Biota and palaeoenvironment of a high middle-latitude Late Triassic peat-forming ecosystem from Hopen, Svalbard archipelago

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Abstract: A siliceous permineralized peat block recovered from Hopen in the Svalbard archipelago hosts a low-diversity Late Triassic flora dominated by autochthonous roots and stems of bennettitaleans and lycophytes, and parautochthonous leaves, sporangia, spores and pollen from a small range of pteridophytes and gymnosperms. Some parenchymatous bennettitalean root cells show interactions with chytrid fungi and bacteria; the remains of other fungi and fungi-like organisms are dispersed within the peat’s detrital matrix. Cavities excavated through some roots and compacted detritus contain abundant coprolites probably derived from sapro-xylophagous oribatid mites, although no body fossils have yet been identified. Sparse larger coprolites containing leaf fragments attest to the presence of invertebrate folivores in the ancient ecosystem. The low-diversity flora, relatively few trophic levels and simple nutritional web, together with sedimentological aspects of the host formation and the peat structure, collectively favour accumulation of the organic mass as a fibric (root-dominated) peat within a temperate (high middle-latitude), well-aerated mire.

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The Late Triassic saw remarkable innovations in gymnosperm reproductive architectures and diversification of several spore-bearing plant groups that would become key components of global floras for the remainder of the Mesozoic (Anderson et al. 1999; Anderson & Anderson 2003). Amongst terrestrial vertebrates, the Late Triassic saw the decline of large synapsids, the origins of true mammals and the rise of dinosaurs, which would dominate the megafauna of terrestrial ecosystems for the next 150 myr (Benton 1993). Amongst terrestrial arthropods, the Late Triassic saw the peak expression of the early component of the Herbivore Expansion 3 of Labandeira (2006a, 2006b). The earliest records of such interactions in Baltica extend back to the late Silurian in the form of coprolites containing land-plant spores (Hagström & Mehlqvist 2012). By the Triassic, arthropods (in tandem with other terrestrial animals) were interacting with all parts of plants via the full gamut of functional feeding strategies (Labandeira 2006a, b). Recent research provides compelling evidence that fungi and fungi-like microorganisms were also important components of early terrestrial ecosystems and were actively interacting with living plants or their remains from the earliest stages of colonization of the land surface (e.g. Taylor et al. 2006, 2015; Krings et al. 2007, 2010; Dotzler et al. 2008; Vajda 2012; Strullu-Derrien et al. 2014). Plants, animals and fungi represent the most
important sources of macro-biodiversity on the planet. These organisms interact in a complex network of relationships that has experienced massive expansion since the initial steps in colonization of the land. However, the fossil record of these interrelationships remains sparsely documented and much of our knowledge of interactions in terrestrial communities derives from a small number of isolated fossils or exceptional Lagerstätten (Ash 1996, 2000; Scott et al. 2004; McLoughlin 2011; Moisan et al. 2012; Strullu-Derrien et al. 2012; Labandeira 2013; Ghosh et al. 2015).

Information on the composition of, and interactions within, Late Triassic terrestrial ecosystems in Europe derives mostly from fossil assemblages located from Italy to Skåne (southern Sweden), which represent low- to lower middle-paleolatitude lowland biotas (Dobruskina 1994; Kustatscher et al. 2010, 2012; Pott & McLoughlin 2011). Recently, Strullu-Derrien et al. (2012) documented evidence of invertebrate interactions with bennettitalean roots in a permineralized peat block derived from the island of Hopen in the Svalbard archipelago, around 2500 km north of Skåne. Together with a leaf adpression flora described from the same formation (Launis et al. 2014; Pott 2014b), these remains represent the only macrofossil expression of higher mid-latitude floras from the Late Triassic of Europe. The study by Pott (2014b) revealed an adpression flora of sphenophytes, ferns, bennettitaleans, caytonialeans and putative peltaspermaleans, and ginkgoaleans. Here, we build on these preliminary studies to describe the flora of a remarkable three-dimensionally preserved permineralized block of peat from Hopen. In addition, we document associated microfossils and traces of saprotrophic and detritivorous organisms in order to begin reconstruction of the trophic levels and biotic interactions in the Late Triassic peatland ecosystems of Svalbard.

Geological setting

This study is based on a single block of silicified peat recovered by Thor Iversen in 1929 (see Iversen 1941) from an undisclosed locality on the shore of Hopen (Hope Island), part of the Svalbard archipelago, located at 76.30° N, 25.01° E (Fig. 1). The precise origin of the sample was not recorded at the time of collection, but one of three localities are strong candidates for the source based on recorded access sites to the island made by Iversen (1941) (Fig. 1). The Svalbard archipelago had a paleolatitude of around 55–65° N in the Late Triassic (Scotese 1997; Torsvik et al. 2002; Feist-Burkhardt et al. 2008). The strata exposed on Hopen belong predominantly to the De Geerdalen Formation (DGF) of Carnian age, although successions of around 50–60 m each of the overlying Flatsalen Formation (Norian) and Svenskøya Formation (Norian–lowermost Jurassic) are exposed in the island’s higher altitudes (Vigran et al. 2014).
The DGF incorporates mostly coarsening-upward cycles of shales to sandstones deposited in a deltaic setting. These strata are overlain transitionally by fully marine mudstones in the upper part, which were designated the Hopen Member by Mørk et al. (2013). Thin coal seams are represented in the lower part of the DGF and dispersed plant matter is common in the eolian sedimentary layers. The overlying mudstone-dominated Flatsalen Formation was deposited in marine settings and contains a fossil invertebrate fauna together with isolated ichthyosaur bones (Vigran et al. 2014); it characterizes a marine transgression represented throughout the Barents Sea region (Vajda & Wigforss-Lange 2009). The succeeding Svenskøya Formation is represented mainly by multistorey, cross-bedded sandstone packages deposited in coastal settings. Further details of the geology of Hopen and Svalbard were outlined by Smith et al. (1975) and Vigran et al. (2014).

