

6. NON-POLLEN PALYNOMORPHS

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Introduction

In pollen preparations other microfossils of various origin are often preserved. Among the microfossils that attracted the attention of palynologists are a variety of organisms, e.g., algae (Korde, 1966; Jankovská & Komárek, 1992, 2000), eggs produced by aquatic flatworms (Haas, 1996), eggs of Tardigrada (Jankovská (1990, 1991), Bacteria (Nilsson & Renberg, 1990) and stomates (MacDonald, this volume). For a period of more than 30 years, deposits of Eemian, Weichselian and Holocene age have been studied palynologically at the University of Amsterdam. The analysis of pollen was combined with the study of all 'extra' microfossils (non-pollen palynomorphs: NPP) with a characteristic morphology. The aim was to discern still unexplored fossils, and this strategy resulted in an increase in the number of palaeoenvironmental indicators. Among the extra fossils were spores of fungi, remains of algae, cyanobacteria (formerly known as blue-green algae) and invertebrates. Most of the deposits studied were situated in Northwest Europe, but some cores from Colombia were also studied. In a series of papers the descriptions and illustrations of the NPP ('Types') were published and their indicator value was discussed. Morphological descriptions were always combined with stratigraphic information, often in the form of pollen and microfossil diagrams. Several hundred Types have now been distinguished, each one with a Type-number (Bakker & van Smeerdijk (1982), Batten & van Geel (1985), Carrion & van Geel (1999), Ellis-Adam & van Geel (1978), Kuhry (1985, 1997), López-Sáez et al. (1998), Pals et al. (1980), van Dam et al. (1988), van Geel (1976, 1978, 1986, 1998), van Geel & Grenfell (1996), van Geel et al. (1981, 1983, 1986, 1989, 1994, 1995). In most cases there was initially no, or hardly any taxonomic/ecological knowledge about the distinguished Types. The identification of the fossils was attempted with the aid of literature and by consulting colleagues in invertebrate zoology, phycology, mycology and plant anatomy. Among the NPP there still are many taxa which are not properly identified, but some of them nevertheless can be used as palaeoenvironmental indicators. In such cases, the ecological information is inferred from the co-occurrence (curve matching) with



identified taxa (e.g., pollen, seeds). Most fungal and algal taxa and cyanobacteria have a much longer geological history than angiosperms and gymnosperms, and, therefore, some of the NPP-studies are also interesting for palynologists specialised in the analysis of pre-Quaternary deposits.

In this chapter only a small selection of NPP taxa is shown. For more information and for morphological descriptions and illustrations, reference is made to the above-mentioned publications. The palaeoecological exploration of NPP in lake deposits is certainly not yet finished. Some egg types of rotifers are shown here as an example of a taxonomic group which still has to be studied in detail (compare Merkt & Müller, 1999), so that the full palaeoenvironmental information can be used in future studies.

Methods used

All the recorded non-pollen palynomorphs were found in pollen samples that had been treated according to the pollen preparation method as described below (compare Bennett & Willis, this volume, Faegri & Iversen, 1989 and Moore et al., 1991):

- 1) Boil the sample (0.5–3 cc) in 10% KOH (or in 10% Na-Pyrophosphate for clayey sediments).
- 2) sieve (meshes 215 μm); pour into centrifuge tubes and centrifuge until a speed of at least 4500 rpm.
- 3) Wash the material with water and centrifuge until the supernatant is clear. NB: the following steps (4–7; 10–11) are undertaken in the fume cupboard.
- 4) Dehydrate with 96% acetic acid and centrifuge.
- 5) Prepare an acetolysis mixture by slowly adding 1 part H_2SO_4 to 9 parts acetic anhydride (stirring and cooling in a water bath is essential; no contact between acetolysis mixture and water!; safety glasses and gloves required).
- 6) Acetolyse the material by heating the sample in the acetolysis mixture to 100 °C for ca 10 minutes in a water bath.
- 7) Cool the sample tubes in a water bath and then centrifuge.
- 8) Wash with distilled water and centrifuge twice.
- 9) Wash with 96% alcohol and centrifuge twice.
- 10) The separation of organic material from sand and clay (if any) is done by using a heavy liquid (bromoform-alcohol mixture, specific gravity 2; gloves!). The procedure for this treatment, if required, is:
- 11) Add the bromoform-alcohol mixture to the sample and centrifuge at 1500 rpm for 10 minutes. Do not use the centrifuge brake in this case and pour the material floating above the bromoform mixture into a tube that is half-filled with 96% alcohol.

- 12) Centrifuge again (until 4500 rpm). Decant and wash the sample into a residue tube, using 96% alcohol. Centrifuge (until 4500 rpm) the residue tubes. Decant and add a drop/drops of glycerine to the residue (dependent upon the residue size).
- 13) Put the residue tube for a night in the oven at 40 °C.
- 14) Prepare microscope slides.

