

Epiphyllous fungi from the Oligocene shallow-marine deposits of the Krabbedalen Formation, Kap Brewster, central East Greenland

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ABSTRACT. Fructifications of epiphyllous fungi were encountered during palynological investigation of the Lower Oligocene shallow-marine deposits of the Krabbedalen Formation at the Savoia Halvø, Kap Brewster, central East Greenland. Six fossil taxa from the family Microthyriaceae (*Phragmothyrites kangukensis* Kalgutkar, *Phragmothyrites* sp., *Plochmopeltinites* sp., *Trichothyrites* cf. *ostiolatus* (Cookson) Kalgutkar & Jansonius, *Trichothyrites* sp. 1, and *Trichothyrites* sp. 2) and one *incertae sedis* fungal remain are reported. Fungal remains from the Krabbedalen Formation represent the youngest, Oligocene occurrence of the epiphyllous fungi in the Palaeogene of the Arctic. The presence of epiphyllous, microthyriaceous fungi in low quantities and in low taxonomical diversity points to a humid and not necessarily warm climate, which is corroborated by data obtained from the analysis of microscopic plant remains.

KEYWORDS: Epiphyllous fungi, fructifications, Microthyriaceae, taxonomy, palaeoecology, Oligocene, Arctic, Krabbedalen Formation, Greenland

INTRODUCTION

During classical palynological investigation of samples from the Lower Oligocene shallow-marine deposits of the Krabbedalen Formation (Kap Dalton Group) from Kap Brewster, Savoia Halvø, Scoresby Sund, central East Greenland (Fig. 1), some specimens of fructifications of epiphyllous fungi were encountered (Birkenmajer et al. 2010). In view of the usefulness of fossil epiphyllous fungi as a palaeoclimatic proxy, we made detailed taxonomic and palaeoecological studies of these fungal fructifications from the Krabbedalen Formation.

GEOLOGY

The Kap Brewster area was mapped and sampled by Krzysztof Birkenmajer during the 1971 Geological East Greenland Expedition organized by the Geological Survey of Greenland

(Birkenmajer 1972). He also described the geology of the area in detail (Birkenmajer & Jednorowska 1997, Birkenmajer et al. 2010). Four main lithostratigraphic units have been distinguished in the Kap Brewster area (Hassan 1953, Birkenmajer 1972, Birkenmajer & Jednorowska 1977, 1997, Birkenmajer et al. 2010): Mesozoic (?Upper Cretaceous) deposits which underlie plateau basalts; plateau-basalts with sediment intercalations (Blosseville Group, Palaeocene–Eocene); older post-basalt deposits (Kap Dalton Group, Eocene–Oligocene); and younger post-basalt deposits (Kap Brewster Formation, Miocene).

The shallow-marine to brackish deposits of the Kap Dalton Group occupy a small fault-bounded depression in the central part of Savoia Halvø. The Krabbedalen Formation (Krabbedalen Member – Birkenmajer 1972; Krabbedalen Formation – Birkenmajer

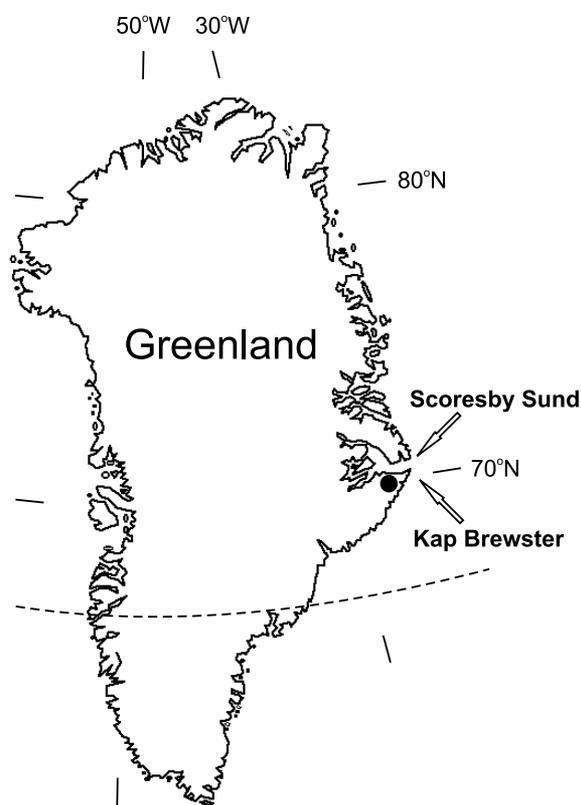


Fig. 1. Location map (black dot) of the samples studied from the Krabbedalen Formation, Kap Brewster, East Greenland. Dashed line – Arctic Circle

& Jednorowska 1977) consists of alternating grey to yellowish marly siltstones and hard calcareous siltstones, often containing single pebbles of basalt and other rocks. According to Hassan (1953), its rich shallow-marine macrofauna probably indicates an Early Oligocene age of the deposits. Foraminiferal study (Birkenmajer & Jednorowska 1977, 1997) confirmed the Early Oligocene age estimates of the Krabbedalen Formation. The dinoflagellate cyst assemblages also suggest an Early Oligocene age of the deposits, while the pollen-spore spectra are less conclusive in this respect, suggesting an Oligocene-Middle Miocene age. Nevertheless, the interpretation rather favours an Early Oligocene age of this assemblage supported by cold-water indicators (foraminifera and dinoflagellates), possibly related to cooling of the Early Oligocene coastal sea by the East Greenland Current (Birkenmajer & Jednorowska 1997, Birkenmajer et al. 2010).

MATERIAL AND METHODS

The samples were collected by Krzysztof Birkenmajer during the 1971 Geological East Greenland Expedition from the deposits of the Krabbedalen Formation,

Kap Brewster, central East Greenland (Birkenmajer 1972).

The samples were processed in the Micropalaeontological Laboratory of the Institute of Geological Sciences, Polish Academy of Sciences, Kraków, according to the palynological protocol entailing 38% hydrochloric acid (HCl) treatment, 40% hydrofluoric acid (HF), heavy liquid ($\text{ZnCl}_2 + \text{HCl}$; density 2.0 g/cm^3) separation, ultrasonic treatment for 10–15 s., and sieving through $15 \mu\text{m}$ nylon mesh. No nitric acid (HNO_3) treatment was applied. Seven samples (810, 811, 812, 813, 814A, 814B, and 815) were prepared, and two microscope slides were made from each sample using glycerine gel as a mounting medium.

The studied samples yielded rich palynological material consisting mainly of sporomorphs (pollen grains and spores) and dinoflagellate cysts. The results of palynological studies were described in detail (Birkenmajer et al. 2010). During the current investigation all these slides were re-examined for the presence of remains of epiphyllous fungi.

Terminology for the morphology of fungal fructifications follows Korf (1958) and Wu et al. (2011). The method of measuring the size of fungal structures depends on their shape; we used diameter measurements for regular, round or broadly elliptical structures, and length and width for quadrangular structures.

Bright field, dark field and phase contrast microphotography of the fossils was done using a NIKON Eclipse E400 microscope fitted with a CANON A640 digital camera.

RESULTS

The classification of fossil and recent fungi follows Kalgutkar & Jansonius (2000) and Wu et al. (2011).

ORDER MICROTHYRIALES G. ARNAUD

Family Microthyriaceae Sacc.