Although the studied peat block was recovered ex situ, its probable stratigraphic source is the lower DGF, based on the interpreted depositional environments of the exposed succession (Riis et al. 2008) and the presence of thin coal seams (Vigran et al. 2014) in this part of the formation (see also Strullu-Derrien et al. 2012). Moreover, fossil woods discovered recently in this unit on Edgeøya, located in the SE part of the main Svalbard archipelago (Fig. 1) to the north of Hopen have similar grades of siliceous permineralization (sampling by A. Mørk pers. comm. 2010). The corresponding abundance of bennettitalean leaf impressions (Pterophyllum and Anomozamites species) in the DGF flora (Høeg 1926; Flood et al. 1971; Vasilevskaya 1972; Smith et al. 1975; Pott 2014b), and of bennettitalean axial remains in the silicified material recovered by Iversen (Strullu-Derrien et al. 2012), provide further circumstantial evidence for this unit being the source of the studied permineralized peat block. A Carnian age is proposed for the DGF based on palynostratigraphic and magnetostratigraphic correlations across the Barents Sea region (Hounslow et al. 2007; Vigran et al. 2014).

**Material and methods**

This investigation is based on a study of 64 thin sections cut from a single block of silicified peat (described as ‘lydian stone’ by Selling 1944, 1945, 1951), which bears the field number 540, collected by Thor Iversen during the Norwegian Svalbard and Arctic Investigation of 1929. These are the same slides used by Strullu-Derrien et al. (2012) to identify roots and selected invertebrate interactions within the peat. The thin sections were prepared at the Department of Palaeobotany (now the Department of Palaeobiology), Swedish Museum of Natural History, in the 1940s by traditional lapidary techniques: 42 slides are held by the Swedish Museum of Natural History, Stockholm (registration numbers NRM S038420-03–05, -08–11, -14, -15, -18, -19, -21, -22, -26, -28, -33–36, -38–42, -44–46, -49, -51, -53–58, -60–66) and 22 slides are registered with the Norwegian Museum of Natural History, Oslo (registration numbers PMO 162.628/01–PMO 162.628/22). Thin sections were analysed and photographed using a Zeiss Axioskop 2 and Olympus BX51 transmitted light microscope with DS 2M Digital Sight camera at the Palaeobiology Department, Swedish Museum of Natural History, and a Leitz Dialux 20 EB transmitted light microscope at the Laboratoire Mycorhizes (Angers, France).

**Terminology**

We refer to various processes of biotic resource acquisition. Since the terminology for these processes varies between previous publications, we outline our application of the terms according to the following definitions:

- detritivory is the process of obtaining nutrients by ingestion of organic detritus (decomposing organic matter) – generally by invertebrates;
- autotrophy is the ability to be self-sustained by generating food from inorganic compounds via photosynthesis or chemosynthesis;
- heterotrophy, for the purposes of this study, is the consumption of a range of other living organisms to obtain nutrients;
- herbivory, for the purposes of this paper, is the consumption of living plant tissues;
- parasitism is defined as a relationship between organisms, in which one (the parasite) benefits at the expense of the other (the host);
- saprotrophy is the process of obtaining food resources from dead organic material by enzymatic reduction, absorption of nutrients and metabolism on a molecular scale; saprotrophs generally include bacteria, fungi and fungi-like organisms;
- xylolphyagy is specifically the consumption of either living or dead woody tissues;
- sapro-xylolphyagy is the consumption of exclusively dead woody tissues;
- mycophagy is the consumption of fungal tissues;
- the term peat is employed for an accumulation of plant material in which the organic constituents represent more than 75% of the sediment mass (Moore 1987);
- mire is used in the sense of Moore (1989) as a general term embracing all peat-forming ecosystems.
Biodiversity of the peat

Plants

Bryophyte sporangia and microspores

Description. Distinctive ellipsoidal microsporangia occur dispersed through the peat matrix as complete sacs with in situ miospores (Fig. 2a), as near-complete microsporangia with penetration of organic detritus (Fig. 2b) and as dispersed sporangial wall fragments (Fig. 2f–h). The sporangia are 400 μm long, 200 μm wide, girdled by a wall consisting of a single layer of robust, radially elongate cells; each cell is approximately 35 μm high and 10 μm wide, with walls 0.4 μm thick. Wall cells are narrowly rectangular in radial view (Fig. 2d, g, h) and circular to elliptical in paradermal section (Fig. 2f). In rare cases, a layer of small (<10 μm) cells is preserved internal to the wall layer (Fig. 2d). Spores within the sporangia are 5–6 μm in diameter, spherical and laevigate, but lack distinct laesurae (Fig. 2e). They have 0.5 μm-thick walls. Several hundred spores are present within each sporangium (Fig. 2c).