In studies by the author, HF treatment in order to remove minerogenic material was never applied. It is not known if HF would destroy any of the NPP occurring in samples which are not treated with HF. Clarke (1994) discussed differential recovery of palynomorphs by three processing techniques. None of the techniques seemed to cause notable deterioration to fungal palynomorphs.

Indicator potential and applications of a selection of non-pollen palynomorphs

Zygnemataceae

Zygnemataceae are unbranched filamentous green algae, inhabiting shallow, stagnant, oxygen-rich freshwater lakes, ponds, small pools or wet soils. The cell walls of the filaments do not fossilize, but the morphologically characteristic and resistant spore walls preserve. Within the family, twelve genera are distinguished, among which are *Mougeotia*, *Zygnema*, *Spirogyra* and *Debarya* (for some examples of fossil spore types see Figure 1(1–10)). Zygnemataceae reproduce sexually by conjugation. During the conjugation process, two filaments become closely aligned and adjoining vegetative cells become connected by a conjugation tube. Conjugation results in the thick-walled zygospores. Apart from zygospores, asexual resting spores (aplanospores) can also be formed. In the temperate climatic zone Zygnemataceae produce their spores during spring in shallow (often less than 0.5 m deep), relatively warm water. Dormant spores of Zygnemataceae may be exposed to (summer) desiccation without damage to the living contents. Spores germinate in the next year in early spring. With the taxonomy of the extant Zygnemataceae, the morphology and number of chloroplasts is important but in most cases the morphological characteristics of the spores (which we find as microfossils) are necessary for identification to species level.

For general information on extant Zygnemataceae, reference is made to Transeau (1951), Randhawa (1959) and Kadlubowska (1984). A research review concerning the morphology, distribution, ecology, reproduction, physiology, biochemistry, cytology, genetics, systematics and phylogeny of the extant Zygnemataceae is given by Hoshaw & McCourt (1988).

The recognition of the zygnemataceous origin of various morphological spore types in palynological slides started with a study by van Geel (1976). An overview of information about Zygnemataceae of relevance for palynologists and palaeolimnologists is given by van Geel & Grenfell (1994). Fossil spores of Zygnemataceae can be very common in pollen preparations and such spores have often been described—especially in pre-Quaternary deposits—as form-taxa of unknown taxonomic affinity. Based on the zygospore record, Zygnemataceae range from the Carboniferous to the present time. The morphological differentiation of the various spore types (*Mougeotia*, *Zygnema*, *Spirogyra*, *Debarya*) may have happened during the Early Carboniferous, or even earlier (van Geel, 1979).

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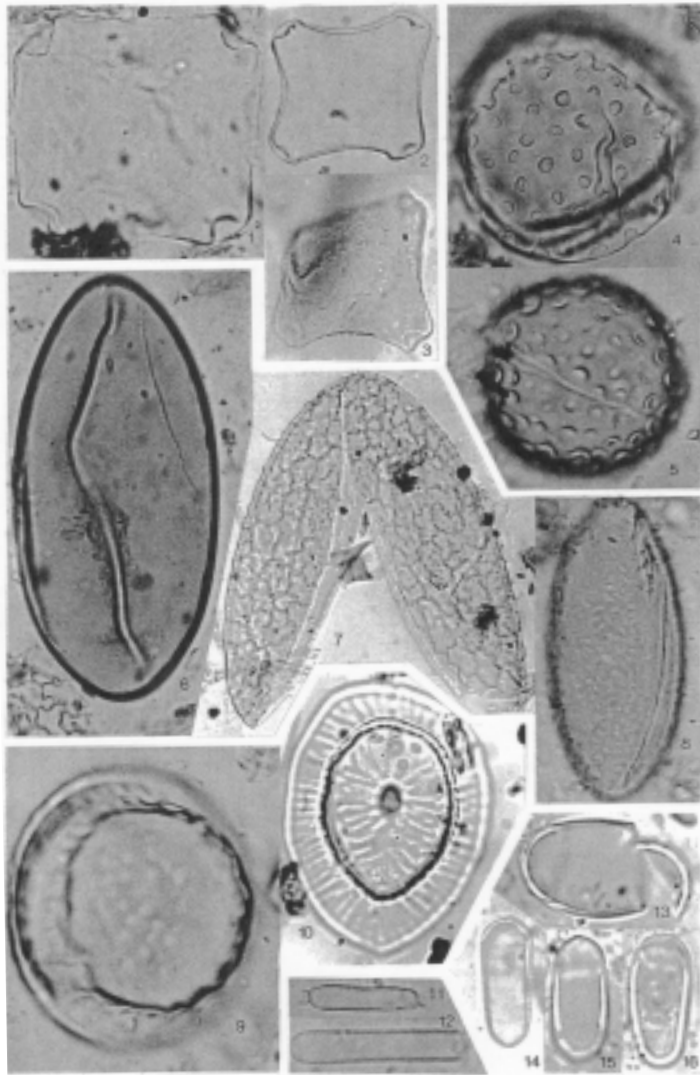


Figure 1. 1–3: *Mougeotia*, zygospores ($\times 1000$). 4 and 5: *Zygnema*-type, zygospores or aplanospores ($\times 1000$). 6–8: *Spirogyra*, zygospores or aplanospores ($\times 1000$, $\times 500$, $\times 750$). 9 and 10: *Debarya*, zygospores ($\times 1000$). 11 and 12: *Aphanizomenon*, akinetes ($\times 1000$). 13–16: *Anabaena*, akinetes ($\times 1000$).