Trichothyrites Rosendahl

Synonyms: *Notothyrites* Cookson,
Sphaerialites Venkatachla & Kar

Trichothyrites cf. *ostiolatus* (Cookson) Kalgutkar & Jansonius

Pl. 1, figs 1a, b

? 1947 *Asterothyrites ostiolatus* Cookson, p. 210, pl. 12, fig. 11.

? 2000 *Trichothyrites ostiolatus* (Cookson) Kalgutkar & Jansonius comb. nov., p. 303, pl. 22, fig. 4.

Material. Slide 144-812(1). One specimen.

Description. Fruiting body fragmentary,

± orbicular, ca 125 µm in diameter, margin irregularly sinuate. Scutellum composed of radiating rows of quadrilateral (*textura prismatica*) nonporate cells, 5.0–7.5 µm long and 2.5–4.0 µm wide. Cell walls ± straight. Ostiole central, roundish, ca 12 µm in diameter. Collar distinct, ca 10 µm wide, collar cells small, isodiametric with very thick and dark walls.

Remarks. This fruiting body is similar to fossil *Trichothyrites ostiolatus* (Cookson) Kalgutkar & Jansonius from Oligocene/Miocene deposits of Victoria, Australia (Cookson 1947, Kalgutkar & Jansonius 2000). The poor state of preservation prevents unequivocal assignment to the discussed species. Almost identical forms were reported as *Notothyrites* (= *Trichothyrites*) *setiferus* Cookson by Kar & Saxena (1976) from the Palaeocene Matanomadh Formation, Kutch district, India. Indeed, there were some similarities with the latter species (correctly *Trichothyrites setifer* (Cookson) Saxena & Misra; Kalgutkar & Jansonius 2000), but the cells of scutellum of *T. setifer* are twice larger than in *T. ostiolatus* and thus the fruiting body described as *Notothyrites setiferus* from the Matanomadh Formation most probably represent different species of the genus *Trichothyrites*.

***Trichothyrites* sp. 1**

Pl. 1, figs 2a, b

Material. Slide 144-812(2). One specimen.

Description. Fragment of fruiting body, ± orbicular/suborbicular, ca 70 µm in diameter, margin ± entire. Scutellum composed of radiating rows of rectangular (*textura prismatica*), nonporate cells, ca 7.5 µm in diameter. Cell walls straight. Ostiole central, ± roundish, ca 10 µm in diameter. Collar easily visible, ca 12 µm wide, collar cells smaller than ordinary cells of scutellum.

Remarks. This specimen is morphologically similar to *Trichothyrites* cf. *ostiolatus* (Cookson) Kalgutkar & Jansonius described above, but the poor state of preservation prevents an accurate comparison.

***Trichothyrites* sp. 2**

Pl. 1, figs 3a, b

Material. Slide 144-812(1). One specimen.

Description. Fruiting body ± orbicular, ca 100 µm in diameter, margin slightly sinuate. Scutellum composed of radiating rows of quadrilateral, usually isodiametric (*textura prismatica*) nonporate cells 4–5 µm in diameter. Cell walls straight, partly rounded. Ostiole central, roundish, 15 µm in diameter. Collar distinct, its cells with thick and dark walls.

Remarks. The fruiting body shows morphology typical of the fossil genus *Trichothyrites* (e.g. radiating cells of scutellum, distinct ostiole). It bears some similarity to *Trichothyrites keralensis* (Rao & Ramanujam) Kalgutkar & Jansonius, described from the Late Miocene of India (Rao & Ramanujam 1976, Kalgutkar & Jansonius 2000). However, *T. keralensis* differs in having a smaller ostiole. *T. hordlensis* Smith, similar in respect of the scutellum structure, differs in having considerably smaller fruiting bodies (Smith 1980).

***Plochmopeltinites* Cookson**

***Plochmopeltinites* sp.**

Pl. 2, figs 1a–c

Material. Slide 144-812(1). One specimen.

Description. Fragment of fruiting body, ± suborbicular, ca 125 µm in size. Scutellum composed of ± radiating rows of elongated, nonporate cells with strongly undulate walls (*textura epidermoidea*). Ostiole central, fragmentary, roundish, 12–17 µm in diameter. Collar distinct, composed of small cells.

Remarks. The morphology of the discussed epiphyllous microthyriaceous fungus corresponds to the genus *Plochmopeltinites* (e.g. scutellum composed of radiating cells with undulate walls, distinct ostiole). In respect of ostiole diameter it resembles both *Plochmopeltinites cooksoniae* Ramanujam & Rao and *Plochmopeltinites masonii* Cookson, and clearly differs from *Plochmopeltinites keralensis* Patil & Ramanujam (Kalgutkar & Jansonius 2000). The poor state of preservation prevents classification as one of the last two species. The fossil thyrithoeceia of the genus *Stomiopeltis* Theissen differ in having a non-radiate structure of the scutellum, which is typical for fruiting bodies of genera of the family Micropeltidaceae (Kalgutkar & Jansonius 2000, Wu et al. 2011).

Family ? Microthyriaceae Sacc.

Phragmothyrites Edwards

Synonyms: *Microthallites* Dilcher

Phragmothyrites kangukensis Kalgutkar

Pl. 2, figs 2a, b

1997 *Phragmothyrites kangukensis* Kalgutkar, p. 223, pl. 3, fig. 16, 21, pl. 4, fig. 1.

Material. Slide 144-812(1). One specimen.

Description. Fruiting body suborbicular, slightly elongated, preserved fragment ca 60 μm in size, entire-margined. Scutellum composed of both isodiametric (central part) and radiate (margin) nonporate cells (*textura angularis/prismatica*) up to 12.5 μm long and ca 5 μm wide. Cell walls straight or rounded. Ostiole absent.

Remarks. Most probably a fragment of a young, not fully developed microthyriaceous fruiting body. The specimen corresponds to average-developed thyrtothecia of *Phragmothyrites kangukensis* Kalgutkar described from Palaeogene deposits of Axel Heiberg Island from the Canadian Arctic (Kalgutkar 1997), confirmed by the characteristic rather large marginal cells of the scutellum.

Phragmothyrites sp.

Pl. 2, figs 3a, b

Material. Slide 144-812(2). One specimen.

Description. Fruiting body orbicular, ca 60 μm in diameter, margin irregularly sinuate. Scutellum composed of both isodiametric (central part) and radiate (margin) nonporate cells (*textura angularis/prismatica*), 7.5–10.0 μm in diameter. Cell walls straight, rarely rounded. Ostiole absent.

Remarks. Fruiting body shows morphology typical of the fossil genus *Phragmothyrites* (e.g. thin-walled, non-porate cells of scutellum, absence of ostiole). The structure of the margin of the fructification is somewhat similar to *Phragmothyrites serratus* Saxena & Khare described from a borehole in Tertiary deposits of Tamil Nadu, India (Saxena & Khare 1992). The discussed *Phragmothyrites* sp. most probably represent a young

stage of development of a microthyriaceous fruiting body (“germling”).

INCERTAE SEDIS FUNGAL REMAIN

Non-pollen palynomorph Type 8G (van Geel 1978), **now HdV-8G** (Miola 2012)

Pl. 3, figs 1a–c

1978 Non-pollen palynomorph Type 8G, van Geel, p. 55, pl. 4, figs 8G: a–f.

Material. Slide 144-811(1). One specimen.