Remarks. These organs differ from leptosporangiate fern sporangia in having walls consisting of a uniform palisade of cells: that is, there is no obvious dehiscence zone or differentiation of specialized annulus cells from the remaining generally thin cells of the sporangial wall. Rather, these Hopen sporangial walls consist of a single layer of brick-shaped, regimented cells. Superficially, this array of cells is similar to those of the pollen sac wall in the cycad Delemaya spinulosa from the Middle Triassic of Antarctica (cf. Klavins et al. 2003, fig. 3d), and the outer pollen sac wall of some modern cycads (Lang 1897). Bennettitaleans have a similar row of robust regimented cells in the outer part of the synangial wall, but differ in having a band of smaller irregular cells (including scalariform-pitted tracheids) on the inner synangial surface, together with thin remnants of the individual sporangial walls (Nishida 1994). Moreover, the miospores contained within the Hopen sporangia are not spindleshaped like typical cycadalean or bennettitalean pollen, and they do not correspond in size or shape to Cycadopites-type pollen dispersed within the peat matrix (described below). The affinities of the Hopen sporangia remain unresolved, but the simple architecture and very small size of the spores favour assignment to the bryophytes. The laevigate sporangial walls are reminiscent of those developed in some liverworts, such as Riccia, Marchantiida and Pellia (Bell & Hemsley 2000), although no elaters can be clearly resolved within the spore masses (a few indistinct linear to spiral structures possibly represent ill-preserved elaters) (Fig. 2e: arrowed). Some mosses also have radially arranged, elongate cells in the spore capsule wall, and the form and distribution of the cells near the sporangium margin (Fig. 2d) are similar to those in some young capsules before the development of the spores (Chadefaud & Emberger 1960).

Macrofossil evidence of mosses is scant in northern European Triassic floras. Liverworts have a patchy record in the Triassic of this region. They are represented by several well-preserved macrofossils in the Late Triassic peat-forming floras of Scania (Lundblad 1950, 1954) but were not recorded from the latest Triassic floras of Scoresby Sound in Greenland (Harris 1937) – these two floras being the closest to Hopen palaeogeographically.

Lycophytes

Axes. Diminutive axes up to 500 μm in diameter (Fig. 3f) are preserved in the peat matrix but the cortical tissues are largely degraded and, in some cases, the stele is crushed (Fig. 3g). The vascular cylinder is stellate in transverse section, with six protoxylem poles (Fig. 3f). Metaxylem tracheids reaching 50 μm in diameter (i.e. up to 10 times the diameter of protoxylem cells) fill the centre of the vascular column, although these can be locally degraded leaving a cavity. Metaxylem tracheids have pervasive scalariform pitting and rare vertical connections between horizontal bars (Fig. 3h). No secondary xylem is developed. A one–two-cell thick layer of phloem and/or pericycle surrounds the xylem. Remnants of the cortical tissues indicate that these cells were relatively thin walled and up to 140 μm in diameter.

Megaspores. Several megaspores are dispersed throughout the peat profile. The distal hemisphere of each megaspore is semi-circular in polar section (Fig. 3a, b, d, e); the proximal hemisphere forms a low dome or pyramid (Fig. 3a, b, e). The equatorial diameter is 450–560 μm and the polar diameter 300–430 μm. The megaspore wall is two-layered, consisting of an 8 μm-thick intine and a 40–110 μm-thick exoexine (Fig. 3c). The distal surface is ornamented with robust coni and rounded bacula up to 60 μm high and 60 μm in basal diameter, set approximately 70 μm apart (Fig. 3b–d). The intine is composed of dense material without obvious structure. The exoexine has a spongy texture consisting of fibrous elements arranged mostly perpendicular to the intine (Fig. 3c). Sculpture on the proximal surface is of similar shape to that on the distal surface but reaches only 35 μm high and 30 μm in basal diameter (Fig. 3a, b, d). Most megaspores show little compression but rare examples are compacted to an extent that the lumen is almost completely lost and a few are fragmentary (Fig. 3i, j). The lumen is typically empty but, in some cases, contains a small amount of organic detritus or...
Fig. 2. Bryophyte and fern remains from the Norian permineralized peat of Hopen: (a) bryophyte sporangium containing immature spores (PMO 162.628/19); (b) ruptured bryophyte sporangium penetrated by organic detritus (NRM S038420-35); (c) cluster of bryophyte spores (PMO 162.628/19); (d) enlargement of the bryophyte sporangial wall, showing spongy cells interior to palisade-like wall cells (NRM S038420-35); (e) enlargement of a cluster of bryophyte spores (possible elaters arrowed: PMO 162.628/19); (f) transverse section of palisade-like bryophyte sporangial wall cells (NRM S038420-41); (g) radial section of a bryophyte sporangial wall fragment (NRM S038420-42); (h) radial section of a bryophyte sporangial wall fragment (NRM S038420-57); (i) robust annulus cells of a fern sporangium (NRM S038420-57). Scale bars: 100 μm for (a), (b), (d), (g); 20 μm for (c), (f), (h), (i); 10 μm for (e).
fungal spores that have apparently entered through the commissure (Fig. 3d). All megaspores occur isolated within the peat matrix.

**Microspores.** Elliptical, cavate, laevigate or slightly scabrate, monolete spores (Fig. 3k–r) are common within the peat. They are small (17–31 μm long, 13–25 μm wide and 12–18 μm in polar diameter), pale, and difficult to recognize and photograph within the peat matrix, commonly being masked by dense accumulations of amorphous organic material (Fig. 3l), opaque resin blebs with contractional haloes and angular cell wall fragments. The proximal hemisphere is trianguloid, whereas the distal surface is hemispherical (Fig. 3o, q). A few of these grains bear an indistinct laesura that extends to the equator (Fig. 3n, p, r). The inner body is ellipsoidal, 13–24 μm long, 9–16 μm wide, 9–14 μm in polar diameter and is typically in contact with the proximal side of the outer spore wall (Fig. 3o, q).