Fossil spores of Zygnemataceae from Quaternary and older sediments have been described and used as palaeoenvironmental indicators by van Geel (1976), van Geel & van der Hammen (1978), Ellis-Adam & van Geel (1978), Rich et al. (1982), van Geel et al. (1989), and Head (1993), as well as others. Within the representatives of extant Zygnemataceae few ecological differences are known. However, different Types of fossil spores often

characterise different habitats (e.g., specific sediment types, different trophic conditions). Such differences in ecological amplitudes for specific spore types become evident when the complete spectrum of micro- and macrofossils from closely spaced samples is considered. Van Geel (1978) observed a succession of three different zygnemataceous spore types at the base of the Holocene raised bog Engbertsdijksveen in The Netherlands. The succession was presumably caused by changing trophic conditions (oligotrophication) under influence of the formation of a peaty layer of increasing thickness. At particular sites, conditions can remain favourable to Zygnemataceae for longer periods (millennia in lakes, or near lake margins; see van Geel & van der Hammen, 1978), or only during very short transitional intervals where Zygnemataceae played a role in the vegetation succession. Van Geel & Grenfell (1994) showed an example of such a short successional phase in which *Mougeotia* zygospores played a pioneer role after a local rise of the water table in the Holocene raised bog Engbertsdijksveen.

Pediastrum

Pediastrum species (Fig. 5(52)) are radially-symmetrical colonial green algae (Batten, 1996; Nielsen & Sørensen, 1992; Jankovská & Komárek, 1982, 1995). The outermost cells each show one or two horns. Records of *Pediastrum* species present in pollen slides seem to indicate a wide range of environmental responses (Batten, 1996). Factors mentioned as causative for the occurrence of *Pediastrum* species in sediments include changes in erosion in the catchment, turbidity, water chemistry, nutrient status, and pH. The range of responses may be due to the fact that in the palynological record often different *Pediastrum* species are lumped together. Further knowledge on the present-day ecology of *Pediastrum* species is needed. According to Crisman (1978) *Pediastrum* species are common in hard-water eutrophic lakes. Cronberg (1982) studied a late Holocene lake deposit in S. Sweden. She showed differences in the responses of various *Pediastrum* species and used those species as indicators of the changing trophic status of the lake. Jankovská & Komárek (2000) and Komárek & Jankovská (in press) illustrated *Pediastrum* species and other coccal green algae and reviewed their palaeoecological indicator value.

Botryococcus

Botryococcus species (Fig. 5(53)) are colonial green algae with densely-packed conical cells radiating and branching from the center of the roughly-spherical colony. Modern *Botryococcus* is widely dispersed in temperate and tropical regions, and is known to tolerate seasonally cold climates. It generally lives in freshwater fens, temporary pools, ponds and lakes, where it may form a thick surface scum, but considerable abundances in variable salinity habitats are also known. For morphological details and palaeoenvironmental significance, reference is made to Guy-Ohlson (1992), Komárek & Marvan (1992), Batten & Grenfell (1996), and Jankovská & Komárek (2000).

Cyanobacteria

The analysis of cyanobacteria allows a better understanding of the changing local environments in lakes and pools in the past. Van Geel et al. (1989) recorded *Gloetrichia*

