et al. 1981, 1983a, b, 2003), often in combination with ascospores of other coprophilous ascomycetes.

Sporormiella sp. (Plate II, 28; van Geel et al. 2003: Type 113)

Ascospores of modern-day *Sporormiella* species are three- to many-septate. Every ascospore cell shows a germ slit, extending over the entire length of the cell. The ascospores easily split up in separate cells and, as a consequence, in the fossil state no observations of complete ascospores can be made. Species identification of *Sporormiella* and similar genera is not possible because fruitbodies, asci and complete ascospores are not available (compare Ahmed & Cain 1972). The representatives of the related, also coprophilous genus *Sporormia* lack germ slits, but as the descriptions of Ahmed & Cain (1972) are based on non-germinated spores, a slit may appear after germination of *Sporormia* spores, and thus we cannot exclude that *Sporormia* is also among our fossil spores. In addition, the genus *Sporormiella* is often merged with *Preussia*. Therefore we refer to the fossil part-spores as *Sporormiella*-like instead of *Sporormiella* as such. Fossil *Sporormiella*-like part-spores were distinguished by Davis et al. (1977), Davis & Turner (1986), Davis (1987), Burney et al. (2003), and by van Geel et al. (2003) who concluded that the spores are a reliable proxy for faunal biomass. Samples from the north Siberian site of the Jarkov mammoth (Mol et al. 2003) are rich in *Sporormiella*-like spores. Fruitbodies found in the intestines of the Yukagir mammoth point to coprophagy (Aptroot & van Geel in press).

Stomiopeltis sp. (Plate II, 29; van Geel et al. 1978: Type 8F)

Fruitbodies were recorded in Holocene raised bog samples from Engbertsdijksveen (van Geel 1978), some of them were found attached to the epidermis of leaves of *Erica tetralix*, *Calluna vulgaris*, *Oxycoccus palustris*, and once on a leaf of *Sphagnum* sect. *Acutifolia*. The fossil fungus is probably *S. callunae* B.Eriksson (1974), which is common on dead leaves of *Calluna vulgaris* throughout Fennoscandia.

Trichoglossum hirsutum (Pers. : Fr.) Boudier (Plate II, 30; van Geel 1978 : Type 77B)

Two ascospores were observed in holocene raised bog peat (van Geel 1978). The spores were probably produced locally in the peat. Transport over long distances is unlikely as the relatively small fruitbodies grow among taller plants. Similar ascospores are produced by *Geoglossum peckianum*, but this species does not grow in *Sphagnum* bogs (Favre 1948, Maas Geesteranus 1964).

Ustulina deusta (Hoffm. : Fr.) Lind (Plate II, 32; van Geel 1978: Type 44)

Ustulina deusta (nowadays often classified as *Kretzschmaria deusta* (Hoffm.) P.M.D.Martin) is a dangerous parasite causing soft-rot of wood. It is of regular

occurrence on a variety of host trees (in northwest Europe: *Abies*, *Acer*, *Aesculus*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Fagus*, *Fraxinus*, *Populus*, *Quercus*, *Salix*, *Taxus*, *Tilia* and *Ulmus*). A full record of host plants is given by Wilkins (1934) and Hepting (1971).

Van Geel & Andersen (1988) compared fossil records of ascospores of *U. deusta* with the pollen records of potential host trees in Eemian deposits from Denmark. Their results indicate that the distance between sample site and forest has a considerable influence on the frequency records of the ascospores. These spores were absent in deposits from large lakes, but in the deposit taken from a small hollow within a forested area they appeared with high frequencies. A close relationship between the incidence of the fungus and the pollen curves of its potential host plants (*Tilia* and *Fraxinus* at the site Egernsund) was evident. The transportation of the ascospores (produced near the forest floor, where wind dispersal is less effective) apparently is far less easy than the dispersal of tree pollen. There are no indications that the fungus has influence on the forest succession (van Geel & Andersen 1988, van Geel et al. 1986). Pals et al. (1980) showed that *U. deusta* spores also can occur (in low frequencies) in marine clay, in combination with other redeposited non-marine plant remains, like *Sphagnum* leaves.

Valsaria cf. variospora (Boudier) Y.-M.Ju & J.D.Rogers (Plate II, 33; van Geel et al. 2003: Type 140)

Ascospores of this type often occur in peat deposits formed under wet eutrophic conditions (van Geel et al. 1983a, van der Wiel 1982).

Valsaria sp. (Plate II, 34; van Geel et al. 2003: Type 263)

Ascospores were recorded in soil samples from a Roman Period settlement site in the Netherlands (van Geel et al. 2003)

Zopfiella lundqvistii Shearer & Crane (Plate II, 35; van Geel et al. 1986: Type 501)

Van Geel et al. (1986) observed ascospores of *Zopfiella lundqvistii* in an Eemian deposit from the Netherlands. P.de Klerk (pers. comm. 1994) found many ascospores in a late Holocene wood peat deposit from near Leerdam, the Netherlands. According to Guarro et al. (1991), the species is known from a series of collections from swamps in Illinois and from paddy field soil in Japan.

Discussion and conclusion

Remains of fossil fungi in Quaternary deposits appear to be almost exclusively ascospores, conidia and chlamydospores (produced by Ascomycetes including their anamorphs). Many of the recorded fungal 'types' were found in peat deposits, especially in peat layers which were formed under relatively dry conditions. In lake deposits, fungal remains are normally of rare occurrence (in open water there is no strictly local production of fungal spores which are preserved as fossils). Another factor that influences the fossil record is the fact that only relatively large fungal

spores with thick walls are normally preserved. Most of the thin-walled spores, which disperse better and are known from the records of spores in the present atmosphere, obviously do not fossilize. Relatively small fruitbodies, like those of *Stomiopeltis* and *Actinopeltis* were never found with ascospores inside, and no spores were found that could have been produced by these taxa. Similarly, fossil asci were never observed.

From the various studies of fossil fungal spores it is evident that the recorded spores in most cases were of strictly local occurrence. They were fossilised at, or near, the place where they had been produced, or the spores were deposited at only a short distance from the place where sporulation took place. Among the analysed fossil fungi are:

(1) Parasitic fungi and saprobes, which are always found in combination with certain host plants or on their remains, like *Meliola ellisii* which always comes together with *Calluna vulgaris*. Records could even be made of *Isthmospora spinosa*, which is a hyperparasite on *Meliola ellisii* (van Geel et al., in press).

(2) Fungi which were present only under certain conditions or incidentally on special hosts, or on their remains, like *Anthostomella fuegiana* which sometimes occurs together with *Eriophorum vaginatum*.

(3) Fungi growing on dung, like *Sporormiella* and various representatives of Sordariales.

(4) Fungi occurring on burnt plant remains like *Neurospora crassa*.

The paleoecological information of fungal remains is not yet fully explored. Most palynologists do not produce records of the observed fungal remains. However, it is our experience that the information is often very useful, especially in studies of peat deposits and when studying material from archaeological sites. Man and domesticated animals will have been responsible for a range of new habitats, and also the mycoflora of settlement sites and the surrounding arable land, pastures and hay-meadows will have had different fungal assemblages relative to undisturbed natural ecosystems. Innes & Blackford (2003) used the fungal spore record of coprophilous taxa, in combination with fossil pollen and charcoal, to study pre-Neolithic woodland disturbances in northeast England. Kuhry (1997) showed that fungal remains initially described in European sites show similar ecological preferences in Canadian bogs.

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