**Remarks.** Following the decline of arborescent lycophytes in the late Palaeozoic and the brief resurgence of shrub-sized Pleurosmatales in the immediate wake of the end-Permian extinction, lycophytes were relegated to subsidiary herbaceous components of younger Mesozoic and Cenozoic floras (Pigg 1992). However, their generally delicate anatomy, diminutive size and low preservational potential of their vegetative components probably contributed to them being overlooked in many floras of this age. In contrast, the abundance of diverse megaspore and microspore suites in numerous deposits suggest that herbaceous lycophytes may have played a greater role in the global Mesozoic vegetation than previously suspected (Batten & Kovach 1990; McLoughlin et al. 2015). Certainly, macrofossil records from sinter deposits, coal balls, permineralized peats and modern peats indicate that herbaceous lycophytes were consistent elements of mire and hot-spring wetland vegetation from the Devonian to present (Kidston & Lang 1920; Fry 1954; Slater 1984; Channing & Edwards 2013; McLoughlin et al. 2015).

This rare and diminutive axis type has a greater number of protoxylem poles than the co-preserved bennettitalean roots described by Strullu-Derrien et al. (2012). Their stellate vasculature in cross-section is similar to that of the main axis of *Paurodendron friaponti*, a diminutive isooetalean lycophyte from the late Palaeozoic (Fry 1954; Schlanker & Leisman 1969; McLoughlin et al. 2015). However, no distinctive isooetalean roots with eccentrically positioned vascular strands (like those of *P. friaponti*) were identified in the Hopen peat. Modern selaginellalean lycophytes tend to possess lobed, reniform or polystelic vascular systems in their axes (Maideen et al. 2013) but it is unclear whether these are recently acquired (apomorphic) characters of the group. Given the similarity in size and vascular architecture to *Paurodendron*, and co-preservation with the megaspores described above, we consider that these axes probably belong to a diminutive herbaceous heterosporous lycophyte but insufficient characters are available from the axes alone to differentiate an isooetalean or selaginellalean affinity.

Selling (1945) described megaspores from this sample under the name *Triletes hopeniensis* and attributed them to isooetales. Their robust conate sculpture is very similar to that of *Echitriteles*? sp. 1 of Fuglewicz (1973) from the Polish Early Triassic and slightly broader than that of *Capillisporites germanicus* Kozur illustrated by Marcinkiewicz (1992) from the Middle Triassic of the same region. Younger (Late Cretaceous) megaspores attributed to *Verrutriteles dubius* (Dijkstra) Potonié from The Netherlands (Batten 1988) also have stout conate to rounded sculptural elements on the proximal and distal surfaces that are similar to the rounded bacula on a few of the Hopen megaspores. Modern *Selaginella* and *Isoetes* produce megaspores with a broad range of granulate, conate, baculare and reticulate exine sculpture (Schelpe &

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**Fig. 3.** Lycophyte remains from the Norian permineralised peat of Hopen. (a)–(e), (i), (j) *Triletes hopeniensis* Selling, 1945: (a) polar section of a megaspore (PMO 162.628/19); (b) near-polar section of a megaspore (PMO 162.628/19); (c) enlargement of a megaspore wall showing distal ornament (PMO 162.628/19); (d) polar section of a megaspore with the interior penetrated by organic detritus and spherical fungal reproductive structures (NRM S038420-28); (e) polar section of a megaspore (PMO 162.628/19); (f) section through a crushed megaspore (NRM S038420-56); (j) bulbous ornament on a megaspore fragment (NRM S038420-28). (f)–(h) Sections through herbaceous lycophyte axes: (f) transverse section of an axis with stellate vasculature (NRM S038420-9); (g) crushed stele (NRM S038420-60); (h) longitudinal sections of xylem tracheids showing scalariform pitting and rare vertical struts connecting horizontal thickenings (NRM S038420-60); (k)–(r) Lycophyte microspores (*Aratrisporites sp.*): (k) polar view of a microspore (NRM S038420-33); (l) cluster of microspores embedded in organic detritus (NRM S038420-33); (m) polar view of a microspore (NRM S038420-28); (n) near-polar view of a microspore with laesurae extending to the margin (NRM S038420-42); (o) polar section of a microspore showing a cavate architecture (NRM S038420-32); (p) near-polar view of a microspore (NRM S038420-41); (q) polar section of a microspore showing a cavate architecture (NRM S038420-42); (r) polar view of a microspore (NRM S038420-33).

Scale bars: 100 μm for (a), (b), (d)–(f), (h)–(j); 50 μm for (c); 20 μm for (g), (m), (n); 10 μm for (k), (l), (o)–(r).
The associated microspores are attributable to *Aratrisporites* Leschik emend Playford & Dettmann, 1965, which is known from several lycophyte strobili of pleuromeian or isoetalean affinity (Balme 1995 and references therein). They are particularly similar to *Aratrisporites scabratus* Klaus, 1960 recorded from the upper DGF on Hopen by Vigran et al. (2014). Given the abundance of this morphotype in the peat and in associated strata (Vigran et al. 2014), it probably represents the microspore affiliate of the megaspores described above.

**Ferns**

*Sporangium.* A single dispersed sporangium (Fig. 2i) was identified in the peat matrix. It consists of a portion of the annulus with large rectangular cells 50 μm long and 20 μm wide, with walls 2 μm thick.

**Spores.** At least two dispersed spore morphotypes are recognizable in the peat matrix but neither is well preserved. The first is represented by a single granulate, acavate spore (Fig. 4a, b) measuring 21 × 15 μm, apparently preserved in oblique orientation with respect to the section such that the laesurae are not evident. Grana, <1 μm in diameter, densely cover the entire surface. The second morphotype has a rounded-triangular amb in polar view. It is 35 μm in diameter, trilete, with gaping laesurae extending to the equator. The sculpture is ill defined but appears scabrate or weakly granulate (Fig. 4e, f).