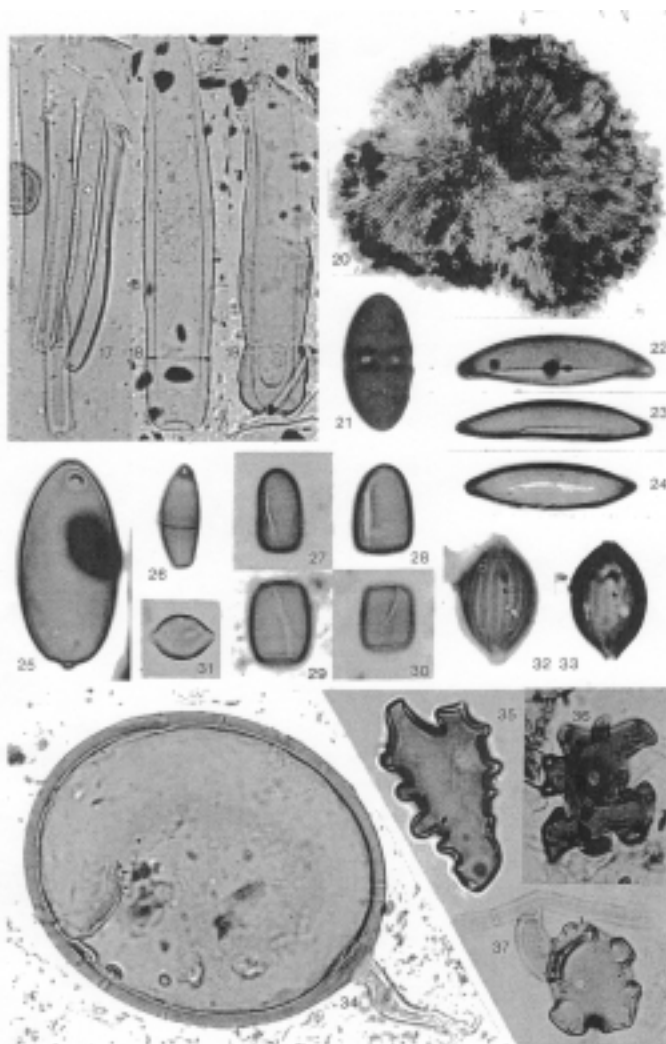


Figure 2. 17: cluster of sheaths of *Gloeotrichia*-type ($\times 400$). 18 and 19: sheaths of *Gloeotrichia*-type ($\times 500$). 20: colony of *Gloeotrichia*-type ($\times 85$; recorded during macrofossil analysis). 21: *Amphisphearella amphisphearioides*, ascospore ($\times 1000$). 22–24: *Ustulina deusta*, ascospores ($\times 1000$). 25: *Podospora*-type, ascospore ($\times 1000$). 26: *Cercophora*-type, ascospore ($\times 1000$). 27–30: *Sporormiella*-type, ascospore cells ($\times 1000$). 31: *Chaetomium*, ascospore ($\times 1000$). 32 and 33: *Neurospora*, ascospore, in high and middle focus ($\times 1000$). 34: *Glomus*, chlamydsopore with hyphal attachment ($\times 500$). 35–37: *Gaeumannomyces*, hyphopodia ($\times 1000$).

(Fig. 2(17–20)) as an aquatic pioneer during the early part of a Late-Glacial deposit in The Netherlands. The records were of crucial importance for understanding the local environmental development during the early Late-Glacial, because *Gloeotrichia* played a pioneer role in nutrient (nitrogen) poor conditions, thanks to its ability to fix nitrogen and thus making conditions suitable for other aquatic plants.

Akinetes of *Aphanizomenon* (Figs. 1(11) and 1(12)) and *Anabaena* (Fig. 1(13–16)) were recorded in the laminated sediments of Lake Gościąg, Poland (van Geel et al., 1994, 1996; see also Findlay et al., 1998), and the record showed that an increasing human impact in the catchment area (evident from the pollen record) had an effect on trophic conditions in the lake water. From ca 1000 AD onwards, *Anabaena* and *Aphanizomenon* were present in enormous quantities. The increases of these cyanobacteria could be interpreted as the effect of the intensification of farming and land fertilization in the area around Lake Gościąg, causing eutrophication of the lake. Phosphorus enrichment in the catchment area of the lake became so high that N-limited growth conditions occurred. In such conditions cyanobacteria could bloom, since they are capable of nitrogen fixation.

Fungi

Most of the fossil fungi appeared to be ascospores, conidia and chlamydospores (produced by, respectively, Ascomycetes and Dematiaceae). 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, however, fungal remains normally are of rare occurrence (in open water there is no strictly local production of fungal spores which do preserve as fossils). Another factor which influences the fossil record is the fact that only relatively big (heavy) fungal spores with thick walls are normally preserved. Most of the thin walled spores, which disperse better and which are known from the records of spores in the present atmosphere, obviously do not fossilize. From the various studies of fossil fungal spores, it became clear 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 were, among others: (1) parasitic fungi and saprophytes, which were always found in combination with certain host plants or on their remains; (2) fungi which were only under certain conditions or incidentally present on special hosts, or on their remains; (3) fungi growing on animal dung; and (4) fungi occurring on burnt plant remains. A selection of examples of fossil fungi is given here:

Amphisphaerella amphisphaerioides, ascospores (Fig. 2(21)): This fungus with its typical ascospores (3–6 pores in the equatorial plane, wall thickened around these pores, especially at the apical sides) is a parasitic species occurring on *Populus*. Van Geel et al. (1981) recorded it in low frequencies in the early Holocene in a deposit with relatively high frequencies of *Populus* pollen. Additional observations in early Holocene deposits by the author (still unpublished) also support the idea of a host-parasite relationship between *Populus* and *A. amphisphaerioides*. In these cases the presence of the ascospores is a valuable extra indication for the presence of *Populus* (the pollen of which is not always easy to recognize; Bennett & Willis, this volume).