Description. Probably a fungal fruiting body, suborbicular, 140 \times 150 μm in size. Scutellum composed of isodiametric cells (*textura angularis*), rather small, ca 2.5 μm in diameter. Ostiole circular, small, ca 5 μm in diameter. Collar absent, cells surrounding ostiole similar to the remaining and differs only in darkened cell walls.

Remarks. The morphology of this specimen points to its fungal affinity, but such forms are not observed among extant epiphyllous fungi of, for example, the families Asterinaceae, Meliolaceae, Micropeltidaceae, and Microthyriaceae. Identical fossil remains were described by van Geel (1978) as fungal non-pollen palynomorph (NPP) type 8G from the Holocene peat bog section of the Engbertsdijkveen, the Netherlands. Van Geel (op. cit.) found them associated with remains of epidermis of a monocotyledonous plant. According to Miola (2012), NPP type 8G, now HdV-8G, has not been reported since it was described. Kar and Saxena (1976) reported almost identical fungal remains as cf. *Notothyrites* sp. from the Palaeocene Matanomadh Formation in India. It differs, however, from the discussed fructification from the Krabbedalen Formation in having larger cells of the scutellum (2–6 μm).

DISCUSSION

In the Oligocene deposits of the Krabbedalen Formation, fruiting bodies of six fossil taxa of epiphyllous fungi from the family Microthyriaceae (*Phragmothyrites kangukensis* Kalgutkar, *Phragmothyrites* sp., *Plochmopeltinites* sp., *Trichothyrites* cf. *ostiolatus* (Cookson) Kalgutkar & Jansonius, *Trichothyrites* sp. 1, and *Trichothyrites* sp. 2) and one *incertae sedis* fungal

remain, probably also a fruiting body (non-pollen palynomorph HdV-8G) were identified. Altogether there are seven fossil taxa but from only three genera. Fossil epiphyllous fungi have been regularly reported from the Palaeogene and Neogene of the Arctic, but most of the reports come from the Canadian Arctic and Alaska. Jansonius (1976), Kalgutkar (1985, 1993, 1995) and McIntyre (1991) reported the occurrence of fungal fructifications from the Palaeogene deposits. Later Kalgutkar (1997) described an abundant association of fossil fungal remains from the Palaeogene (Palaeocene/Eocene) Iceberg Bay Formation from Axel Heiberg Island in the Canadian Arctic. The numerous microthyriaceous fructifications found there were represented by the species *Callimothallus pertusus* Dilcher, *Euthyrites oleinites* Cookson, *Microthallites lutosus* Dilcher, *Microthyriacites* sp., *Paramicrothallites canadensis* Kalgutkar, *Phragmothyrites kangukensis* Kalgutkar, *Plochmopeltinites cooksoniae* Ramanujam & Rao, and *Trichothyrites* sp. In Palaeogene (Eocene) deposits of the Amphitheatre Formation, Yukon Territories, Canada, Kalgutkar (1999) also found ascocarps of *Callimothallus pertusus*, *Paramicrothallites canadensis*, *Phragmothyrites eocenicus*, and *Plochmopeltinites cooksoniae*. From Palaeogene deposits of the Caribou Hills in northern Canada, Parsons (2000) described a rich assemblage of epiphyllous fungi representing the genera *Callimothallus* Dilcher, *Desmidiospora* Thaxter, *Microthallites* Dilcher, *Paramicrothallites* Jain & Gupta, *Phragmothyrites* Edwards, *Plochmopeltinites* Cookson, and some other forms of fungal fructifications besides abundant remains of fungal spores. Recently Vickulin et al. (2010) reported thyriothecia of microthyriaceous fungi from needles of *Metasequoia occidentalis* from Palaeogene (Eocene) deposits of Axel Heiberg Island in the Canadian High Arctic.

Unlike all the mentioned assemblages of epiphyllous fungi from the Arctic, the fungal remains from the Krabbedalen Formation represent the youngest, Oligocene occurrence of the fungal fructifications in the Palaeogene of the Arctic. Most of the earlier-recorded taxa originate from Palaeocene and Eocene deposits. This is also the first report on the occurrence of fungal fruiting bodies in the Tertiary deposits in this part of East Greenland. From Western Greenland, Hansen (1980) described fossil remains considered to be fossil algae *Ulvella*

nannae Hansen. However, putative *Ulvella nannae* probably represents non-ostiolate fungal fructifications of the genera *Callimothallus* and *Phragmothyrites*. Moreover, they were found in considerably older, Cretaceous deposits. Fructifications described as *Ulvella nannae* were also reported from the Late Palaeocene to earliest Eocene Thyra Ø Formation in eastern North Greenland (Lyck & Stemmerik 2000).

In terms of taxonomic composition the assemblage of fungal remains from the Krabbedalen Formation is most similar to the Palaeogene assemblage from the Iceberg Bay Formation of Axel Heiberg Island in the Canadian Arctic (Kalgutkar 1997). All fungal fruiting body genera from the Krabbedalen Formation are present in the Iceberg Bay Formation, but the latter shows much greater taxonomic diversity. The fungal assemblage of the Krabbedalen Formation is significantly impoverished, probably due to global and local climate cooling in the Early Oligocene (Śliwińska & Heilmann-Clausen 2011). The other localities with fungal remains differ from the assemblage from the Krabbedalen Formation in the absence of epiphyllous fungi representing the genus *Trichothyrites*.

Outside the Arctic, Kar and Saxena (1976) described an assemblage comprising very similar fungal fruiting bodies, from the Palaeocene Matanomadh Formation, Kutch District, India. *Notothyrites* (= *Trichothyrites*) *setiferus* Cookson and cf. *Notothyrites* sp. from the Matanomadh Formation are almost identical to *Trichothyrites* cf. *ostiolatus* and the non-pollen palynomorph HdV-8G, respectively, from the Krabbedalen Formation. Another locality with a fungal assemblage similar to East Greenland is the Miocene Cullen Formation, Tierra del Fuego, southern Argentina (García-Massini et al. 2004). Particularly similar are fructifications described from both localities as *Plochmopeltinites* sp. Also showing some resemblance are *Phragmothyrites eocenicus* Edwards from the Cullen Formation (especially the specimen illustrated in fig. 2P, García-Massini et al. 2004) and *Phragmothyrites kangukensis* from the Krabbedalen Formation.

The presence of the fruiting bodies of epiphyllous fungi is very useful for reconstructing the palaeoclimate and palaeoenvironment of East Greenland during the period of deposition of the Krabbedalen Formation. Their existence in a fossil state is correlated with a rather humid,

warm temperate to tropical climate (Dilcher 1965, Lange 1976, Elsie 1978, Sherwood-Pike 1988, Kalgutkar 1997, Kalgutkar & Jansonius 2000, García-Massini et al. 2004, Limaye et al. 2007, Lee et al. 2012). Modern epiphyllous fungi are encountered in areas characterized by humid climate and fairly stable temperature throughout the year (Schmiedeknecht 1995, Hofmann 2010, Kumar et al. 2011, Piepenbring et al. 2011). Most important for their growth are wet climatic conditions such as high annual rainfall and high air moisture (Selkirk 1975, Johnson & Sutton 2000, Limaye et al. 2007). There are, however, distinct differences in the ecology between certain families of epiphyllous fungi. Asterinaceae and plant-parasitic Microthyriaceae are generally restricted to subtropical and tropical areas, while saprotrophic and hyperparasitic Microthyriaceae are also found in temperate regions of the world (Hofmann 2010). Epiphyllous obligate parasitic Meliolaceae also prefer humid tropical to subtropical climate (Schmiedeknecht 1995). Unlike Meliolaceae, some microthyriaceous epiphyllous fungi do not require tropical to subtropical thermal conditions (Hofmann 2010), as some extant members of this family occur even in polar areas with wet climate (Lind 1928, Dennis 1968, Holm & Holm 1984). As a rule, however, epiphyllous fungi in extant communities show high abundance and taxonomic diversity in warm, humid subtropical and tropical regions (Reynolds & Gilbert 2005, Thaug 2006, Piepenbring et al. 2011). This pattern extends to the fossil state (Rao et al. 2013). Finally, extant epiphyllous fungi (both parasitic and saprophytic) seem to prefer coriaceous leaves (live or fallen) of evergreen plants, even in areas with temperate climate (e.g. Eriksson 1974, Kirk & Spooner 1989). For fungal taxa growing on the surface of living leaves, perennial leaves apparently provide a better substrate for fungal growth, allowing them to complete the life cycle (Flessa et al. 2012).