**Remarks.** The prominent annulus indicates that the dispersed sporangium derives from a

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**Fig. 4.** Fern and conifer/pteridosperm remains from the Norian permineralized peat of Hopen: (a) & (b) granulate fern spore in surface and marginal focus (NRM S038420-34); (c) bisaccate pollen in transverse section (NRM S038420-41); (d) portion of bisaccate pollen with a reticulate wing structure (NRM S038420-33); (e) & (f) scabrate trilete spore (NRM S038420-34); (g) section through bisaccate pollen showing hollow sacci (NRM S038420-35); (h) bisaccate pollen (NRM S038420-35); (i) section through bisaccate pollen showing hollow sacci (NRM S038420-41); (j) portion of bisaccate pollen with dense corpus and reticulate wing structure (NRM S038420-33). Scale bars: 10 μm for (a), (b); 20 μm for (c)–(j).
leptosporangiate fern but its affinities cannot be resolved further. Granulate acavate spores are produced by a wide range of ferns and bryophytes (Balme 1995). The single small granulate spore identified in the peat has a morphology reminiscent of *Trachysporites fuscus* Nilsson from the Hettangian of northern Europe (Larsson 2009). The larger scabrate spore is similar to *Baculatisporites comauensis* (Cookson) Potonié figured by Larsson (2009), which has possible osmundaceous affinities (Raine et al. 2011), and to *Conbaculatisporites hopensis* Bjaerke & Manum, 1977 recorded from the upper DGF on Hopen (Vigran et al. 2014).

**Bennettitales**

*Roots and stems.* Small (0.65–1.10 mm diameter) axes are very common within the peat (Fig. 5s, t). Selling (1944) originally assigned these organs to *Protojuniperoxyylon arcticum* and inferred a cupressacean (coniferous) affinity. Strullu-Derrien et al. (2012) re-analysed this material and illustrated the axial anatomy in detail. They concluded that the axes, preserving only primary tissues, represent distal bennettitalean rootlets based on their tracheid pitting characters together with other anatomical features. These authors also recognized fragments of larger, branched, axes containing up to 3 years of secondary growth (Fig. 5m) that were interpreted as more mature roots and fragments of subaerial axes of bennettitalean within the peat matrix.

*Leaves.* Very sparse foliar remains occur within the peat. One specimen cut in oblique section bears at least seven vascular strands about 220 μm apart, positioned equidistant from the lamina surfaces (Fig. 5l). The abaxial and adaxial mesophyll layers are of roughly equal thickness and consist of spongy parenchyma (i.e. no obvious palisade layer is developed). The epidermis is not well preserved on either side of the leaf. Details of the vasculature are indistinct. Another section reveals two narrow (1.5–1.8 μm wide, 270–460 μm thick) leaf or pinnule transverse sections (Fig. 5o). The vasculature is indistinct and the mesophyll consists of unspecialized parenchyma. A degraded 27 μm-thick epidermis is evident on these leaves. The leaf margins are arched or slightly enrolled.

*Seed.* A single distorted structure isolated in the peat matrix has a distinctive wall architecture. This organ is 4 mm long and 540 μm in maximum width at its base, but it is strongly deformed such that its original dimensions are uncertain (Fig. 5n). Its outer wall is 81 μm thick and is transparent, having lost any cellular anatomy. The inner side of this layer is bounded by an opaque band up to 27 μm thick, which encloses an inner zone of mostly crushed brown organic material. Robust and thick-walled cells occur at the base of the organ and reach maximum dimensions of 55 × 215 μm.

**Reproductive or vegetative buds.** Several circular to elliptical structures within the peat consist of tightly bound overlapping bract-like structures (Fig. 5p–r). These structures reach 0.7–1.35 mm in maximum diameter. Each bract-like component is 37–62 μm thick in its mid-region and has tapered margins. In some cases, the bracts are so tightly interlocked that they become indistinguishable (Fig. 5r). Few structural details are evident within the bracts apart from the presence of thinly layered cells. Most examples of these elliptical structures are surrounded by dense, thick-walled periderm and poorly preserved fibrous tissues (Fig. 5r), but a few occur isolated within the peat matrix (Fig. 5p).

*Pollen.* Laevigate monosulcate pollen grains are the most abundant sporomorphs in the peat matrix. They are commonly obscured by detritus, and are difficult to photograph with clarity (Fig. 5a–k). These pollen grains are 13–29 μm long and 7–14 μm wide, with acutely pointed to rounded termini and a sulcus that extends the length of the grain. Monosulcate pollen grains commonly occur in loose clusters within the peat matrix (Fig. 5k) but have not been identified within pollen sacs.

**Remarks.** The poor preservation provides few diagnostic features for confident identification of the leaves. The arched leaf margins are reminiscent of the downwardly curved margins of pinnules on small bennettitalean leaves assigned to *Otozamites*, *Ptilophyllum* or *Pterophyllum* species (Harris 1969; Douglas 1969). Similar-width, multi-veined *Pterophyllum* (bennettitalean) leaves were documented as impressions from Hopen by Pott (2014b).

The putative seed is very poorly preserved but is interpreted to have a broad chalazal end bearing a pad of thick-walled cells similar to many seeds described from the late Palaeozoic and early Mesozoic (Taylor & Taylor 1987; Yao et al. 1997). The bulk of the brown internal matter may represent crushed gametophytic or embryonic tissues. Bennettitalean seeds are typically of similar length to this organ and are narrowly tubular or vasiform (Sharma 1977; Nishida 1994), making them vulnerable to distortion with compaction.