Ustilina deusta, ascospores (Fig. 2(22–24)): This ascomycete is a mild parasite, causing soft-rot of wood, on several tree species (in NW-Europe: *Abies*, *Acer*, *Aesculus*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Fagus*, *Fraxinus*, *Populus*, *Quercus*, *Salix*, *Taxus*, *Tilia* and *Ulmus*). The pollen of these trees is transported over relatively long distances from the source and can be analysed in sediment samples from lakes and in peat deposits. The

ascospores of *U. deusta*, however, are common at a short distance (several metres) from the trees, but the spores are scarce or almost absent in samples from relatively large lakes and bogs (van Geel & Andersen, 1988).

Some coprophilous fungi: Cercophora-type, Podospora-type and Sporormiella-type: Fossil ascospores of *Cercospora*-type (Fig. 2(26)) were first recognized by van Geel (1978) and records were made by van Geel et al. (1981), Bakker & van Smeerdijk (1982) and by Witte & van Geel (1985). According to Lundqvist (1972), representatives of the sordariaceous genus *Cercophora* are coprophilous or occur on decaying wood and on herbaceous stems and leaves. The fossil record thus far (e.g., van Geel et al., 1981; Witte & van Geel, 1985; Mateus, 1992; Buurman et al., 1994) shows circumstantial evidence that the presence of ascospores of the *Cercophora*-type can often be used as an indicator for dung in the surroundings of the sample site.

Although always present in low frequencies, ascospores of the *Podospora*-type (Fig. 2(25)) are regularly recorded in archaeological samples (van Geel et al., 1981; 1983; Buurman et al., 1994; van Geel, unpublished). A relation with the presence of humans or cattle (providing dung as a substrate) for this sordariaceous genus (see Lundqvist, 1972) seems probable. Further observations of ascospores of the *Podospora*-type were made (by the author) in deposits containing remains of *Mammuthus* in The Netherlands (Moershoofd Interstadial; Cappers et al., 1993), in Norwegian *Calluna-Sphagnum* peat deposits with palynological evidence for grazing (project P. E. Kaland, Bergen University), in a Roman Iron Age site in The Netherlands (van Geel, unpublished) and in late Holocene deposits from Mexico (van Geel, unpublished).

Ascospores of extant *Sporormiella* species are three- to many-septate. Every ascospore cell shows a germ slit, extending 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 (Fig. 2(27–30)). Species identification of *Sporormiella*-type is not possible because fruitbodies, asci and complete ascospores are not available (compare Ahmed & Cain, 1972). The representatives of the related, coprophilous genus *Sporormia* are without 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. Therefore we refer to the fossil spores as *Sporormiella*-type instead of *Sporormiella*. Fossil spores of *Sporormiella*-type were distinguished by Davis et al. (1977), Davis & Turner (1986), Davis (1987) and by van Geel (archaeological sites; unpublished) who concluded that increased quantities of the spores can be used as indicators of dung, produced by relatively high population densities of domestic herbivores. Samples from the N-Siberian site of the Jarkov mammoth (van Geel, unpublished) are rich in spores of the *Sporormiella*-type.

Chaetomium spec., ascospores (Fig. 2(31)): *Chaetomium* species are strong decomposers of cellulose and occur wherever this substrate is abundant, such as on plant remains and dung. Apart from the occurrence of the lemon-shaped ascospores in peat deposits representing strictly natural habitats, *Chaetomium* species also appeared to be indicators for human impact in the past (Buurman et al., 1995; van Geel, unpublished). In settlements there will have been extra dung, damp straw, clothes, leather and other suitable substrates.

Neurospora spec., ascospores (Figs. 2(32) and 2(33)): The dark ascospores of *Neurospora* with their longitudinal grooves are rare, but their morphology is so characteristic and the indicator value so evident that it is worth while recording their presence. Shear & Dodge (1927) and Dennis (1968) mention *Neurospora* on vegetable matter, developing often after it has been charred by fire. Van Geel (1978) found *Neurospora* ascospores in a layer of charred *Molinia* remains in the Holocene bog Engbertsdijksveen, The Netherlands. *Neurospora* is an indicator for local fires (see also Bakker & van Smeerdijk, 1982, p. 134), but it is also evident that often *Neurospora* ascospores are absent in the charred layers that represent former fires in fens and bogs. The occurrence of ascospores in lake deposits is possible, but no records are available yet.

