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NON-POLLEN PALYNOMORPHS FROM MID-HOLOCENE PEAT OF THE RAISED BOG BORSTELER MOOR (LOWER SAXONY, GERMANY)

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Abstract

In order to reconstruct regional vegetation changes and local conditions during the fen-bog transition in the Borsteler Moor (northwestern Germany), a sediment core covering the period between 7.1 and 4.5 cal kyrs BP was palynologically investigated. The pollen diagram demonstrates the dominance of oak forests and a gradual replacement of trees by raised bog vegetation with the wetter conditions in the Late Atlantic. At ~ 6 cal kyrs BP, the non-pollen palynomorphs (NPP) demonstrate the succession from mesotrophic conditions, clearly indicated by a number of fungal spore types, to oligotrophic conditions, indicated by *Sphagnum* spores, *Bryophytomyces sphagni*, and testate amoebae *Amphitrema*, *Assulina* and *Arcella*, etc. Four relatively dry phases during the transition from fen to bog are clearly indicated by the dominance of *Calluna* and associated fungi as well as by the increase of microcharcoal. Several new NPP types are described and known NPP types are identified. All NPP are discussed in the context of their palaeoecological indicator values.

Key words: pollen, fungal spores, microbiomorphs, palynology, bog development.

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INTRODUCTION

The Borsteler Moor (Lower Saxony, Germany) is a typical raised bog of the northwestern German Plain (Fig. 1). Until drainage in 19th and 20th centuries, this area was a vast peat-dominated landscape. About one third of the lowland area between the North Sea coast and the Central Uplands had been covered by raised bogs up to 10 m in height (Behre 2008; Grosse-Brauckmann 1997). These abundant raised bogs had developed from former fens or directly on nutrient-poor glacial sands particularly since about 9 kyrs BP due to a rapid increase of the sea-level (Behre 2004; Eckstein *et al*. 2011). Such remarkable landscape changes influenced vegetation successions and vegetation cover in the region.

Within the project "Dendroecological studies of subfossil pine-forests in Lower Saxony", the Borsteler Moor was studied in order to investigate the transition from fens to *Sphagnum* bogs in this region. Dendrochronological studies clearly reveal several establishment and dying-off phases of pines in the raised bog (ongoing study), raising the question of whether the transition to *Sphagnum* bog was gradual or interrupted by dry phases, requiring further palaeoenvironmental reconstructions of bog development. Therefore, a section from the early formation of the Borsteler Moor raised bog was palynologically investigated in order to reconstruct the local development during the fen-bog transition. For this, locally produced microscopic plant, fungal and animal remains, known as non-pollen palynomorphs (NPP), are very suitable (e.g. Hesmer 1929; Frey 1964; van Geel 1978) and often better than pollen, as this can be transported over long distances. Numerous studies of NPP from raised bog profiles in the Netherlands and northern Germany (e.g. van Geel

Fig. 1. Location of the Borsteler Moor core (star). a) map of Europe with Germany and position of the Borsteler Moor; b) Google Earth map of the Borsteler Moor; c) schematic diagram of location of the core and pine root plates used for establishment of the age-depth model.

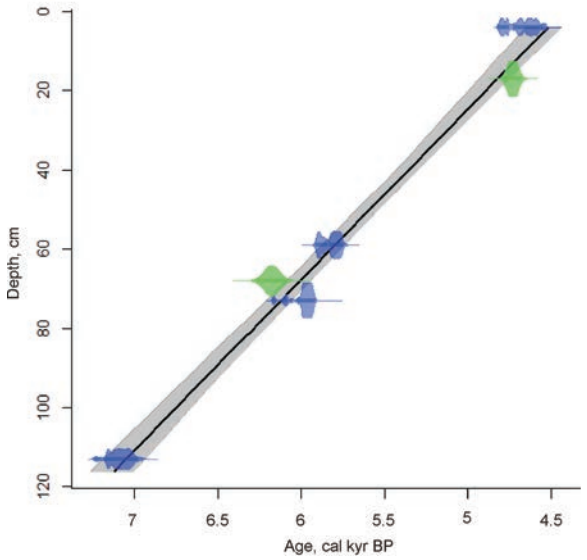

Fig. 2. Age-depth model of the Borsteler Moor based on radiocarbon dating of peat bulk (blue) and dendrochronological dating (green).

1978; Kuhry 1985; Blaauw, Mauquoy 2012) have demonstrated the usefulness of these microfossils in the reconstruction of local hydrological conditions, nutrient status, and diseases of plants or fungi. In this paper we provide the results of the palynological investigation of the Borsteler Moor with special emphasis on NPP.

MATERIAL AND METHODS

Peat coring was carried out in the Borsteler Moor in June 2013. The coring site (52°38'19.73"N, 8°58'19.49"E, 36.21 m a.s.l.) was chosen on a peat surface exposed by peat extraction close to in situ pine root plates needed for additional age control. Coring was performed with a Gouge corer (coring chamber 100 cm) on the same position in two sections (0-87 cm and 87–116 cm). The upper 13 cm were not collected because of the visible mixing, therefore a zero depth of the core is located 13 cm under the surface. Geographical coordinates were taken with Leica GNSS System, Antenna GS 15 and Handheld CS 15 with Satellite Reference of Ascos (error estimates ± 2 cm).

Age-depth model

The age-depth model for the Borsteler Moor core is based on two dendrochronological and four radiocarbon dates (Table 1, Fig. 2). For the dendrochronological control, pines 745-33 (52°38'19.69"N 8°58'19.28E; 35.40 m a.s.l.) and 745-187 (52°38'19.66"N 8°58'19.65"E; 35.91 m a.s.l.) were dated by H. Leuschner (Göttingen) to the age of 6223–6130 and 4760–4702 cal yr BP (year 1950 as the present), respectively. Based on the GPS coordinates and field observa-

Table 1

Chronological control of the peat core from Borsteler Moor

Core depth, [cm]	Dating method	Dated material	Lab. No.	Age ^{14}C yrs BP	Age cal yrs BP (probability)
4–5	AMS ^{14}C	peat bulk	Poz-60932	4130 ± 30	4533–4544 (2.1) 4546–4558 (2.3) 4567–4728 (63.2) 4738–4740 (0.4) 4750–4820 (26.9)
$17_{estimated}$	dendrochronology	pine tree-rings	M745-187	–	4760–4702
59–60	AMS ^{14}C	peat bulk	Poz-60933	5090 ± 35	5747–5833 (57.3) 5840–5913 (37.5)
$68_{estimated}$	dendrochronology	pine tree-rings	M745-33	–	6223–6130
73–74	AMS ^{14}C	peat bulk	Poz-60934	5225 ± 35	5912–6023 (82.5) 6053–6061 (0.9) 6079–6113 (7.6) 6154–6174 (3.9)
113–114	AMS ^{14}C	peat bulk	Poz-60935	6190 ± 40	6977–7179 (90.2) 7198–7238 (4.8)

tions, the positions of the pine root plates were estimated at 68 and 17 cm depth of the Borsteler Moor core, respectively. For AMS radiocarbon dating, four bulk samples of one-centimeter thickness were analyzed at the Poznań Radiocarbon Laboratory. As the core was taken from the (vegetation-free) freshly cut peat several meters below the former bog surface, the risk of erroneously young radiocarbon dates caused by modern roots was excluded. The age-depth model (Fig. 2) was conducted within the free R package CLAM (Blaauw 2010) applying the implemented linear regression model to all age and depth data (Table 1). For the age-depth model, the radiocarbon age calibration curve IntCal13 was used (Reimer *et al.* 2013) and calculations were made using 95% confidence ranges. All ages given in the text are calibrated data.