The bud-like structures are superficially similar to tightly bound pinnule masses, such as those evident in the fern *Cycnopterus patagoniensis* Vera, 2010. However, vascular strands are not distinct and the laminar structures are more tightly bound in the Hopen specimens. They are here interpreted to represent vegetative bud apices or immature (unexpanded) bennettitalean reproductive structures. The tightly bound laminar components are interpreted to represent unexpanded leaves or a combination...
Fig. 5. Bennettitalean remains from the Norian permineralized peat of Hopen: (a)–(j) isolated monosulcate pollen (*Cycadopites* sp. (NRM S038420-42, -35, -34, -34, -60, -33, -35, -35, -42, -34)); (k) cluster of *Cycadopites* sp. in the peat matrix (NRM S038420-41); (l) transverse section of a leaf with regularly spaced central vascular bundles (NRM S038420-56); (m) transverse section of a portion of an axis with several years of secondary xylem development (NRM S038420-38); (n) longitudinal section of a deformed seed (NRM S038420-56); (o) transverse section of two degraded leaves (NRM S038420-56); (p) bud-like structure of enrolled bracts (NRM S038420-57); (q) enlargement of bract cross-sections in a bud-like structure (NRM S038420-57); (r) spirally arranged bracts in degraded bud-like structure (NRM S038420-28); (s) transverse section of root with initial secondary tissue development (NRM S038420-28); (t) transverse section of ultimate rootlet with well-preserved primary tissue anatomy (NRM S038420-42). Scale bars: 10 μm for (a)–(k), 100 μm for (p), (q); 1 mm for (l)–(o), (r)–(t).
of sterile protective bracts (outer zone) and possibly incompletely developed microsporophylls (inner zone). If these are reproductive structures and were bisexual (as are at least some williamsoniacean fertile organs: Pott 2014a), then they are at a very early stage of development because no ovule-bearing receptacle is evident in the central region. Delevoryas (1960) illustrated apparently more developed cycadeoid ‘cone buds’ with clearly separated bracts, rhombic in cross-section, but also lacking the central ovuliferous dome. The monosulcate pollen falls within the circumscription of Cycadopites Wodehouse, 1933, although some published examples of Chasmatosporites species are also similar (Larsson 2009; Vigran et al. 2014). Such monosulcate grains from the Mesozoic were produced by Cycadales, Bennettitales, Ginkgoales and Pentoxylales (although the last of these is typically a Gondwanan group: Balme 1995). Given that the only gymnospermous macrofossils identified in the peat are attributed to Bennettitales, these relatively common pollen grains probably belong to that group, and are certainly similar to examples illustrated by Wieland (1899), Zavialova et al. (2009) and Osborn & Taylor (2010) recovered from reproductive organs of that clade. However, ginkgoalean leaves are also known from adpression floras of the host formation, so derivation of the pollen from this group cannot be excluded entirely.

**Conifers or ‘pteridosperms’**

**Pollen.** Several haploxy lonoid to slightly diploxy lonoid bisaccate pollen grains, 49–68 μm wide and with a darkened non-tenui tate corpus 36–40 μm long (Fig. 4g, i, j), are preserved in the Hopen block. Sections transecting the grains show the sacci to be arched distally (Fig. 4c), hollow (Fig. 4c, g, i) and with a reticulate ornament (Fig. 4d, j).

**Remarks.** Potential parent plants of the bisaccate pollen include voltzi alean and pinalean conifers, Peltaspermales, Caytoniales and even Corysto spermales (Balme 1995). The size, ornament and shape of the grains fall within the defined ranges of several northern European Triassic pollen morpho species, such as Pinuspollenites minimus (Couper) Kemp, 1970 and Alisporites radi alis (Leschik) Lund, 1977 but insufficient diagnostic characters are available to permit definite identification.

**Bacterial activity, fungi and unknown organisms**

**Bacterial activity**

**Description.** Scattered throughout the peat matrix, in parenchymal cells, in tracheids, in mega spore lumens and bordering roots, are dark spherical glo bules and granules (Fig. 6a–d). Some appear to be embedded in mucilaginous residues or what were originally gelatinous decay products (Fig. 6a). Globules and granules are 3–60 μm in diameter and are usually rimmed by a contractional halo (0.5–10 μm thick). Where globules and granules occur within the root parenchyma or ray cells, they occur in isolation or in loose aggregations (Fig. 6c, d). Some root parenchyma cells are locally deformed around such bodies (Fig. 6d). The smallest granular bodies (3–6 μm diameter) commonly occur in dense aggregations (Fig. 6c). All such bodies are essentially structureless.

**Remarks.** The identity of the globules and granules is unclear. They appear to be organic structures based on their colour and intimate association with cellular tissues. They are typically distributed within areas of decayed matrix detritus and degraded plant cell walls, where bacterial cells may have acted as nucleation sites for mineral precipitation. These opaque bodies with pale rims may also represent simply organic gels that were entrapped during the silicification process, and contracted slightly with solidification/desiccation producing clear shrinkage halos. In living plants, mucilage produced by root cells forms a gel upon root contact with the soil. This mucilage consists of diffusible material, and facilitates interactions between the plant and soil; it commonly contains cell debris and bacteria (Uren 1993). The globule/granule-containing mucilage masses may represent the fossilized remnants of such exudates. Similar haloed opaque globules in ray parenchyma of wood were interpreted by Taylor et al. (2009, fig. 3.86) as resinous exudates representing a plant response to fungal colonization but, in the Hopen sample, such features are also widely dispersed in the detrital peat matrix, suggesting a link to general bacterial degradation.