Glomus spec. (Fig. 2(34)): The globose chlamydospores of *Glomus* (extremely variable in size: 18–138 μm in diameter, exclusive of the hyphal attachment) are of regular occurrence on pollen slides. *Glomus* spores recorded at the Late-Glacial site Usselo (van Geel et al., 1989) closely resembled those of *Glomus fasciculatum*; a relationship of this mycorrhizal fungus (occurs on a variety of host plants) with the roots of local stands of *Betula* at Usselo was probable. Anderson et al. (1984) identified *G. fasciculatum* in post-glacial lake sediments in Maine (U.S.A.). The fungus became established with tundra vegetation on newly developing soils soon after the melting of Wisconsin ice. It was postulated by Anderson et al. (1984) that erosion in the area around the lake accounted for the abundance of *Glomus* in Late-Glacial sediments, and the reduced abundance in Holocene sediments was attributed to a decrease in the rate of soil erosion (and related sedimentation in the lake) after the establishment of forest.

Gaeumannomyces spec. (Fig. 2(35–37)): The lobed hyphopodia of *Gaeumannomyces* appeared to be characteristic for the local occurrence of *Carex* species. As *Carex* species often play a role in lake margins, and shallow phases of lakes, records of the hyphopodia could be useful in palaeolimnological studies. A comparison of the curve of fossil hyphopodia of *Gaeumannomyces* with the curves of macrofossils and the Cyperaceae pollen curve in a Holocene deposit was made by Pals et al. (1980). A correspondence in the representation of *Gaeumannomyces* and local *Carex* species in the core was obvious. Van Geel et al. (1983) observed and illustrated fossil hyphopodia of *Gaeumannomyces*, still in contact with the epidermis of *Carex*. The corresponding presence of *Gaeumannomyces* and *Carex* species has interesting implications for the palynological analysis of, e.g., Late-Glacial 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 Late-Glacial deposits, the answer to the question whether Cyperaceae constituted an element of the local vegetation is a crucial piece of information (Bennett & Willis, this volume). The local presence/absence, of *Carex* species becomes evident from the analysis of hyphopodia of *Gaeumannomyces* during microfossil analyses.

Rotifers

Resting eggs of rotifers are of regular occurrence in lake deposits, but normally no records are made. In his study of the Otterstedter See, Müller (1970) recorded resting eggs of

rotifers. Müller tried to explain their changing frequencies by a comparison with records of other taxa which indicated changes in lake conditions and human impact in the landscape.

Among the taxa that can be identified are *Anuraeopsis fissa* (Fig. 3(38–40)), *Brachionus* (Figs. 3(41) and 3(42)), cf. *Conochilus hippocrepis* (Figs. 3(43) and 3(44)), *Conochilus natans*-type (Fig. 4(45)), *Filinia longiseta*-type (Fig. 4(46)), *Keratella* (Fig. 4(47)), *Hexarthra mira* (Fig. 4(48)), cf. *Polyarthra dolichoptera* (Fig. 4(49)) and *Trichocerca cylindrica* (Fig. 4(50)). For relevant literature on extant and fossil rotifers see Bogoslovsky (1967, 1969), Pontin (1978), Ruttner-Kolisko (1972), Voigt (1956–1957), Voigt & Koste (1978), Müller (1970), Ralska-Jasiewiczowa & van Geel (1992) and van Geel (1998).

Many rotifer taxa pass the winter as resting eggs. Some rotifers live in shallow puddles. For such species the resting egg is a stage which can survive when the puddle dries up. Van Geel (1998) focussed on the species *Hexarthra mira*. It is a cosmopolitan warmth-demanding planktonic organism. In Europe the species has its optimum habitat in the temperature range of 13 to 28 °C, when the pH of its environment is higher than 7. It occurs in lakes and pools where it feeds on detritus. Koste (1979) showed the distribution of *H. mira* in Holocene deposits of two lakes in NW-Germany.

The resting eggs of the planktonic species *Trichocerca cylindrica* showed a sharp decline and disappeared in the Otterstedter See in historical time when several pollen curves showed that human impact in the surroundings increased considerably (Müller, 1970). Also in Lake Gościąg *T. cylindrica* decreased in historical time and this is probably also related to human-induced changes of environmental conditions in the lake (van Geel, unpublished).

Filinia longiseta-type comprises the eggs of *F. longiseta* and *F. passa* (H. Müller, Hannover, pers. comm., 1990). Detailed drawings of the eggs of both species are given by Bogoslovsky (1967). *Filinia longiseta* and related varieties are planktonic taxa (Voigt & Koste, 1978) and, according to Ruttner-Kolisko (1972), *Filinia* also occurs in brackish water. The eggs of *Filinia* are of regular occurrence in lake deposits. In the Otterstedter Lake (Müller, 1970), eggs of *Filinia* showed the highest representation during the Atlantic and early Subboreal. Increased human impact in the surroundings of the lake apparently had a negative effect on *Filinia*, at least on its egg production. Merkt & Müller (1999) showed that Late-Glacial climate changes, as evident from the pollen record of Hämelsee (Germany), were also reflected in the oscillating frequencies of rotifer remains.