Palynological investigations

In total, 45 subsamples of one cm^3 were collected from the Borsteler Moor core at intervals of 2 cm in the upper part (0–64 cm), and 4–6 cm in the lower part (64–116 cm). The subsamples were treated with cold 10% HCl and acetolysis with sieving using metal sieve with a 200 µm mesh size. In order to calculate concentrations, two tablets of *Lycopodium* spores (Batch number 1031) were added at the beginning of treatment. Prepared subsamples were stored in glycerin. Sums of total pollen grains counted up to a minimum of 1000 grains were used to calculate the percentages of pollen and NPP. Pollen identification and taxonomy follows Beug (2004). NPP identification is based on van Geel (1978, 1981), Bakker, van Smeerdijk (1982) and Kuhry (1985). In the palynological diagram and the discussion, the identified NPP taxa are given taxonomical names, whereas the naming of unidentified NPP taxa follows Miola (2012). New NPP types are described with taxonomical names or using the abbreviation BM (Borsteler Moor) with a number. The diagram (Fig. 3) was constructed using C2 version 1.5 (Juggins 2007). Pollen zonation was carried out visually based on changes in dominant pollen, spores and NPP taxa. NPP are presented following their indicator value for the nutrient status as well as for wet and dry phases (van Geel 1978; Kuhry 1985; van Geel, Aptroot 2006). Supplementary data are available at doi:10.1594/PANGAEA.846695.

RESULTS AND INTERPRETATION

NPP types

The majority of NPP types in the present study were identified following van Geel (1978) and Kuhry (1985). These NPP are briefly summarized in this section, emphasizing their ecological interpretation with regard to the Borsteler Moor environment. The description of new NPP types (pollen infected by dark-coloured hyphae, pollen with sporangia of chytridiomycetes, BM-1, BM-2, BM-3, *Dictyosporium australiense* = BM-4, Zygospores of *Mucor* = BM-5), the taxonomic identification of types with existing descriptions, and the discussion of their ecology as well as the microphotographs presented are arranged by organismic groups and morphology with animal remains followed by plant remains, NPP of unknown origin and then by fungal remains and spores arranged by their number of cells.

1) Animal remains

Testate amoebae are represented by ***Amphitrema flavum*** Archer 1842**,** ***Assulina muscorum*** Greeff 1888 and ***Arcella* sp.** (Fig. 4A, C, D). *A. flavum* is an indicator of actively growing *Sphagnum* bogs (Frey 1964). Maxima in the Borsteler Moor coincide with wet *Sphagnum*-phases (Fig. 3b). Interestingly, the highest maximum of *A. flavum* (30%) occurred during the first *Sphagnum* phase. In the following *Sphagnum* phases, the amount of *A. flavum* does not exceed 4%, in contrast to *A. muscorum* and *Arcella* spp. Since *Arcella* species are not sphagnophilous and can live in different mosses (Frey 1964), such a mixed assemblage might indicate drier or more nutrient-rich conditions.

Loricae of the rotifer ***Habrotrocha angusticolis*** (Murray) (Fig. 4B) are common in *Sphagnum* peat bogs (Frey 1964) and other mossy (Warner, Chengalath 1988) and wet habitats (van Geel 1978 in Borradaile *et al.* 1963). However, most of its palaeorecords are from *Sphagnum* peat, possibly due to good preservation under acid conditions (Frey 1964). A strong correlation of *H. angusticollis* and *Sphagnum* mosses was recently reported from a peat bog from NE Iran, connected with the discovery of subfossil remains of *Sphagnum squarrosum*, which was documented for the first time in Iran (Kürschner *et al.* 2015). A recent study of rotifer communities in peat bogs of Poland (Bielańska-Grajner *et al.* 2011) demonstrate that the presence of *H. angusticolis* correlates positively with the total organic content and nitrate. In the Borsteler Moor, *H. angusticollis* is characteristic for the wet phases, mostly coinciding with maxima of *Sphagnum* spores, the *Sphagnum* parasite *Bryophytomyces sphagni* and testate amoebae.

Copepod spermatophores (Fig. 4E) are well-known from peat (e.g. Rudolph 1917, Hesmer 1929, Frey 1964, van Geel 1978). Hesmer (1929) found the copepod *Canthocamptus* with spermatophores inside and provided the first description of this palynomorph. He stated that other copepods might have similar spermatophores and later authors list them as spermatophores of (harpacticoid) copepods (Frey 1964). Due to the lifecycle of copepods, their spermatophores are indicators for the (temporary) presence of open water (van Geel 1978). In the Borsteler Moor, spermatophores occur first in the mesotrophic swamp (zone Borstel-2), and increase during *Sphagnum* peat development (zone Borstel-4) but show maxima during the first two dry phases. Together with Rhabdocoela cocoons they nevertheless indicate open water at the site (Hesmer 1929).

2) Plant remains

Pollen infected by dark-coloured hyphae (Fig. 4G, H) are pollen grains, the apertures and/or insides of which are covered by dark-coloured fungal hyphae or are filled by pigmented fungal spores. The observed hyphae are concentrated in the aperture areas. In Angiosperm pollen, these are pores and colpi (Fig. 4G), thin regions in the pollen wall supposed to be passed by the germination tube and therefore not entirely covered by the very inert sporopollenin layer of the outer pollen wall (Punt *et al.*, 2007). In the gymnosperm pollen, aperturoid areas and major occurrence of hyphae are located at the distal side between the two air-sacs of the pollen