**Fungi**

**Description.** Two types of fungal structures are evident in the root cells. The first type is represented by large globose structures (70–75 μm in diameter) attached to tiny filaments (2.5 μm in diameter), which occur in some parenchymatous root cells (Fig. 6e, f). Other similar bodies are not linked to filaments (Fig. 6g). The second type is represented by elongate structures attached to broad (0.35 μm diameter) filaments that are aseptate and branch dichotomously in some cases (Fig. 6h, i). The reproductive structures have a tubular base, 12 μm long; a septate junction is evident at the contact with the filament. It is difficult to ascertain the precise location of these structures with respect to plant tissues because they were found disarticulated. However, they appear to develop on the surface rather than within the root parenchyma cells (Fig. 6i).
Remarks. These microfossils probably represent fungal reproductive structures. We interpret the first type to be endobiotic fungal sporangia attached to rhizoids and resting sporangia. These features are similar to the reproductive structures produced by chytrids, a group of fungi that produces flagellate zoospores (Webster & Weber 2007), and to putative root-colonizing Blastocladiomycota from the Rhyne chert (Strullu-Derrien et al. 2015).

Chytridiomycetes are considered to be basal (plesiomorphic) among the fungi. They are the only phylum of true fungi that reproduces via motile spores. The most prominent morphological feature of the chytrid body, or thallus, is the sporangium, which produces zoospores. Zoosporangia are thin-walled, whereas resting spores, which may germinate to produce a sporangium after a dormant period, are thick-walled structures (James et al. 2006). Originally grouped within the Chytridiomycota, recent molecular phylogenetic studies have segregated Blastocladiomycota and Neocallimastigomycota as separate major basal clades of flagellate fungi (James et al. 2006; Hibbett et al. 2007). Blastocladiomycota include more complex organisms that develop a branched thallus where several sporangia are formed (Webster & Weber 2007). Some root cells in the Hopen material contain large endobiotic sporangia attached to rhizoids (Fig. 6e, f). A few spherical bodies are devoid of rhizoids and probably represent resting sporangia (Fig. 6g). The association of fungal tissues in these cells may represent a monocentric endobiotic thallus. These structures resemble those produced by some modern fungi, such as Olpidium. Olpidium, previously linked to Chytridiomycota, is a genus in which the phylogenetic position is poorly constrained. Sekimoto et al. (2011) provided strong support for Olpidium as the closest living flagellated relative of the terrestrial fungi. Several chytrids described from the Rhyne chert are morphologically similar to modern members of the Olpidiaceae and Spizellomycetaceae (Taylor et al. 2015).

The second fungal type may represent sporangia derived from a sporothallus. Although the fossil remains are fragmentary, they resemble features evident in the sporothallus of the fossil Palaeoblastoclusia milleri (Remy et al. 1994; Taylor et al. 1994) and in extant Microallomyces dendroides (Emerson & Robertson 1974) assigned, respectively, to Paleoblastocladiomycota and Blastocladiomycota.

Modern Chytridiomycota represent a large and diverse group that is essentially cosmopolitan and common to many ecosystems, occurring in soil and water. They function as important primary biodegraders and are probably vital to nutrient recycling in their respective ecosystems. Others parasitize insects, nematodes, fungi, algae and plants (Barr 1990; Powell 1993). The chytrid fossil record extends back to examples from the Early Devonian Rhyne chert (Strullu-Derrien et al. 2015; Taylor et al. 2015). Several chytrid fossils have also been found in Carboniferous deposits (see references in Taylor et al. 2015) and there are some records from younger strata (e.g. Daugherty 1941; Bradley 1967; García-Massini et al. 2012). The new discoveries add to the sparse fossil record of chytrid fungi and are significant in revealing their infestation of bennettitalean roots. We favour a saprophytic status for the observed colonizations.

Hyphae and other filaments

Description. Four forms of filaments are readily distinguishable in the peat. The first form consists of small (1–3 μm wide), essentially structureless, ramifying or shredded filaments with surface encrustations that occur both within cells and, less commonly, within the peat matrix (Fig. 7d).

The second form is represented by filaments (<2 μm wide), sporadically branching once, which invade the parenchymatous cells of the roots (Fig. 7f). Filaments typically radiate inwards from the plant cell walls and taper distally. They represent localized colonization: commonly only an isolated cell within a tissue is invaded by these filaments.

The third form consists of stellate arrays of unbranched filaments (1–3 μm wide) radiating from a central opaque mass (Fig. 7g). The filaments are straight and structureless or slightly beaded.

The fourth form consists of irregularly branched filaments (2–5 μm wide), locally forming thick- enings but otherwise featureless (Fig. 7h). They typically occur as irregular filamentous networks within plant cells.

Remarks. The first form may represent hyphae showing encrustation, similar to features described by Gadd (2007). Free-living and symbiotic
fungi play an important role in modern soils through precipitation of secondary minerals, and through nucleation and deposition of crystalline material on and within cell walls, notably oxalates and carbonates (Gadd 2007 and references herein). This is possibly the case for these filaments found in the Hopen material.

Fossils similar to the second form were described by Taylor et al. (2012) as Cashhickia acuminata, a fungus colonizing the calamite root Astromyelon, and consisting of asceptate, branched hyphae with acuminate tips that appear to enter the host from the exterior and initially extend through the apoplast of the cortical cells. Although some specimens display an extensive intracellular presence of the fungus, with almost all of the cortical cells affected, others show more localized infections in which only one or a few adjacent cells contain hyphae. The colonization is similarly localized in our material.

The dearth of diagnostic morphological features makes the third and fourth forms difficult to identify. The third form has basic similarities to stellate filaments in fungal taxa such as modern Asterosroma but, alternatively, it may have been generated by mineral precipitation. The fourth form, characterized by a filamentous network with localized thickenings may represent a fungal saprotroph.