The fungal remains from the Oligocene of the Krabbedalen Formation at the Savoia Halvø were accompanied by rich palynological material, consisting of sporomorphs (pollen grains and spores) and dinoflagellate cysts (Birkenmajer et al. 2010). The pollen spectra were dominated by gymnosperms (mainly bisaccates), with a low share of angiosperms in terms of both diversity and relative frequency. Pollen grains of gymnosperms were

represented by bisaccate *Pinus sylvestris* type (mainly *Pinuspollenites labdacus*), *Pinus haploxylon* type/*Cathayapollis*, *Picea (Piceapollis)*, *Cedrus (Cedripites)*, *Abies (Abiespollenites)* and others, and non-bisaccate *Sciadopitys (Sciadopityspollenites)*, *Tsuga (Zonalapollenites)*, *Taxodium/Glyptostrobus (Inaperturopollenites)*, and *Sequoia (Sequoiapollenites)*. Among the angiosperms Ericaceae (*Ericipites*) were most common. Also recorded were single specimens of *Diervillapollenites* sp., *Intratropopollenites microreticulatus*, *Lonicerapollis gallwitzii*, *?Pistillipollenites mcgregori*, *Quercoidites* sp., *?Saxonipollis* sp., and *Tricolporopollenites* sp. Spores represented mainly taxa of the families Lycopodiaceae (*Retitriletes*), Selaginellaceae (*Echinatisporis*), and Osmundaceae (*Baculatisporites* and *Rugulatisporites*) as well as others related to Schizaeaceae/Cyatheaceae (*Leiotriletes*), Polypodiaceae/Davalliaceae (*Laevigatosporites* and *Perinomonoletes*), and Pteridaceae (*Cryptogrammasporis* sp.).

The palynoflora most resembles the Oligocene and Miocene spectra from the Hovgård (Hovgaard) Ridge, Greenland Sea (Boulter & Manum 1996), especially from its Oligocene part. It also shows some similarities to the middle Oligocene spore-pollen assemblages from Sarsbukta, Spitsbergen (Manum 1962, Boulter & Manum 1996) and the Miocene (Early and early Middle Miocene) pollen and spore assemblages described from the Baffin Bay (Head et al. 1989). The state of preservation of some sporomorphs (e.g. spores of *Selaginella* in tetrads) suggests that the distance to the terrestrial source was relatively short.

The composition of the pollen spectra accompanying epiphyllous fungi points to the presence of coniferous forests dominated by *Pinus* species, accompanied by *Picea*, Cupressaceae and others, with a minor share of angiosperms. Probably the forest understory was composed of ferns, Lycopodiaceae and Selaginellaceae, or these plants grew on open areas and at the edges of open water. Similar fossil plant communities were described from other Tertiary Arctic localities (Boulter & Fisher 1994) but it is difficult to reconstruct the type of northern subarctic palaeoflora because there are no modern equivalents of the Tertiary palaeoenvironment of the Arctic (Boulter & Manum 1996). The climate was then temperate with periodic light reduction (a few months of reduced light and even darkness each year). These conditions

surely demanded a special physiology and lifestyle for their inhabitants (Basinger et al. 1994, Boulter & Manum 1996).

Similar conclusions about climate can be inferred from the fungal remains. The presence of epiphyllous microthyriaceous fungi in low quantities and in low taxonomical diversity points to a humid and not necessarily warm climate. Thus the results previously obtained from the analysis of microscopic plant remains are confirmed by data gleaned from epiphyllous fungal fructifications.

Today the discussed area (East Greenland Sea) is characterised by cold (but with relatively mild winters) and moderately humid polar climate (Alt 1987). Epiphyllous microthyriaceous fungi are now rare in this part of the Arctic but were reported from nearby Iceland as *Trichothyrina* (= *Lichenopeltella*) cf. *nigroannulata* (Webst) J.P. Ellis, *Stomiopeltis dryadis* (Rehm) Holm, *Morenoina* sp., *Schizothyrium* sp., Holm & Holm (1984), and from more distant Spitsbergen as *Microthyrium arcticum* Oudem. (= *Ronnigeria arctica* (Oudem.) Petr.), Lind (1928), Petrak (1947).

The age of the deposits from the Krabbedalen Formation could not be inferred from the fungal remains, as stratigraphically relevant taxa do not occur in the assemblage.

CONCLUSIONS

- Six fossil taxa from the family Microthyriaceae (*Phragmothyrites kangukensis* Kalgutkar, *Phragmothyrites* sp., *Plochmopeltinites* sp., *Trichothyrites* cf. *ostiolatus* (Cookson) Kalgutkar & Jansonius, *Trichothyrites* sp. 1, and *Trichothyrites* sp. 2) and one *incertae sedis* fungal remain are reported here from the Oligocene Krabbedalen Formation.

- The fungal remains from the Krabbedalen Formation represent the youngest, Oligocene occurrence of the fungal fructifications in the Palaeogene of the Arctic. This is also the first report on the occurrence of fungal fruiting bodies in the Tertiary deposits of discussed part of Eastern Greenland.

- In respect of its taxonomic composition the assemblage of fungal remains from the Krabbedalen Formation is most similar to the Palaeogene assemblage of the Iceberg Bay Formation from Axel Heiberg Island in the Canadian Arctic (Kalgutkar 1997). Assemblages from outside the

Arctic that comprised very similar fungal fruiting bodies were described from the Palaeocene Matanomadh Formation, Kutch District, India (Kar and Saxena 1976), and from the Miocene Cullen Formation, Tierra del Fuego, southern Argentina (García-Massini et al. 2004).

- The composition of pollen spectra accompanying epiphyllous fungi from the Krabbedalen Formation suggests the presence of coniferous forest dominated by *Pinus* species, accompanied by *Picea*, Cupressaceae and others, with a minor share of angiosperms. Probably the forests understory was composed of ferns, Lycopodiaceae and Selaginellaceae, or else these plants grew on open areas and at the edges of open water. The climate was then temperate with periodic light reduction (a few months of reduced light and even darkness each year). The presence of the fruiting bodies of epiphyllous fungi is generally correlated with rather humid, warm temperate to tropical climate. The low quantities and low taxonomic diversity of epiphyllous fungi found in the Krabbedalen Formation point to humid and not necessarily warm climate, a suggestion in conformity with earlier results from analysis of microscopic plant remains.