Vegetative remains of Nymphaeaceae

Nymphaeaceae have mucilaginous hairs. The suberized basal cells of these hairs (Fig. 4(51)) with their central pore and concentric rings are very common in pollen slides from deposits of lakes and pools where *Nuphar* and/or *Nymphaea* played a role in the local vegetation (Pals et al., 1980). Also the trichosclereids are characteristic, but those are less frequent. The high frequency of the suberized basal cells is in strong contrast with the often rare pollen of (entomophilous) Nymphaeaceae. Ralska-Jasiewiczowa et al. (1992) showed that the rise of the suberized cells at the Late-Glacial/Holocene transition in the Polish Lake Gościąg is a better indication for the increase of the thermophilous Nymphaeaceae than pollen of *Nuphar* and *Nymphaea*.

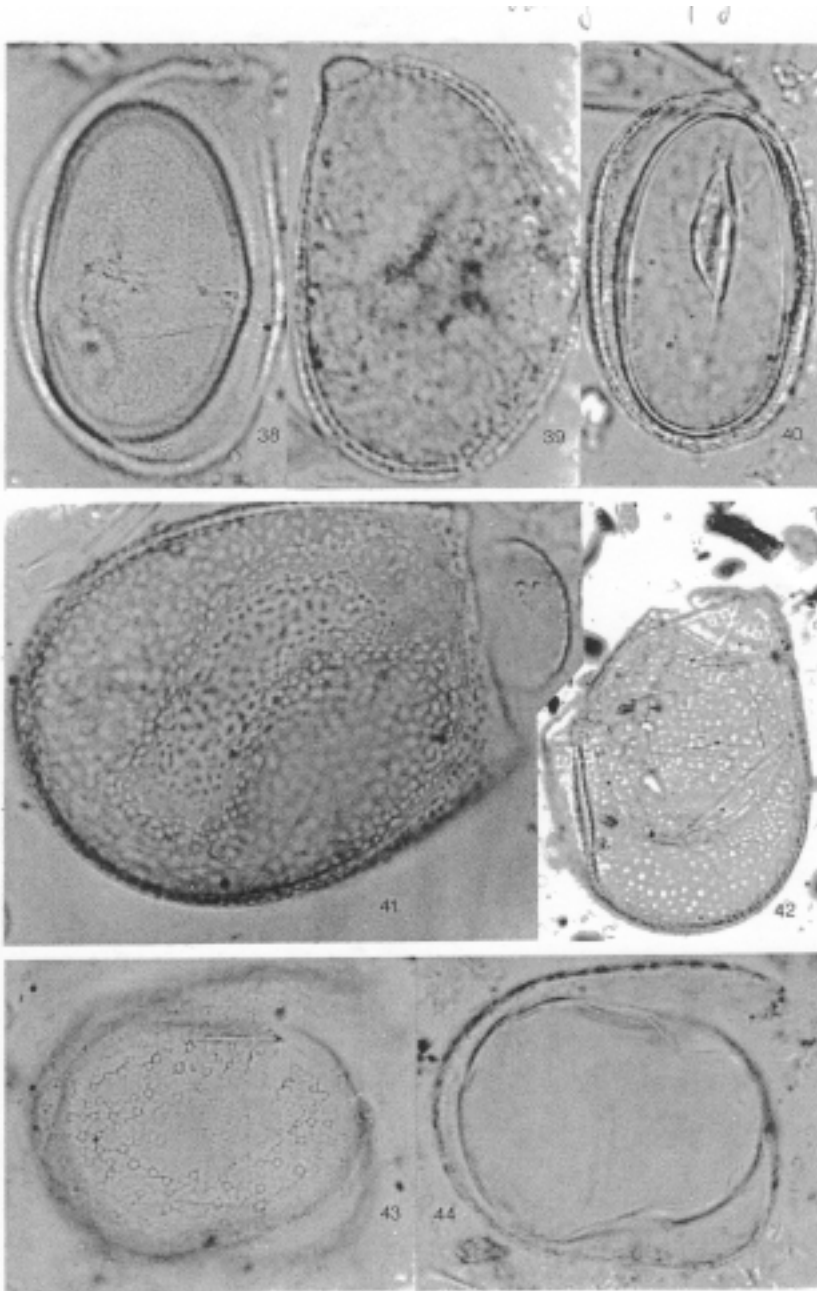


Figure 3. 38–40: *Anuraeopsis fissa*, eggs ($\times 1000$). 41 and 42: *Brachionus*, eggs ($\times 750$ and $\times 500$). 43 and 44: cf. *Conochilus hippocrepis*, egg, in high and middle focus ($\times 750$).