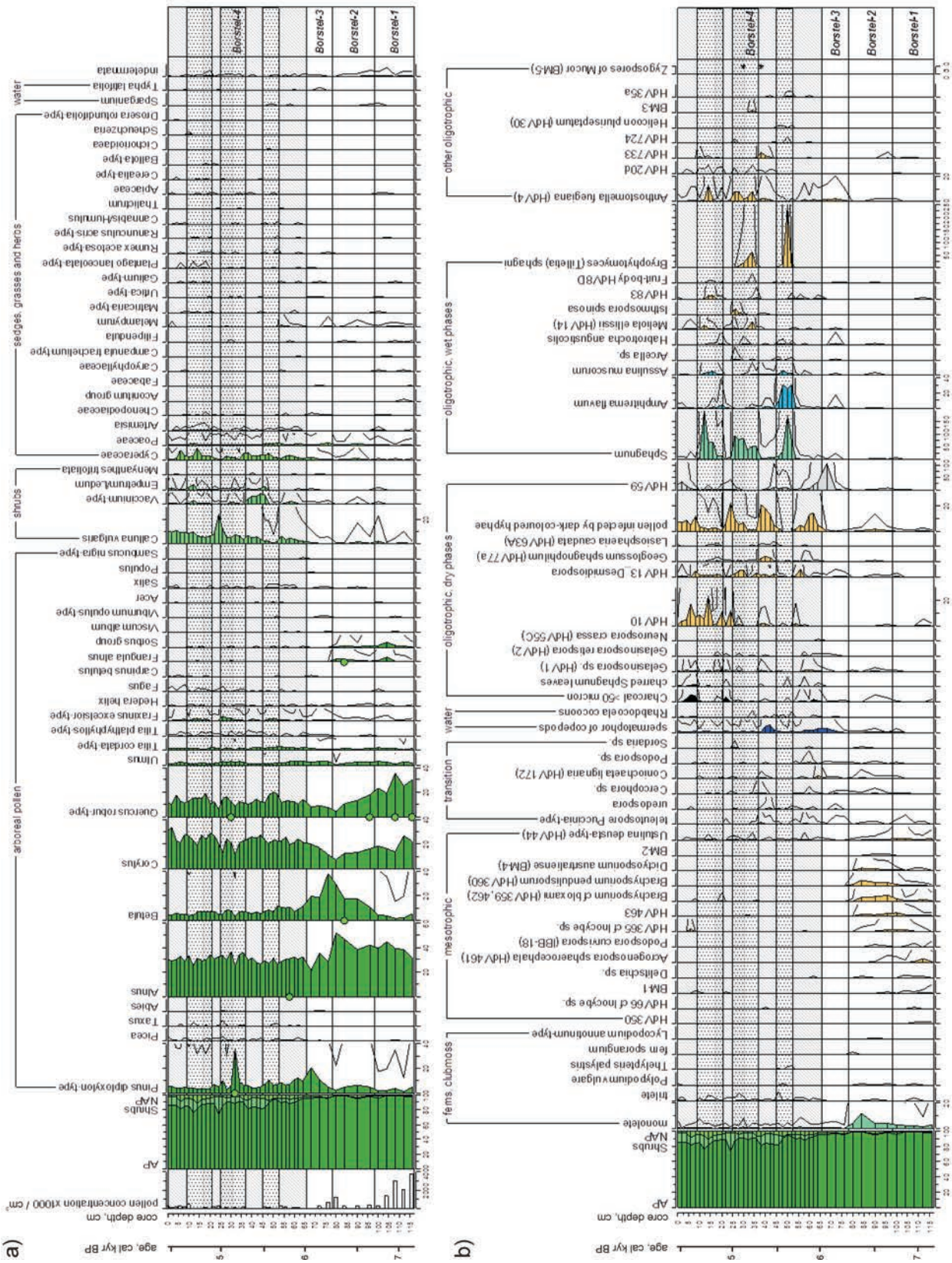

Fig. 3. Pollen (a), spores and non-pollen palynomorphs (b) percentage diagram of the Borsteler Moor. Circles at some curves indicate presence of pollen clumps. AP – arboreal pollen, NAP – non-arboreal pollen. Solid grey line for each taxa means multiplication by factor 10. Textured areas in the zone Borstel 4 indicate wet (points) and dry (hatching) phases as explained in the text.

grains (Fig. 4H). Pollen infected by dark-coloured hyphae, described here for the first time, occur mainly during the dry phases, suggesting increased saprotrophic activity of fungi.

Other pollen grains contain hyaline spheroid to prolongate objects in some cases connected to the inner pollen wall (Fig. 4I). We have identified these objects as **pollen with sporangia of chytridiomycetes** (e.g. Braune *et al.* 1999). Chytridiomycetes are well-known parasites of pollen grains, belonging to the Oomycetes. In the palynological literature, Hesmer (1929) documented and identified remains of chytridiomycete sporangia of *Olpidium pendulum* and other unidentified taxa in *Pinus* and *Picea* pollen grains for the first time. Although spores with chytrid sporangia occurred rather frequently in the Borsteler Moor, they were not counted and their palaeoecological meaning remains unclear until further investigations are carried out.

Charred fragments of *Sphagnum* leaves (Fig. 4F) with clearly visible former chlorophyll and hyaline (water-) cells occur during dry phases of bog development (Fig. 3).

3) NPP of uncertain origin

BM-1 (Fig. 4J, K, L) is globose, hyaline with an inner diameter of 30-32 µm and with bent protuberances of 3–4 µm length and <1 µm thickness, arranged 3–4 µm from each other. The protuberances are covered by a hyaline undulated membrane. BM-1 occurs mostly during the mesotrophic and rarely under dry oligotrophic conditions.

Globose hyaline microfossila of 24–30 µm diameter with curved protuberances of 3–8 µm (Fig. 4M, N) found here are similar to **HdV 59**, described from sandy subsoil below peat (van Geel 1978). Bakker, van Smeerdijk (1982) found HdV 59 mainly in oligo- to ombrotrophic peat. In the Borsteler Moor, HdV 59 clearly corresponds to dry phases of oligotrophic peat. Possibly it is a moss spore.

HdV 35 is a globose or oval structure fractured in a pentagonal or hexagonal pattern with an overall diameter of 30–55 µm (van Geel 1978). In the Borsteler Moor, HdV 35 was found at the beginning of oligotrophic conditions. The palaeoecological meaning is uncertain; possibly of animal origin.

4) Fungal remains

Fruiting-bodies of **HdV 8D** (Fig. 5A) were originally found attached to the epidermis of *Trichophorum caespitosum* and on a leaves of *Sphagnum* section *Cymbifolia* (van Geel 1978). In the Borsteler Moor, HdV 8D is clearly associated with wet *Sphagnum* phases.

HdV 13 (Fig. 5B; van Geel 1978) was first found attached to the leaves of *Polytrichum alpestre*, *Aulacomnium palustre*, *Scheuchzeria palustris*, *Calluna vulgaris*, and *Andromeda polifolia* as well as inside the water-cells of *Sphagnum imbricatum* leaves (van Geel 1978). Van Geel (1978) conclude that HdV 13 might represent sporangia of cf. *Entophlyctis lobata* Willoughby & Townley (Chytridiales), agreeing with a previous identification of similar microfossils of Eocene age by Bradley (1967). Sherwood-Pike (1988) doubts this identification as well as the hypothesis of a hyphopodia origin, and suggests that this problematic microfossil might be a structure formed during germination of a single propagule. For example, germinating spores of *Colletotrichum* form short hyphae with dark thick-walled apressorium or conidia of *Desmidiospora myrmecophila* Thaxt. (Sherwood-Pike 1988). Following Kalgutkar, Jansonius (2000), we name this type ***Desmidiospora***. However, this microfossil type remains problematic. Like other records (van Geel 1978, Kuhry 1997), in the Borsteler Moor the type is characteristic for oligotrophic stages especially during dry phases.

Hyaline spores with typical protuberances (Fig. 5C) were described as **HdV 66** (van Geel 1978). Van Geel (1978) notes that HdV 66 includes smaller specimens of 19–21 µm with 8 or 12 protuberances and bigger ones of 30–34 µm with about 8 protuberances. We found the smaller ones. Van Geel (1978) reports HdV 66 from mesotrophic conditions and absent in oligotrophic *Sphagnum* peat. However, we found single spores during the mesotrophic stage and during the dry phase of oligotrophic stage. In contrast to the suggestion that HdV 66 might be zygospores of *Penium* (Desmidiaceae) (van Geel 1978), it seems very likely that they are basidiospores of some ***Inocybe*** species.

Bryophytomyces sphagni (Navashin) Cif. (formerly *Tilletia sphagni*) (Fig. 5D) is a pathogen ascomycete (Helotiaceae, Helotiales) on *Sphagnum* (Bauch 1938, Eckblad 1975). *B. sphagni* produces its anamorph spores within the *Sphagnum* sporophyte capsules, replacing the moss spores and using the explosive dispersal mechanism of the capsules for its own spreading (Davey, Currah 2006). The fungus parasitizes *S. capillifolium*, *S. central*, *S. cuspidatum*, *S. recurvum*, *S. russowii*, *S. squarrosum* and *S. teres* (Chau 1979). The globose *B. sphagni* spores with a typical channel-like reticulum are well-known objects from Holocene peats. Van Geel (1978, HdV 27) states that the spores do not correlate with species of *Sphagnum* sect. *Acutifolia* such as *S. papilosum* and *S. imbricatum*, but they do correlate with *S. cuspidatum,* which confirms observations from recent mosses (Chau 1979). Van Geel (1978) found maxima of *B. sphagni* spores at the transitions from drier to wetter conditions. In the Borsteler Moor, maxima of *B. sphagni* coincide with the first two *Sphagnum* spore maxima, whereas single spores occur throughout the oligotrophic section.

HdV 724 (Fig. 5E, F; Bakker, van Smeerdijk 1982) was documented for open water conditions similar to copepod spermatophores (HdV 28). In the Borsteler Moor, HdV 724 often corresponds with oligotrophic conditions.

Van Geel, Aptroot (2006) found spores of ***Gelasinospora* sp**. (Fig. 5H; van Geel 1978: HdV 1) in highly decomposed peat, formed under dry, oligotrophic conditions and with the occurrence of charcoal. Lundqvist (1972) note that *Gelasinospora* species are mainly coprophilous, but also carbonicolous and lignicolous. In the Borsteler Moor, *Gelasinospora* sp. occurs together with ***Gelasinospora retispora*** Cain (Fig. 5G; van Geel 1978: HdV 2) and ***Neurospora crassa*** Shear & B.O. Dodge (van Geel 1978: HdV 55C) in layers rich in microcharcoal and charred *Sphagnum* leaves (Fig. 4F), emphasizing their value as an indicator for dry phases during the development of oligotrophic *Sphagnum* peat (zone Borstel-4).