- No deductions on the deposition age of the Krabbedalen Formation could be drawn on the basis of the fungal remains, as stratigraphically relevant taxa do not occur in the assemblage.

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REFERENCES

- ALT B.T. 1987. Arctic climates: 82–90. In: Oliver J.E. & Fairbridge R.W. (eds), *The Encyclopedia of Climatology*. Van Nostrand Reinhold New York.

- BASINGER J.F., GREENWOOD D.R. & SWEDA T. 1994. Early Tertiary vegetation of Arctic Canada and its relevance to paleoclimatic interpretation. In: Boulter M.C. & Fisher H.C. (eds), *Cenozoic Plants and Climates of the Arctic*. NATO Adv. Sci. Inst. Ser., 127: 175–213.
- BIRKENMAJER K. 1972. Report on investigations of Tertiary sediments at Kap Brewster, Scoresby Sund, East Greenland. Grønlands Geologiske Undersøgelse, Rapport, 48: 85–91.
- BIRKENMAJER K. & JEDNOROWSKA A. 1977. Foraminiferal evidence for the East Greenland Current during the Oligocene. Grønlands Geologiske Undersøgelse, Rapport, 85: 86–89.
- BIRKENMAJER K. & JEDNOROWSKA A. 1997. Early Oligocene foraminifera from Kap Brewster, East Greenland. *Ann. Soc. Geol. Pol.*, 67: 155–173.
- BIRKENMAJER K., GEDL P. & WOROBIEC E. 2010. Dinoflagellate cyst and spore-pollen spectra from Lower Oligocene Krabbedalen Formation at Kap Brewster, East Greenland. *Pol. Polar Res.*, 31(2): 103–140.
- BOULTER M.C. & FISHER H.C. (eds) 1994. *Cenozoic Plants and Climates of the Arctic*. Springer Verlag, Heidelberg.
- BOULTER M.C. & MANUM S.B. 1996. Oligocene and Miocene vegetation in high latitudes of the north Atlantic: Palynological evidence from the Hovgård Ridge in the Greenland Sea (site 908). In: Thiede J., Myhre A.M., Firth J.V., Johnson G.L. & Rudiman W.F. (eds), *Proc. of the Ocean Drilling Program, Scientific Results*, 151: 289–296.
- COOKSON I.C. 1947. Fossil fungi from Tertiary deposits in the Southern Hemisphere, Part I. *Proc. Linn. Soc. N.S.W.*, 72: 207–214.
- DENNIS R.W.G. 1968. Fungi from South Georgia. *Kew Bull.*, 22(3): 445–448.
- DILCHER D.L. 1965. Epiphyllous fungi from Eocene deposits in western Tennessee, USA. *Palaeontographica*, B, 116(1–4): 1–54.
- ELSIK W.C. 1978. Classification and geologic history of the microthyriaceous fungi. In: *Proc. of the IV International Palynological Conference, Lucknow (1976–77)*, 1: 331–342.
- ERIKSSON B. 1974. On ascomycetes on Diapensiales and Ericales in Fennoscandia. 2. Pyrenomycetes. *Sven. Bot. Tidskr.*, 68: 192–234.
- FLESSA F., PERŠOH D. & RAMBOLD G. 2012. Annuality of Central European deciduous tree leaves delimits community development of epifoliar pigmented fungi. *Fungal Ecol.*, 5(5): 554–561.
- GARCÍA MASSINI J.L., ZAMALOA M.D.C., & ROMERO E.J. 2004. Fungal fruiting bodies in the Cullen Formation (Miocene) in Tierra del fuego, Argentina. *Ameghiniana*, 41(1): 83–90.
- van GEEL B. 1978. A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. *Rev. Palaeobot. Palynol.*, 25(1): 1–120.
- HANSEN J.M. 1980. Morphological characterization of encrusting, palynomorph green algae from the Cretaceous-Tertiary of central West Greenland and Denmark. *Grana*, 19(1): 67–77.
- HASSAN M.Y. 1953. Tertiary faunas from Kap Brewster, East Greenland. *Medd. Grøn.*, 111(5): 1–42.
- HEAD M.J., NORRIS G. & MUDIE P.J. 1989. Palynology and dinocyst stratigraphy of the Miocene in ODP Leg 105, Hole 645E, Baffin Bay. In: Srivastava S.P., Arthur M., Clement B., et al. (eds), *Proc. of the Ocean Drilling Program, Scientific Results*, 105: 467–514.
- HOFMANN T.A. 2010. Plant parasitic Asterinaceae and Microthyriaceae from the Neotropics (Panama). PhD thesis. The faculty of biological sciences at the JW Goethe-University, Frankfurt am Main, Germany.
- HOLM K. & HOLM L. 1984. A contribution to the mycoflora of Iceland. *Acta Bot. Isl.*, 7: 3–11.
- JANSONIUS J. 1976. Palaeogene fungal spores and fruiting bodies of the Canadian Arctic. *Geoscience and Man*, 15(1): 129–132.
- JOHNSON E.M. & SUTTON T.B. 2000. Response of two fungi in the apple sooty blotch complex to temperature and relative humidity. *Phytopathology*, 90(4): 362–367.
- KALGUTKAR R.M. 1985. Fossil fungal fructifications from Bonnet Plume Formation, Yukon Territory. *Curt. Res. B, Geol. Surv. Can. Pap.*, 85–1B: 259–268.
- KALGUTKAR R.M. 1993. Paleogene fungal palynomorphs from Bonnet Plume Formation, Yukon Territory. *Contrib. Can. Paleontol., Geol. Surv. Can. Bull.*, 444: 51–105.
- KALGUTKAR R.M. 1995. An overview of fossil fungal assemblage from the Iceberg Bay Formation, Eureka Sound Group, at Kanguk Peninsula, Axel Heiberg Island, Northwest Territories. *Proc. of the Oil and Gas Forum '95 Energy from Sediments. Geol. Surv. Can. Open File*, 3058: 205–209.
- KALGUTKAR R.M. 1997. Fossil fungi from the lower Tertiary Iceberg Bay Formation, Eureka Sound Group, Axel Heiberg Island, Northwest Territories, Canada. *Rev. Palaeobot. Palynol.*, 97(1): 197–226.
- KALGUTKAR R.M. 1999. Paleogene fungal spores and fructifications from the Amphitheatre Formation, Yukon Territories, Canada. In: *Abstracts of the proceedings of the thirty-first annual meeting of the American association of stratigraphic palynologists, Ensenada, Baja California, Mexico, 27–31 October 1998*. *Palynology*, 23(1): 247–269.
- KALGUTKAR R.M. & JANSONIUS J. 2000. Synopsis of fossil fungal spores, mycelia and fructifications. *Am. Assoc. Strat. Palynol. Contrib. Ser.*, 39: 1–429.
- KAR R.K. & SAXENA R.K. 1976. Algal and fungal microfossils from Matanomadh Formation (Paleocene) Kutch, India. *Palaeobotanist*, 23: 1–15.