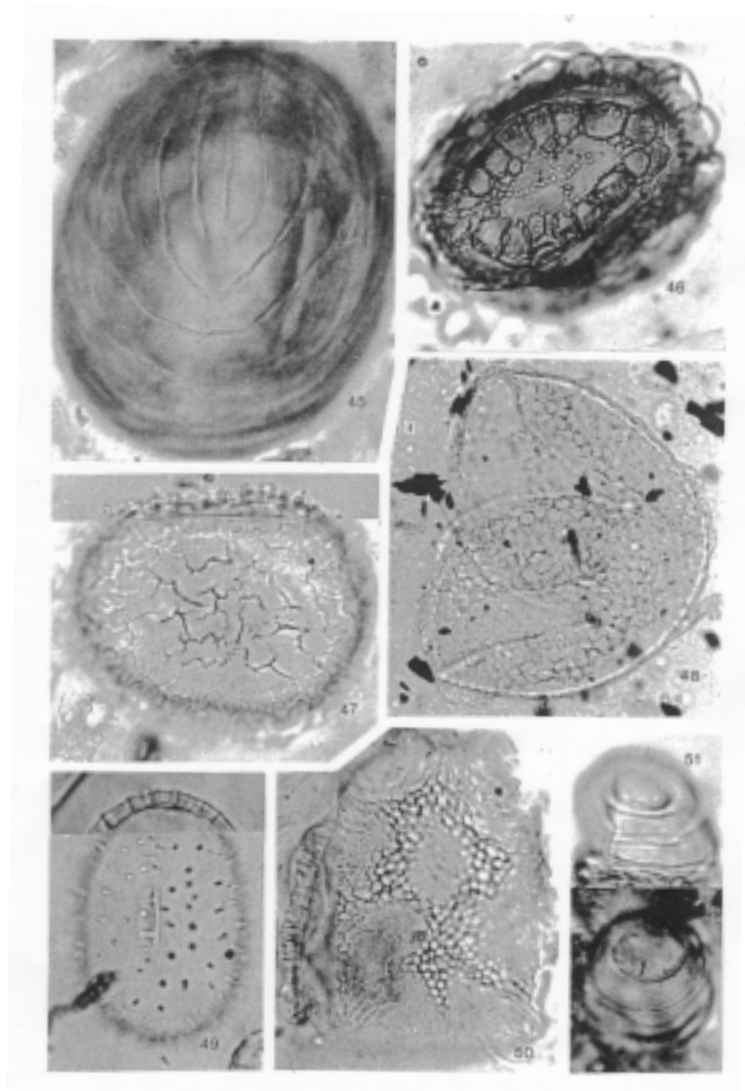


Figure 4. 45: *Conochilus natans*-type, egg ($\times 750$). 46: *Filinia longiseta*-type, egg ($\times 750$). 47: *Keratella*, egg, in high and middle focus ($\times 750$). 48: *Hexarthra mira*, egg ($\times 500$). 49: cf. *Polyarthra dolichoptera*, egg, in high and middle focus ($\times 750$). 50: *Trichocerca cylindrica*, egg, in high and middle focus ($\times 750$). 51: Nymphaeaceae, suberized basal cells of mucilaginous hairs ($\times 1200$).

Conclusions and future directions

Palynologists often restrict themselves to the study of fossil pollen only. A full or selected analysis of non-pollen palynomorphs (which have demonstrable indicator value) on the same pollen slides may result in useful additional palaeoenvironmental information.

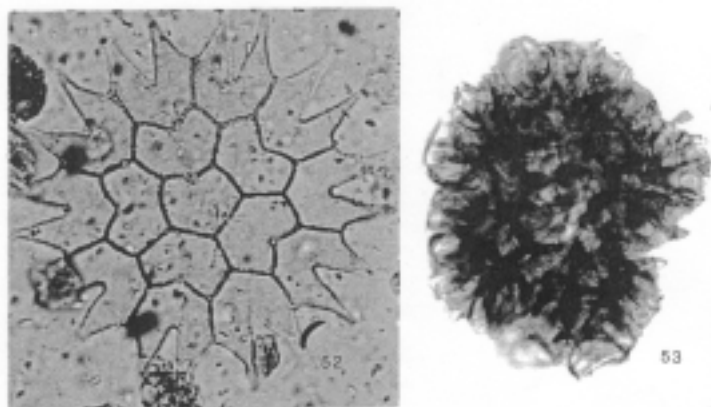


Figure 5. 52: *Pediastrum* ($\times 750$). 53: *Botryococcus* ($\times 1000$).

Summary

A selection of non-pollen palynomorphs is shown and discussed. Spores of Zygnemataceae are common in shallow water deposits, and based on the records of fossil spores, it is evident that the various spore types occur under different environmental conditions. Remains of cyanobacteria appear to be valuable indicators of nitrogen-poor conditions. Such conditions can occur when there is a general low level of nutrients. An extra input of phosphorus-components in lakes (as a consequence of human impact in the catchment area) can also result in the blooming of cyanobacteria. Among the fossil fungi there are (1) parasites indicating the presence of their host plants, (2) indicators for dung, (3) indicators for fires, (4) indicators for the local terrestrialization by *Carex*, (5) soil inhabiting taxa whose presence in lake deposits points to erosion. Eggs of rotifers, which may be present in pollen slides, are also important because of their potential palaeoenvironmental indicator value.

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