Black spores of 25-26 × 21-22 µm with a truncate base (Fig. 5I), described as **HdV 461** (Kuhry 1985), are morpho-

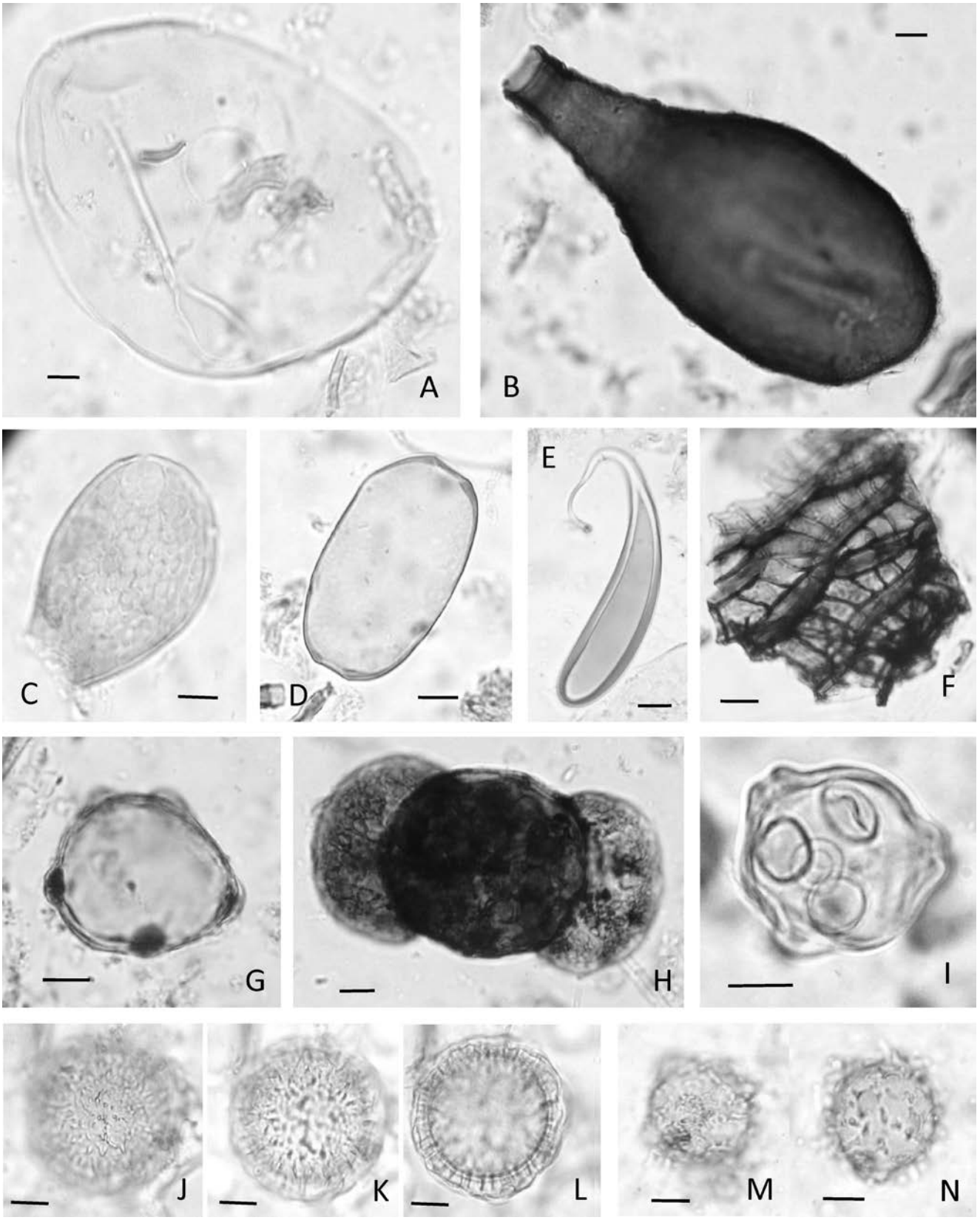

Fig. 4. A *Arcella* sp. (26 cm), B *Habrotrocha angusticolis* lorica (20 cm), C *Assulina muscorum* (16 cm), D *Amphitrema flavum* (18 cm), E spermatophore of copepods (6 cm), F charred *Sphagnum* leaves (6 cm), G *Carpinus betulus* infected by dark-coloured hyphae (4 cm), H *Pinus diploxylon*-type with inner covered by dark-coloured hyphae (38 cm), I *Betula* pollen with chytridiomycetes sporangia (96 cm), J–L BM-1 (10 cm), M–N HdV 59 (4 cm). Bar scale 10 µm. The indication in cm refers to the position in the core.

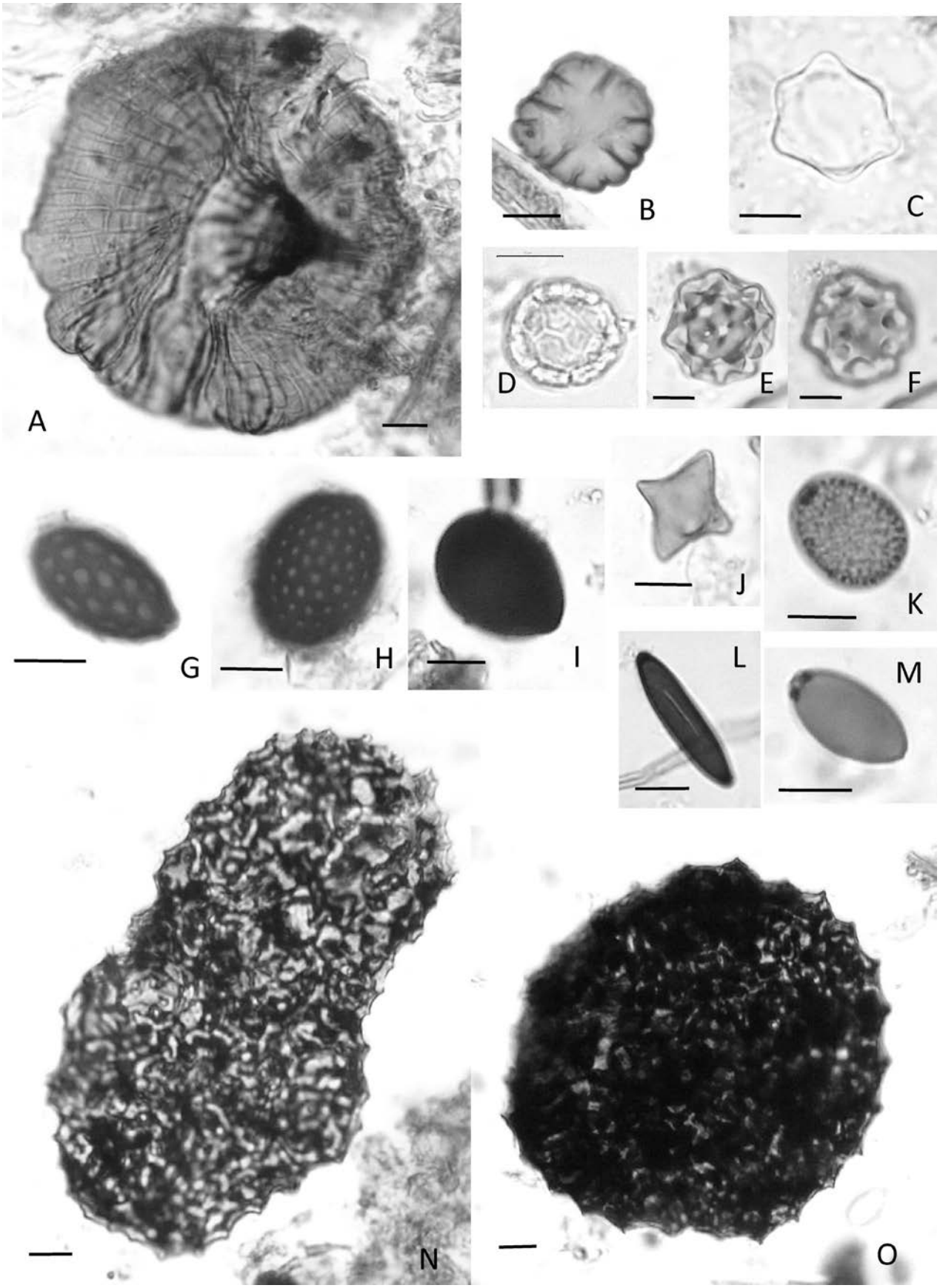

Fig. 5. A Fruiting-body of HdV 8D (56 cm), B HdV 13 *Desmidiospora* (4 cm), C HdV 66 cf. *Inocybe* sp. (6 cm), D *Bryophytomyces sphagni* (50 cm), E–F HdV 724 (30 cm), G *Gelasinospora retispora* (6 cm), H *Gelasinospora* sp. (4 cm), I *Acrogenospora sphaerocephala* (112 cm), J HdV 365 cf. *Inocybe* sp. (104 cm), K HdV 733 (10 cm), L *Ustulina deusta* (26 cm), M *Podospora* sp. (30 cm), N–O zygospores of *Mucor* sp. (BM-5) (38 and 30 cm, respectively). Bar scale 10 μm. The indication in cm refers to the position in the core.