- KIRK P.M. & SPOONER B.M. 1989. Ascomycetes on leaf litter of *Laurus nobilis* and *Hedera helix*. *Mycol. Res.*, 92(3): 335–346.
- KORF R.P. 1958. Japanese Discomycete Notes I—VIII. *Sci. Rep. Yokohama Nat. Univ., Sec. 2, Biol. Sci.* 7: 7–35.
- KUMAR S., SINGH R., GOND D.K., SAINI D.C. & KAMAL. 2011. Indian Forests: A Natural Paradise for Biodiversity of Foliar Fungi. In: National Conference on Forest Biodiversity: Earth's Living Treasure, 22 May 2011: 134–140.
- LANGE R.T. 1976. Fossil epiphyllous “germlings”, their living equivalents and their palaeohabitat indicator value. *Neues Jahrb. Geol. Palaeontol. Abh.*, 151: 142–165.
- LEE D.E., CONRAN J.G., LINDQVIST J.K., BANISTER J.M., & MILDENHALL D.C. 2012. New Zealand Eocene, Oligocene and Miocene macrofossil and pollen records and modern plant distributions in the southern hemisphere. *Bot. Rev.*, 78(3): 235–260.
- LIMAYE R.B., KUMARAN K.P.N., NAIR K.M., & PADMALAL D. 2007. Non-pollen palynomorphs as potential palaeoenvironmental indicators in the Late Quaternary sediments of the west coast of India. *Curr. Sci.*, 92(10): 1370–1382.
- LIND J.V.A. 1928. The micromycetes of Svalbard. *Skr. Svalbard Ishavet*, 13: 1–61.
- LYCK J.M. & STEMMERIK L. 2000. Palynology and depositional history of the Paleocene? Thyra Ø Formation, Wandel Sea Basin, eastern North Greenland. *Geol. Greenl. Surv. Bull.*, 187: 21–49.
- MANUM S. 1962. Studies in the Tertiary flora of Spitsbergen, with notes on Tertiary floras of Ellesmere Island, Greenland, and Iceland. A palynological investigation. *Norsk Polarinst. Skr.*, 125: 1–127.
- McINTYRE D.J. 1991. Palynology (Appendix 3). In: Ricketts B.D. (ed.), *Delta Evolution in the Eureka Sound Group, western Axel Heiberg Island: the Transition from Wave-dominated to Fluvial-dominated Deltas*. *Geol. Surv. Can. Bull.*, 402: 66–72.
- MIOLA A. 2012. Tools for Non-Pollen Palynomorphs (NPPs) analysis: A list of Quaternary NPP types and reference literature in English language (1972–2011). *Rev. Palaeobot. Palynol.*, 186: 142–161.
- PARSONS M.G. 2000. Palynology of Paleogene strata in the Caribou Hills, Beaufort-MacKenzie Basin, northern Canada. PhD Thesis. Department of Geology, University of Toronto, Canada.
- PETRAK F. 1947 *Ronnigeria*, n.gen., eine neue Gattung der Leptopeltineen. *Sydowia*, 1(4–6): 309–312.
- PIEPENBRING M., HOFMANN T.A., KIRSCHNER R., MANGELSDORFF R., PERDOMO O., RODRÍGUEZ JUSTAVINO D., & TRAMPE T. 2011. Diversity patterns of Neotropical plant parasitic microfungi. *Ecotropica*, 17: 27–40.
- RAO K.P. & RAMANUJAM C.G.K. 1976. A further record of microthyriaceous fungi from the Neogene deposits of Kerala in South India. *Geophytology*, 6(1): 96–104.
- RAO M.R., SAHNI A., RANA R.S. & VERMA P. 2013. Palynostratigraphy and depositional environment of Vastan Lignite Mine (Early Eocene), Gujarat, western India. *J. Earth Syst. Sci.*, 122(2): 289–307.
- REYNOLDS D.R. & GILBERT G.S. 2005. Epifoliar fungi from Queensland, Australia. *Aust. Syst. Bot.*, 18(3): 265–289.
- SAXENA R.K. & KHARE S. 1992. Fungal remains from the Neyveli Formation of Tiruchirapalli District, Tamil Nadu, India. *Geophytology*, 21: 37–43.
- SCHMIEDEKNECHT M. 1995. Environmental tolerance range of Meliiales as mirrored in their horizontal and vertical distribution patterns. *Microbiol. Res.*, 150(3): 271–280.
- SELKIRK D.R. 1975. Tertiary fossil fungi from Kian-dra, New South Wales. *Proc. Linn. Soc. N.S.W.*, 97: 141–149.
- SHERWOOD-PIKE M.A. 1988. Freshwater fungi: fossil record and paleoecological potential. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 62(1): 271–285.
- SMITH P.H. 1980. Trichothyriaceous fungi from the Early Tertiary of southern England. *Palaeontology*, 23(1): 205–212.
- ŚLIWIŃSKA K.K. & HEILMANN-CLAUSEN C. 2011. Early Oligocene cooling reflected by the dinoflagellate cyst *Svalbardella cooksoniae*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 305(1): 138–149.
- THAUNG M.M. 2006. Biodiversity of phylloplane ascomycetes in Burma. *Australas. Mycol.*, 25(1): 5–23.
- VIKULIN S.V., UPCHURCH G.R., LEPAGE B.A. & KARATYGIN I.V. 2010. Predstavitel' semeistva Microthyriaceae (Dothideales, Ascomycota) iz paleogena Kanadskoï Arktiki (summary: New data on the Arctic Conifers from the Early Cenozoic of the North America). *Bot. Zhurnal*, 95(7): 897–909.
- WU H.X., SCHOCH C.L., BOONMEE S., BAHKALI A.H., CHOMNUNTI P. & HYDE K.D. 2011. A reappraisal of Microthyriaceae. *Fungal Divers.*, 51(1): 189–248.