logically similar to ***Acrogenospora sphaerocephala*** (Berk. & Broome) M.B. Ellis or ***Acrogenospora ovalia*** Goh, K.D. Hyde & K.M. Tsui (Ellis, Ellis 1985, Goh *et al.* 1998, Seifert *et al.* 2011). *A. sphaerocephala* (teleomorph *Farlowiella*) is a saprobic fungi of worldwide distribution (Goh *et al.* 1998) growing on the rotten wood of *Acer, Alnus, Betula, Cornus, Prunus spinosa, Quercus, Sambucus, Taxus* (Ellis, Ellis 1985), submerged *Phragmites* culms (Goh *et al.* 1998) as well as on other fungi (Seifert *et al.* 2011). As *A. ovalia* is known only for Hong Kong (Goh et al. 1998), HdV 461 might be related here to ascospores of *A. sphaerocephala*. Similar to the Amtsven section (Kuhry 1985), our findings are restricted to the humic sand layer at the base of the core and might indicate the presence of rotten wood.

Similar to HdV 66, spores of another species of ***Inocybe*** can be considered as the origin of **HdV 365** (Fig. 5J; van Geel *et al.* 1981), which occurs in the Borsteler Moor during the mesotrophic stage.

HdV 733 (Fig. 5K) was first described from mesotrophic peat (Bakker, van Smeerdijk 1982). In the Borsteler Moor, HdV 733 is present at low frequencies during the mesotrophic stage and reaches its maximum of 5% during a dry hummock phase, but also occurs during hollow phases.

Ustulina deusta (*Kretzschmaria deusta*, Fig. 5L) is an ascomycetous plant pathogen causing soft-rot of living wood and contributing to decay after the host tree death (van Geel 1978: HdV 44). It was described from *Fagus* and regularly occurs on a variety of tree taxa such as *Abies, Acer, Aesculus, Alnus, Betula, Carpinus, Castanea, Fraxinus, Populus, Quercus, Salix, Taxus, Tilia* and *Ulmus* (van Geel 1978, Ellis, Ellis 1985). In the Borsteler Moor, spores of *U. deusta* are present throughout indicating the lasting presence of host trees or dead wood in the immediate vicinity. The spores are more common during the swamp conditions before the bog development, when *Quercus* trees were growing in the area.

The swamp-bog transition assemblage includes ascospores of ***Cercophora* sp., *Coniochaeta lignaria, Podospora* sp.** (Fig. 5M); ***Delitschia* sp.** (Fig. 6C) and ***Sordaria* sp.**, which belong to mostly facultative coprophilous groups, including some species that also grow on other kinds of decaying organic material (Lundquist 1972, Richardson 2001, Krug *et al.* 2004).

Type IBB-18 (Montoya *et al.* 2010) is morphologically similar to the dark-brown 11–13(17) × 8–10 µm ascospores of ***Podospora curvispora*** (Cain) Cain, which are strongly curved, concave on one side and convex on the other, with an apical germ pore of 1 µm in diameter (Mirza and Cain 1969). *P. curvispora* is similar to *Podospora selenospora* Stchigel, Guarro & M. Calduch; however, the latter has a germ pore on the convex side of the spore (Stchigel *et al.* 2002). In contrast to most other *Podospora* species, *P. curvicola* grows on decaying plant substrates other than dung (Mirza, Cain 1969). In the Borsteler Moor, *P. curvispora* is present in the lowest sandy peat (Borstel-1) together with other decaying fungi (Fig. 3b).

BM-5 (Fig. 5N, O) are round to elongated brown to dark-brown objects of 73–137 µm with 2–4 µm protuberances at regular intervals of 8–13 µm from each other. This type is similar to ***Mucor*-type zygospores**, especially the pigmented zygospores of e.g. *Mucor hachijoensis* Watanabe and *M. meguroense* Watanabe or of *Zygorhynchus moelleri* Vuill. (Watanabe 2010).

Spores of ***Anthostomella fuegiana*** Speg. (van Geel 1978: HdV 4) are suggested as indicators of the local presence of *Eriophorum vaginatum* plants (van Geel 1978, Kuhry 1985). In the Borsteler Moor, *A. fuegiana* spores are more common in the *Sphagnum* peat with *Eriophorum*. However, the correlations of the plant remains and fungus maxima are rather weak, whereas Cyperaceae pollen and *A. fuegiana* spores show a negative correlation.

BM-2 (Fig. 6A) are 3-celled rhomboid fungal spores, 27–28 × 10–12 µm. The upper two brown-coloured cells are divided by a septum with a dark-brown rim of 6–7 µm breadth and the lower cell is hyaline with a pore of 1 µm. As BM-2 coincides with maximum of wood-decaying fungal spores, the type might represent conidiospores of saprotrophic fungi.

Van Geel (1978) correlated findings of **HdV 83** (Fig. 6B) with those of type HdV 106, a representative of relatively wet, oligotrophic bog conditions later identified as eggs of the oribatid mite *Rhysotritia ardua* (C.L. Koch) (Bakker, van Smeerdijk 1982). In the Borsteler Moor, HdV 83 occurs more often especially in wet phases of the *Sphagnum* peat (Borstel-4).

HdV 359 (van Geel *et al.* 1981) and **HdV 462** (Kuhry 1985) are morphologically very similar and assumed to represent phragmoconidia of *Brachysporium* species like *B. obovatum* (Berk.) Sacc. and *B. bloxami* (Cooke) Sacc. or of *Bactrodesmium betulicola* M.B. Ellis (van Geel *et al.* 1981, Kuhry 1985). Finds in the Borsteler Moor (Fig. 6D) are most similar to spores of ***Brachysporium bloxami***, a fungus living on the decaying wood of *Acer*, *Alnus*, *Betula*, *Castanea*, *Fagus*, *Fraxinus*, *Pinus*, *Prunus*, *Quercus* (Ellis, Ellis 1985), or to spores of ***Brachysporium brevius*** Hol.-Jech., which is an anamorphic stage of *Cryptadelphia brevior* Réblová & Seifert and is known from decayed wood of *Fagus sylvatica* (Réblova, Seifert 2004). In agreement with the findings of Kuhry (1985), this type occurs in the humic sandy material (zone Borstel-2), but also occasionally during dry oligotrophic phases.

HdV 360 was also attributed to the genus *Brachysporium* (van Geel *et al.* 1981) and described as a fungal spore of 19–22 × 14–17.5 µm excluding the hyaline cells (1–3) situated at either end. The spore body is strongly pigmented, with a granulated inner wall side, and sometimes a hyaline "episporium" is seen. This type (Fig. 6E) is very similar in morphology and size to conidiospores of ***Brachysporium pendulisporum*** S. Hughes, which are fusoid to limoniform, overall 30–42.5 × 15–17.5 µm, 4–5-septate, with a brown to dark-brown central cell that is separated by thick septa from the small hyaline polar cells (Réblova, Seifert 2004; Markovskaja, Treigien 2007). *B. pendulisporum* (anamorph of *Cryptodelphia pendulispora* Réblová & Seifert) is known from decaying wood from North America, Canada, and Eastern Europe (Markovskaja, Treigien 2007). Our findings and those of van Geel *et al.* (1981) indicate that this fungus also existed in Germany and the Netherlands during the Holocene.

The swamp-bog transition assemblage includes **uredospores** and teleutospores of the ***Puccinia*-type** (Fig. 6F; van Geel *et al.* 1981: HdV 357).

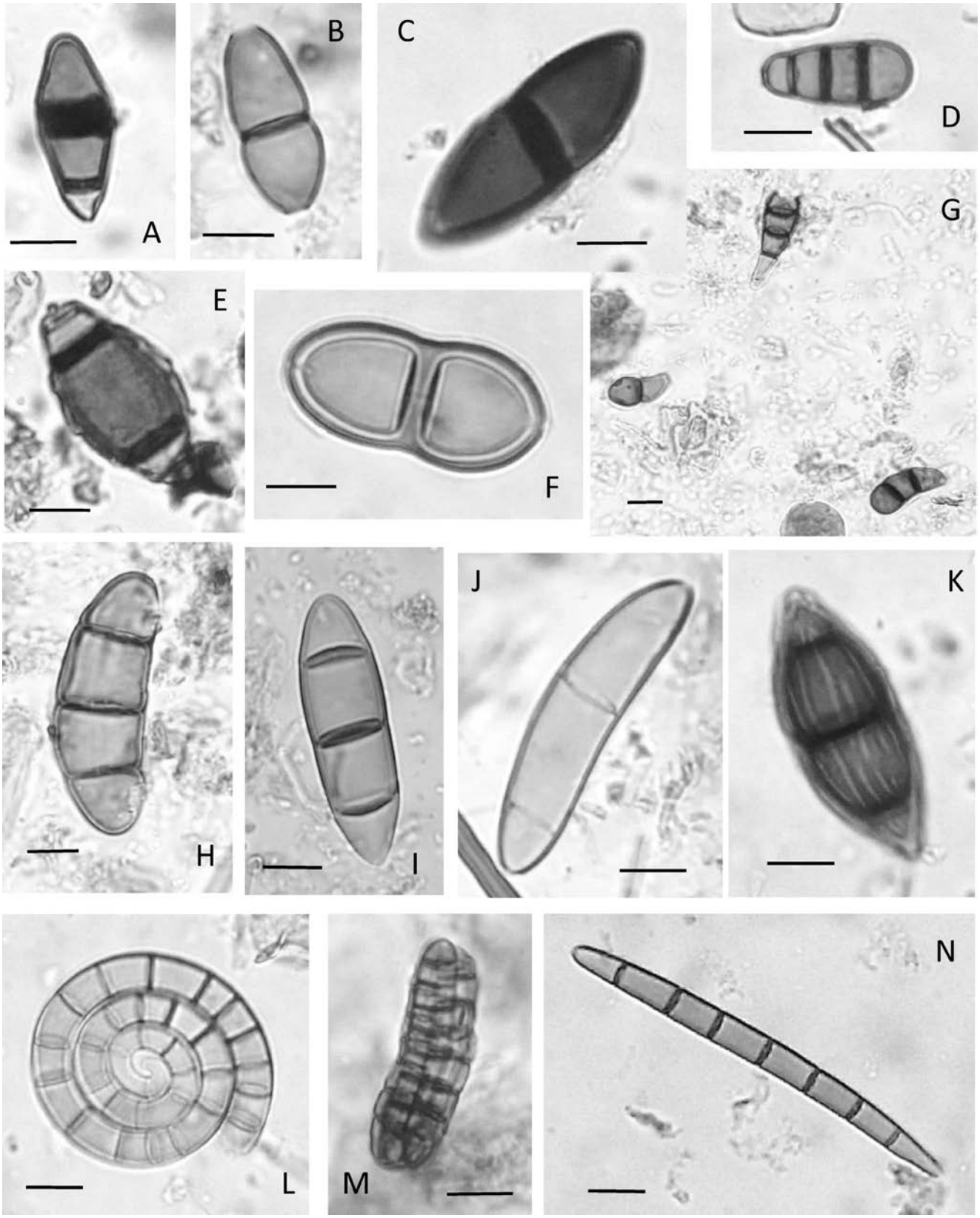

Fig. 6. A BM-2 (96 cm), B HdV 83 (14 cm), C *Delitschia* sp. (84 cm), D *Brachysporium bloxami* (84 cm), E *Brachysporium pendulisporum* (96 cm), F *Puccinia*-type (38 cm), G HdV 10 (4 cm), H *Meliola ellisii* (4 cm), I HdV 20d (4 cm), J BM-3 (32 cm), K HdV 463 (108 cm), L *Helicoon pluriseptatum* (52 cm), M *Dictiosporium australiense* (BM-4) (112 cm), N *Geoglossum sphagnophilum* (40 cm). Bar scale 10 µm. The indication in cm refers to the position in the core.

A strong correlation of **HdV 10** (Fig. 6G) with *Calluna vulgaris* pollen, seeds, leaves and possibly roots has been demonstrated in several records (van Geel 1978). HdV 10 is therefore a good indicator of locally dry conditions in raised bog peats (e.g. van Geel 1978, Kuhry 1985). HdV 10 can also correlate with *Erica tetralix* remains (Bakker, van Smeerdijk 1982). In the Borsteler Moor, this type occurs during increases of *Calluna vulgaris* pollen.

Another fungal spore associated with *Calluna vulgaris* is the ascomycete ***Meliola ellisii*** Roum (Fig. 6H), which was suggested to have been a common parasite on *C. vulgaris* in peat bogs during the Atlantic to Subatlantic period (van Geel 1978: HdV 14). In the Borsteler Moor, spores of *Meliola ellisii* are characteristic for *Sphagnum* peat, confirming that *Calluna vulgaris* growing on mineral soils is not infected (van Geel 1978). Moreover, maxima of *Meliola ellisii* occur during the wet phases, suggesting that *Calluna vulgaris* is less resistant to parasites under stressful wet conditions. Higher numbers of spores of the *Meliola ellisii* hyperparasite ***Isthmospora spinosa*** F. Stevens (van Geel *et al.* 2006) coincide with a small maximum of *Meliola ellisii* (Fig. 3b).

HdV 20d (Fig. 6I) is characterized by tapering apical ends, in contrast to the three-septate ascospores of HdV 20 (van Geel 1978). Van Geel (1978) suggested *Empetrum* as possible host of HdV 20. In the Borsteler Moor, HdV 20d occurs in low frequencies during the oligotrophic phase.

BM-3 (Fig. 6J) is a 3–4-septate, pale, slightly curved fungal spore of 51–52 × 10 µm, with rounded ends, each end with an apical pore of 1.5 µm. The septa are very thin, sometimes displaced or dissolved. In the Borsteler Moor, BM-3 occurred in just one sample (34 cm) during a wet phase of the oligotrophic stage.

We also found **HdV 463** (Fig. 6K) described from the Amtsven section (Kuhry 1985) and assumed to be a *Stuartella* species. Following the figures in Müller (1962), this identification might be doubtful.

Helicoon pluriseptatum van Beverwijk (Fig. 6L) is known from peat bogs and marshy places on birch leaves, pine needles, pine cones, leaves of red oak, and grass blades (Van Beverwijk 1954 in van Geel 1978: HdV 30). In the Borsteler Moor, *H. pluriseptatum* is restricted to the first wet *Sphagnum* phase.

Type **BM-4** (Fig. 6M) has pale brown conidia of 38–40 × 10–12 µm, consisting of one truncate cell with 3 vertical straight or slightly curved cylindrical 8-septate arms of more or less similar length, arranged close to each other. Morphologically, the type is very similar to ***Dictyosporium australiense*** Sutton 1985 (Sutton 1985, Goh *et al.* 1999). Smooth-walled, euseptate conidia produced from determinate conidiogenous cells is a generic characteristic of the whole genus *Dictyosporium* (Goh *et al.* 1999). These hyphomycetes occur worldwide on dead wood, decaying leaves and palm material. The teleomorphic stage is unknown. The systematic identification of species is based on their specific conidiospores (Goh *et al.* 1999), and allows the identification of this type to *Dictyosporium australiense*, known from dead wood (Goh *et al.* 1999). The spores of this fungus occur together with other decaying fungi in zone Borstel-2. Spores of the genus *Dictyosporium* (but another species, *D.* cf. *heptasporum* = HdV 1053) were identified in a palaeoecological context from Lake Challa in southeastern Kenya (van Geel *et al.* 2011).