PLATES

Plate 1

Trichothyrites cf. ostiolatus (Cookson) Kalgutkar & Jansonius

1a. Fructification, specimen No. 144-812(1) 43/98.5

1b. Fructification, specimen No. 144-812(1) 43/98.5

Trichothyrites sp. 1

2a. Fructification, specimen No. 144-812(2) 40.5/100

2b. Fructification, specimen No. 144-812(2) 40.5/100

Trichothyrites sp. 2

3a. Fructification, specimen No. 144-812(1) 36/105

3b. Detail of scutellum structure, specimen No. 144-812(1) 36/105

2b, 3b: scale bar – 10 μm ; 1a, 1b, 2a, 3a: scale bar – 20 μm

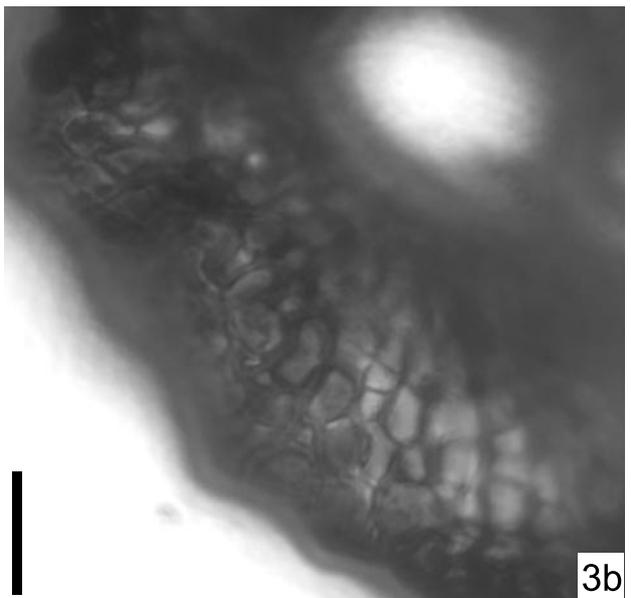
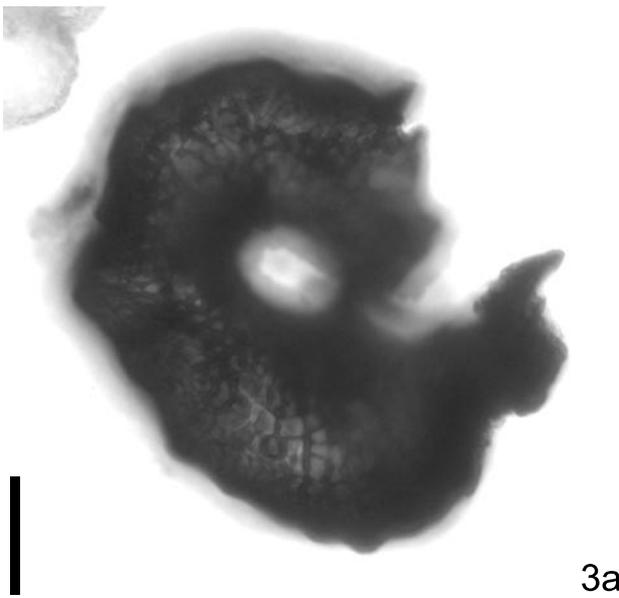
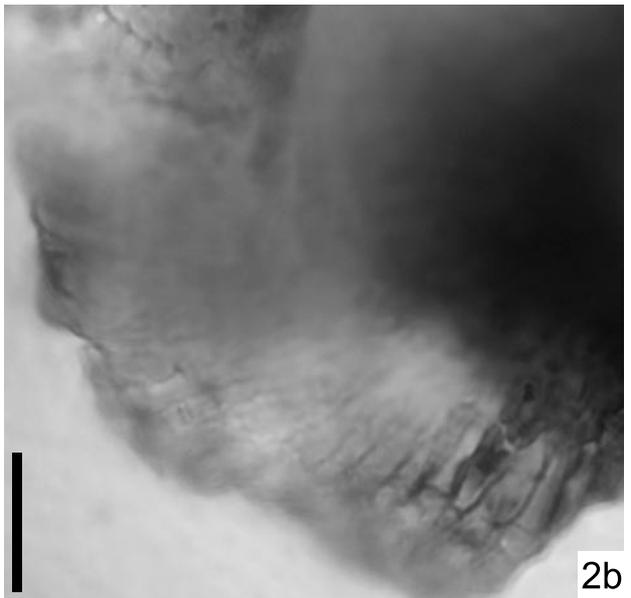
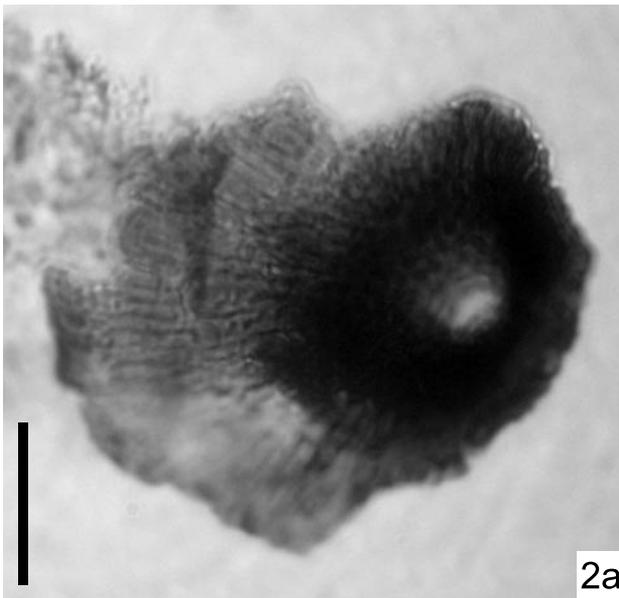
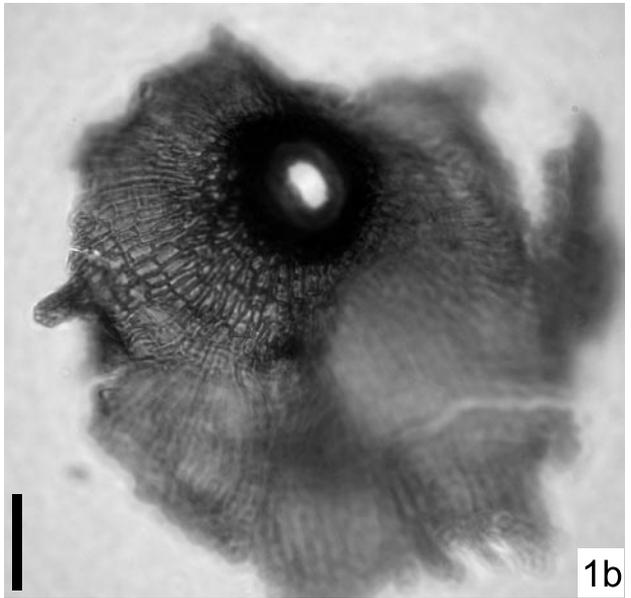
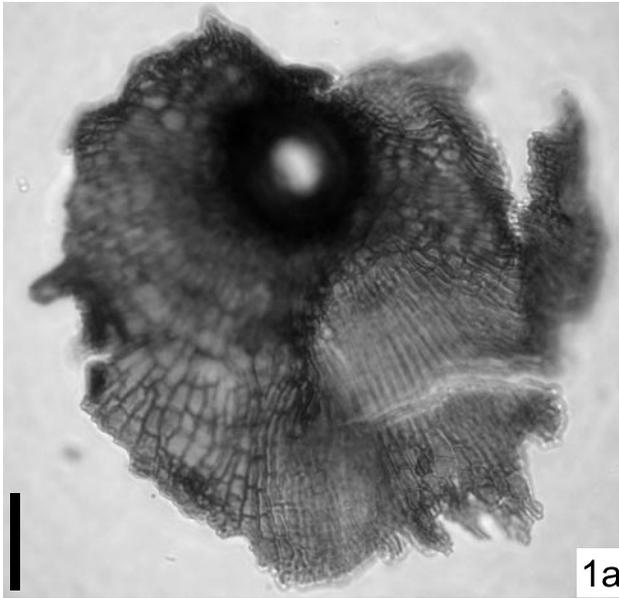


Plate 2

Plochmopeltinites sp.

- 1a. Fructification, specimen No. 144-812(1) 43/109
- 1b. Detail of ostiole, specimen No. 144-812(1) 43/109
- 1c. Detail of scutellum structure, specimen No. 144-812(1) 43/109

Phragmothyrites kangukensis Kalgutkar

- 2a. Fructification, specimen No. 144-812(1) 35/100.5
- 2b. Fructification, specimen No. 144-812(1) 35/100.5

Phragmothyrites sp.