Geoglossum sphagnophilum Ehrenb. (Fig. 6N) is reported to grow among *Sphagnum* and its spores were found with *Sphagnum* remains (van Geel 1978: Type 77A). The spores were encountered from the Atlantic and Subboreal periods, especially in the upper parts of hummocks, just before the wet *Scheuchzeria palustris* overgrowing phases and in a layer characterized by *Scheuchzeria palustris, Oxycoccus palustris* and *Andromeda polifolia* (van Geel 1978). In the Borsteler Moor, *G. sphagnophilum* maxima occur during dry phases rich in *Vaccinium*-type.

Ascospores of ***Lasiosphaeria caudata*** (Fuckel) Sacc. (van Geel 1978: HdV 63A) were recorded with low frequencies in Holocene raised bog deposits (van Geel, Aptroot 2006). *L. caudata* grows on decaying wood of *Picea* (Munk 1957 in van Geel 1978) and its spores correlate to the most recent rise of *Picea* pollen in a raised bog in Denmark, underlining a host-parasite relationship (van Geel and Aptroot 2006). The presence of *Picea* pollen together with *L. caudata* spores in the Borsteler Moor suggests the presence of spruce relatively close to the site. This contrasts with the general view of a very late distribution of *Picea* in northern Germany caused by forestry management. Nevertheless, subfossil wood of *Picea* in *Sphagnum* peat of Lower Saxony (Leuschner, unpubl.) underline a much earlier presence of spruce.

HdV 350 (van Geel *et al.* 1981) occurs in the Borsteler Moor under mesotrophic conditions. Van Geel *et al.* (1981) found this type mainly in a layer rich in the mycorrhizal roots of *Pinus*.

THE PALYNOLOGICAL DIAGRAM

The palynological diagram was divided in four local pollen zones (Fig. 3a, b).

The lowest zone Borstel-1 (116–98 cm; ~7.2–6.8 kyr BP) is characterized by the dominance of *Alnus* (31–44%), *Quercus robur*-type (19–35%) and *Corylus* (14–27%), accompanied by *Sorbus* group and *Frangula alnus* (Fig. 3a), indicating presence of an open oak forest in the wider surroundings and a swamp with mesotrophic conditions at the core site. Occurrence of pollen clumps of *Quercus robur*-type suggests the presence of oaks at the core site. NAP does not exceed 2%, indicating only a small role of herbs in the ground vegetation, mainly represented by *Melampyrum* and accompanied by ferns (3%). The fungal assemblages consist of HdV 461, 359/462, 463, 360 and the *Delitschia*-type (Fig. 3b), indicating presence of decaying wood. *Sphagnum* spores are very rare.

In the zone Borstel-2 (98–78 cm; ~6.8–6.3 kyrs BP), percentages of *Alnus* reach a maximum of 53%, *Betula* and *Pinus* increase up to 29 and 7%, respectively, and *Quercus robur* type (4–18%) and *Corylus* (8–16%) decrease to the end of the zone (Fig. 3a). The spread of the pioneer species *Betula* possibly reveals leaching of soils or an increase in the ground water level. Pollen clumps suggest the presence of *Quercus, Betula* and *Frangula alnus* at the core site. The presence of open water at the site is indicated by copepod spermatophores (Fig. 3b). The presence of pollen of the *Sorbus* group, *Frangula alnus, Melampyrum* and of fern spores and

fern sporangia accompanied by the fungal spores HdV 359/462 and 463 suggest a swamp with mesotrophic conditions similar to the previous zone. However, more frequent occurrence of *Sphagnum* spores accompanied by sphagniphilous indicators such as *Amphitrema flavum* and *Habrotrocha angusticollis* (Fig. 3b) points to the presence of *Sphagnum* mosses at the core site and the possible spread of *Sphagnum* peat in the area.

The zone Borstel-3 (78–66 cm; ~6.3–5.9 kyrs BP) is characterized by an increase of *Pinus diploxylon*-type from 4 to 20% and of *Corylus* from 12 to 20% and by the decrease of *Betula* from 39 to 20% (Fig. 3a). *Frangula alnus*, *Sorbus* group, fern spores as well as fungal assemblages of the previous zones disappear, clearly indicating a change in the environmental conditions. Spermatophores of copepods and Rhabdocoela oocytes indicate open water conditions at the site (Fig. 3b). A slight increase in *Calluna vulgaris*, Cyperaceae and *Sphagnum* indicate the further development of *Sphagnum* peat. The fungal assemblages change considerably and now consist of *Antostomella fuegiana* (HdV 4), HdV 13, *Cercophora, Coniochaeta, Podospora*-type (Fig. 3b). HdV 59 reaches its maximum of 105%.

Zone Borstel-4 (66–0 cm; ~5.9–4.5 kyrs BP) is dominated by *Alnus* (25–37%), *Corylus* (12–34%), *Quercus robur*-type (6–20%). Percentages of *Betula* and *Pinus diploxylon*-type vary between 3 and 11% (Fig. 3a). The *Pinus diploxylon*-type maximum of 35% at 35 cm depth might be explained by a local presence of pine, as indicated by the occurrence of corresponding pollen clumps. *Calluna vulgaris* plays an important role in the zone, increasing from 1–5% in the lower to 10% in the upper part. A maximum of 24% of *Calluna vulgaris* at 24 cm core depth suggests the local presence of heathland plants. Besides *Calluna vulgaris*, additional ericaceous pollen of *Vaccinium*-type and *Empetrum/Ledum* indicate raised bog conditions. Cyperaceae reach up to 10%, possibly indicating the local presence of *Eriophorum vaginatum*. Furthermore, the zone Borstel-4 is characterised by pollen of *Picea, Taxus, Fagus* and *Carpinus betulus* as well as of many herbs such as *Artemisia*, Chenopodiaceae, *Plantago lanceolata*-type, Cerealia-type, *Rumex acetosa*-type and *Ranunculus acris*-type. Such increased diversity of arboreal and non-arboreal pollen can be explained by increased anthropogenic influence in the region and/or more open conditions by the spreading peat bog and therefore more long-distance transport signals.

The zone Borstel-4 is rather heterogeneous. NPP grouping reveals four dry and three wet phases during the period (Fig. 3b). Dry phases occur at 66–53 cm (5.9–5.7 kyrs BP), 45–37 cm (5.5–5.3 kyrs BP), 31–17 cm (5.1–4.8 kyrs BP) and 9–0 cm (4.6–4.5 kyrs BP) and are characterized by higher percentages of microcharcoal (up to 15,000 particles / cm^3), fungal spores such as HdV 4, 10, 13, *Gelasinospora*, but also *Lasiosphaera caudata* as well as of HdV-59 and pollen with dark-coloured hyphae (Fig. 3b). The wet phases at 53–45 cm (5.7–5.5 kyrs BP), 37–25 cm (5.3–5 kyrs BP) and 21–9 cm (4.9–4.6 kyrs BP) are characterized by the dominance of *Sphagnum* spores, the parasitic fungus *Bryophytomyces sphagni*, testate amoebae *Amphitrema flavum*, *Assulina*, *Arcella,* and rotifer loricae of *Habrotrocha angusticolis* (Fig. 3b).

The oligotrophic conditions started at ~6 kyrs BP with a relatively dry phase indicated by *Calluna vulgaris* and *Vaccinium*-type, fungal spores of *Meliola ellisii* and HdV 10. Furthermore, this phase is characterized by a fungal assemblage including ascospores of *Gelasinospora, Cercophora, Coniochaeta lignaria, Podospora* and *Sordaria* (Fig. 3b). Pollen grains with dark-colored hyphae reach their first maximum of 14%. Large amounts of fungal remains indicate increased saprotrophic activity.