- 3a. Fructification, specimen No. 144-812(2) 44/100.5
- 3b. Fructification, specimen No. 144-812(2) 44/100.5

1b, 1c, 2a, 2b, 3a, 3b: scale bar – 10 μm ; 1a: scale bar – 20 μm

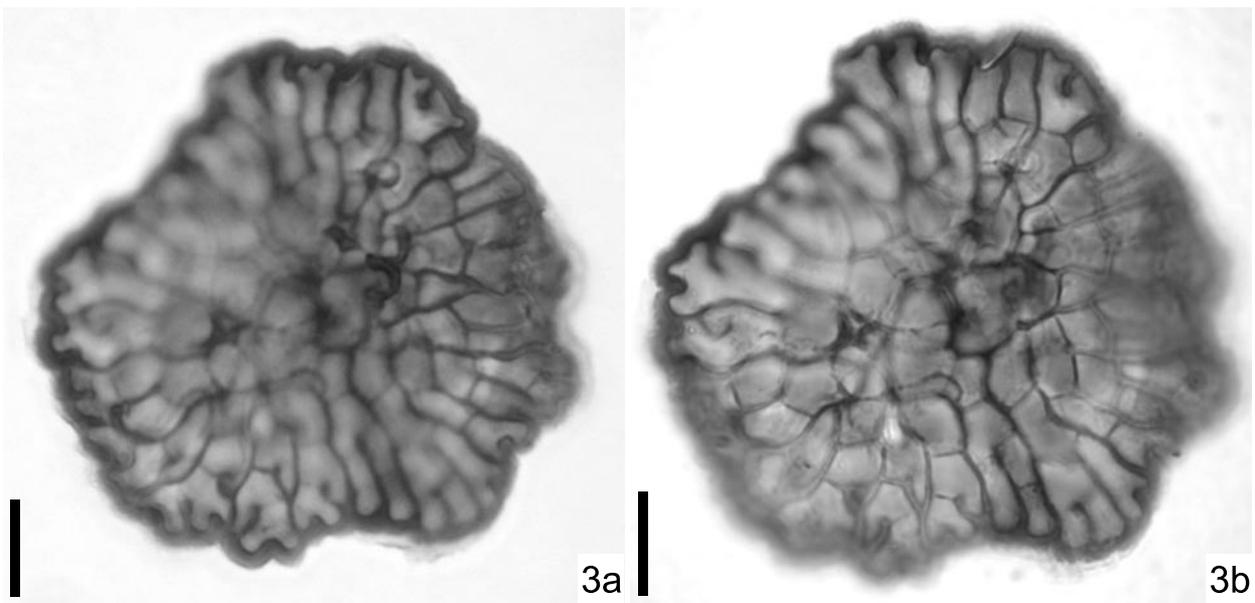
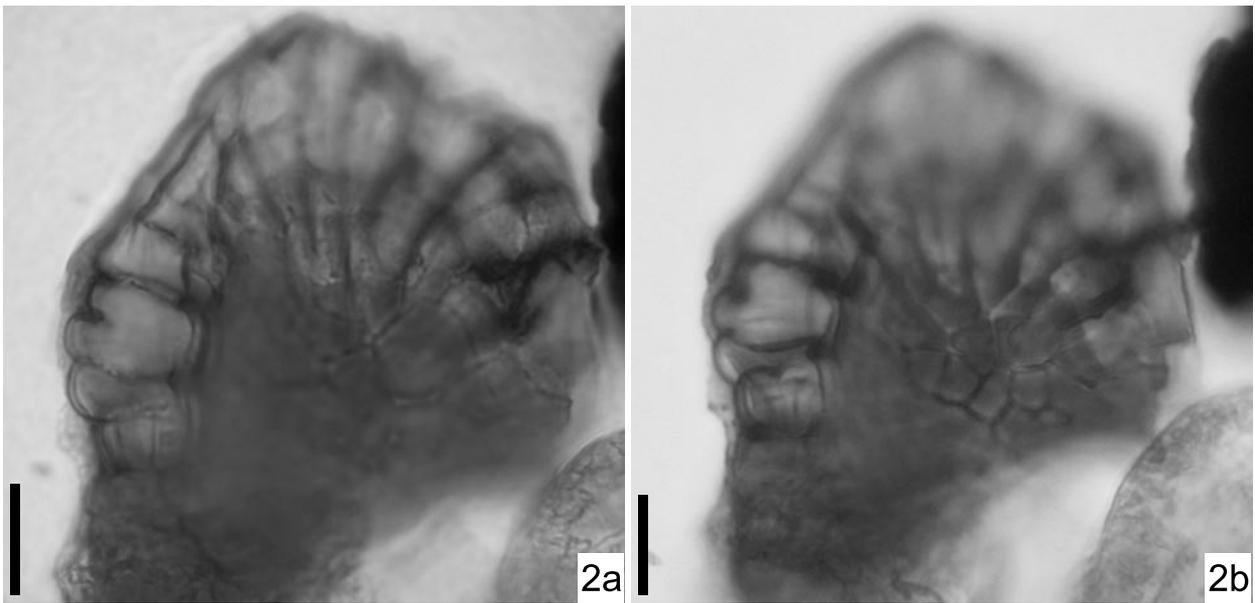
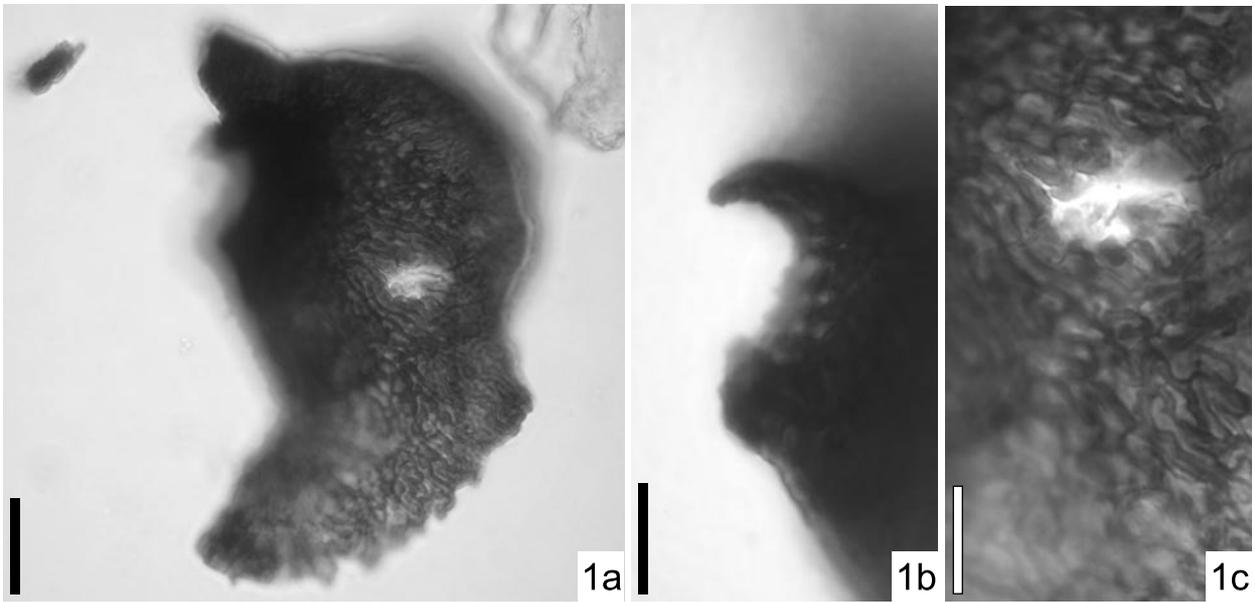


Plate 3

Non-pollen palynomorph Type 8G (van Geel 1978),
now HdV-8G (Miola 2012)

1a. Fructification, specimen No. 144-811(1) 42.5/111.5

1b. Detail of ostiole, specimen No. 144-811(1) 42.5/111.5

1c. Detail of scutellum structure, specimen No. 144-811(1) 42.5/111.5

1b, 1c: scale bar – 10 μm ; 1a: scale bar – 20 μm