At ~5.7 kyrs BP, the community with *Sphagnum* and sphagnophilous indicators such as *Amphitrema, Habrotocha angusticollis* and *Sphagnum* pathogen *Brachyosporium sphagni* indicate the establishment of relatively wet conditions (Fig. 3b). This phase lasted ~180 years until 5.5 kyrs BP, and was replaced by a dry community with *Vaccinium, Calluna vulgaris* and Cyperaceae (possibly *Eriophorum vaginatum*) (Fig. 3a). Similar to the first dry phase, the second is again characterized by an increase of saprotrophic fungal remains and pollen attacked by fungi. Copepod spermatophores indicate the (temporary) presence of open water at the site.

The second *Sphagnum* phase at 5.3–5 kyrs BP is characterized by lower numbers of testate amoebae but also the presence of the *Calluna vulgaris* parasite *Meliola ellisii* and its hyperparasite *Isthmospora spinosa* (Fig. 3a). The end of this wet phase overlaps in the diagram with the third dry phase 5.1–4.8 kyrs BP. *Calluna vulgaris* dominated the vegetation again, the local presence of which is indicated by HdV 10. Higher charcoal concentrations (up to 7,600 particles / cm^3) together with fungal spores and pollen attacked by fungi indicate drier conditions with fires as well as increased saprotrophic activity.

The last *Sphagnum* phase (4.9–4.6 kyrs BP) overlaps with the prevailing relatively dry phase. This *Sphagnum* phase is characterized by the same NPP assemblages as the previous wet phase but lacks *Bryophytomyces sphagni* and contains a large amount of HdV 10, indicating the presence of *Calluna vulgaris* (Fig. 3a, b). The pollen spectra of the youngest documented dry phase (4.6–4.5 kyr BP) are characterized by high values of *Calluna vulgaris* and Cyperaceae as well as by maxima of microcharcoals, saprotrophic fungal spores, pollen attacked by fungi and type BM-1.

DISCUSSION

The Borsteler Moor core contains a high diversity of NPP, including 6 animal, 3 plant, 34 fungal and 3 unknown types. The higher numbers of the fungal remains is likely to be explained by their greater resistance to environmental chemical and biological degradation as well as to laboratory treatments.

The diverse and numerous fungal remains form distinct fungal assemblages corresponding to mesotrophic and oligotrophic stages. Even though the prevalence of well-preserved spores and the lack of thin-walled hyaline specimens mean that our understanding of the former fungal communities is limited, we can nevertheless analyze trends in the fungal fossil assemblages. During the mesotrophic stage, the assemblage contains a variety of soil and wood decay fungi such as *Brachysporium bloxami*, *Brachysporium pendulisporum*, *Podospora curvispora*, *Dictyosporium australiense*, *Acro-*

genospora sphaerocephala. These fungi are present in zones Borstel-1 and 2 and disappear in zones Borstel-3 and 4, which could be explained either by disappearance of suitable substrate or a change in environmental conditions or both. The changes in the fungal assemblages clearly correspond to changes in the pollen composition. Mesotrophic fungal communities correlate well with the presence of *Quercus*, *Betula* and *Frangula alnus* on site, revealed by occurrence of their pollen clumps (Fig. 3a). With the development of heathland and *Sphagnum* peat bog, the substrate changes considerably and includes degradation-resistant sclerophyllous species. In combination with the high water content and acidification caused by *Sphagnum*, this leads to the restriction of the "decomposer" community from the lignicolous to mainly facultative coprophilous communities represented by *Podospora*, *Cercophora*, *Coniochaeta*, *Gelasinospora*, *Neurospora*. These fungi profit from dung, which contains a high concentration of available nutrients, but they can also decompose other organic substrates as well (Krug *et al.* 2004). Such a large change in the assemblage of fungal decomposers indicates an important change in the nutrient status of the ecosystem, which obviously became more dependent on nutrient inputs from outside because organic material cannot be easily decomposed any more. This could be the reason for increased hyphal attack on pollen, as this provides easily available nutrients in large quantities in spring (Shumilovskikh *et al.* in revision). This trend is additionally seen by the fact that diversity of the oligotrophic assemblage increases mainly through parasitic fungi such as *Bryophytomyces sphagni*, *Geoglossum sphagnophilum*, *Meliola ellissii*, *Isthmospora spinosa*, *Lasiosphaeria caudata*, *Anthostomella fuegiana*, clearly indicating the presence of their hosts (van Geel 1978, van Geel and Aptroot 2006). In general, the fungal assemblage of the oligotrophic stage is more diverse and consists of fungi occurring in either (1) dry or (2) wet phases and of (3) fungi of all moisture levels. The oligotrophic dry phase assemblage is indicated by the presence of charcoal and carbonifilous fungi (*Gelasinospora* sp., *Gelasinospora reticulispora*, *Neurospora*) as well as by fungi associated with *Calluna vulgaris* such as type 10, *Meliola ellisii* and *Isthmospora spinosa* (van Geel 1978). The oligotrophic wet phase assemblage includes mainly parasitic fungi *Bryophytomyces (Tilletia) sphagni* growing on *Sphagnum* (Fig. 3b).

Chronologically, the development of the bog at the Borsteler Moor site started with an accumulation of organic material on sand at ~7.1 kyrs BP, most probably due to an increase in the water table caused by a rising sea-level (Behre 2004). Pollen data suggest the presence of an oak forest with hazel, alder and *Frangula alnus* until 6.7 kyrs BP, when the first 15 cm of the humic layer accumulated. This mesotrophic peat was covered by ferns, possibly *Rubus* (*Sorbus* group) and *Melampyrum*. The remains of decomposer and soil fungi indicate soil development, and high pollen concentrations reveal a high decomposition rate at the site. A further increase in the water table and the growing *Sphagnum* peat led to the degradation of the oak forest and the spread of the pioneer trees *Betula* and *Pinus* (6.7–6.2 kyrs BP). Percentage maxima of decaying fungi as well as their high concentrations of up to 20,000 spores / cm^3 (not shown) suggest the presence of dead wood, which possibly was an important source of peat formation. Between 6.2 and 6 kyrs BP, a *Pinus-Betula* carr replaced a *Betula-Quercus* forest. *Rubus* and *Frangula alnus* disappeared and ferns decreased. The light levels increased and Cyperaceae, Poaceae, *Calluna vulgaris* and possibly mosses (type BM-1) became more abundant. A further increase of the water table led to at least the temporary presence of open water at the site after ~6.1 kyrs BP. Typical bog vegetation spread and started to build a raised bog from ~6 kyr BP onwards. Thereby, the succession proceeded as an alternation between dry (6–5.7, 5.5–5.3, 5.1–4.8, 4.6–4.5 kyrs BP) and wet (5.7–5.5, 5.3–5, 4.9–4.6 kyrs BP) phases. During the dry phases the strong increase in spores of decaying fungi confirms observations of previous palaeoecological investigations about increased fungal activities and accelerated decomposition rates (e.g. van Geel 1978; Bakker, van Smeerdijk 1982; Kuhry 1985; Middeldorp 1986; Willemsen *et al.* 1996).

Considering pine germination and die-off phases, it is possible to suggest that the establishment of pines could occur during these dry and nutrient-rich phases. However, percentage (Fig. 3a) and concentration (not shown) maxima of *Pinus* pollen as well as AP in general do not clearly correlate with dry or wet phases. There are multiple possible reasons for this mismatch of dry phases in bog development and pine establishment, and their discussion goes beyond of the scope of the present paper.

In summary, our palynological study of the sediment core from the Borsteler Moor clearly reveals a change from mesotrophic to nutrient-poor conditions at ~6 kyrs BP, coinciding with vegetation development from oak forests to *Calluna* heathland and *Sphagnum* peat. According to the NPP, the establishment of *Sphagnum* peat was not gradual but it was interrupted by four dry phases, characterized by accelerated decomposition rates.

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