Unknown microorganisms

Spinose structures

Description. These structures are elliptical or oblong in longitudinal section, most commonly 70–80 \( \mu \text{m} \) long, 35–40 \( \mu \text{m} \) wide, and occur within the matrix of the peat (Fig. 7a, b). The wall is thin (\(<2 \mu \text{m}\)), single layered and bears spines that branch several times in three dimensions (Fig. 7a) producing stellate tips in plan view. The spines are equi-spaced at 7–15 \( \mu \text{m} \) apart. Some specimens contain a circular body 25 \( \mu \text{m} \) in diameter (Fig. 7b). These spinose bodies possess a distinctive truncate base (20–25 \( \mu \text{m} \) large), which appears to be the site of an attachment.

Remarks. Spinose structures similar to those documented here were described by Williamson (1880) from British Carboniferous coal measures as Zygosporites (?) oblongus, which he interpreted as some form of land plant spore because some specimens appeared to be clustered within a sporangium. Williamson (1883) argued that the name Zygosporites was superfluous and suggested that the genus be deleted from the record (Taylor et al. 2015). The multi-furcate spinose ornamentation of the Hopen specimens closely resembles that of the oogonia of Combresomyces, a peronosporomycete (oomycete) widely dispersed in peat-forming communities from the Carboniferous to Triassic (Klings et al. 2007, 2011; Dotzler et al. 2008; Schwendemann et al. 2009; Strulu-Derrien et al. 2011; Slater et al. 2013). However, the Hopen specimens are more oblong compared to the globose form of most Combresomyces oogonia, the site of attachment is generally broader (although proportionally similar to that illustrated in at least some specimens of Galtierella biscalithecae from the Pennsylvanian of France: Klings et al. 2011, fig. 2i) and the cell wall is thinner in our specimens than is typical of established Combresomyces species. The specimens have not been found attached to hyphae; however, an intriguing feature is the common occurrence of an inner circular body, which has been interpreted as an oosphere or oospore in Combresomyces (Dotzler et al. 2008; Strulu-Derrien et al. 2011). If these structures are Peronosporomycetes oogonia, then they differ in architecture from any established forms and would represent a second Triassic record for that group (Schwendemann et al. 2009; Slater et al. 2013).

Some tardigrade eggs are superficially similar to these spinose bodies (see e.g. Macrobiotus furciger of Gibson et al. 2007) in size, and spinose ornament. However, water bear eggs are typically more spherical and have broadly conate appendages: the distal branches of those cones are simple, lacking the multiple furcations evident in the bodies described here.

Root galls or fungal sporocarps

Remarks. Strulu-Derrien et al. (2012, fig. 5K–M) illustrated gall-like structures within axis fragments preserved within the Hopen peat. These structures have multi-layered encasements composed...
of small, densely packed cells and have anatomies similar to the walls of a range of modern plant galls. No infecting organism was preserved within these structures, so a parasitic agent remains unknown. Modern gall-inducing organisms in plants include a broad range of arthropods, nematodes, fungi, bacteria and viruses (Mani 1964, 1992; Shorthouse et al. 2005). An alternative interpretation is that these thick-walled structures represent fungal sporocarps embedded within decaying plant tissues. Broadly similar, although generally smaller, fossil sporocarps have been identified by White & Taylor (1989, 1991) from Triassic permineralized peats of Antarctica.

Arthropod traces

Coprolites

Description. Two types of arthropod coprolites are recognized within the peat. The first form is spherical to ellipsoidal, with minor-axis diameters of 8–80 μm and major-axis diameters of 8–205 μm (Fig. 7c). They incorporate mainly fine unidentifiable detritus but, sporadically, also contain isolated small, spherical fungal or bryophyte spores (Fig. 7c). These coprolites occur either loose within the peat matrix or clustered within discrete cavities cut through roots or compacted detritus. The second coprolite morphotype is substantially larger (c. 1.35 mm in diameter) and roughly spherical (Fig. 7i), with a darkened rim and incorporating distinct angular fragments (up to 220 μm in diameter) of small-diameter xylem tissues (Fig. 7j). This form occurs only as isolated pellets within fine plant detritus of the peat matrix.

Remarks. The first coprolite morphotype is abundantly represented in the peat samples and was fully described by Strullu-Derrien et al. (2012). They attributed this type of coprolite to oribatid mites based on their shape, size, texture and occurrence in discrete elongate excavations within both bennettitalean tissues and compacted peat detritus. Given this distribution and the lack of reaction tissue in the roots, Strullu-Derrien et al. (2012) proposed a sapro-xyllophytic lifestyle for the Hopen oribatid mites. Such pellets are similar to coprolites widely illustrated from subaerial rootlets of bennettitaleans (Crepet 1974; Osborn & Taylor 2010), and the axes of a range of other plant groups from the late Palaeozoic and Mesozoic (Scott & Taylor 1983; Scott et al. 1985; Chalonier et al. 1991; Scott 1992; Zavada & Mentis 1992; Labandeira et al. 1997; Weaver et al. 1997; Kellogg & Taylor 2004; D’Rozario et al. 2011; Slater et al. 2012).

The producer of the second coprolite morphotype was obviously a larger invertebrate. The small-diameter xylem components within the coprolite may represent non-digestible vein tissues from leaves. We suggest that these coprolites derive from a folivore and were only incorporated sporadically within the peat without close association to any plant organ or other trace.

Discussion

Preservation

The preservational quality of plant remains within the peat is variable. Much of the matrix consists of finely macerated plant tissues and gel residues, in some cases degraded by fungal and bacterial action. Other components (e.g. some of the distal rootlets of bennettitaleans) show almost pristine cellular preservation and minimal compaction, probably because these roots are younger than the organic detritus through which they penetrated. Robust cells, particularly xylem tracheids, mucilage sacs and sclerenchyma, typically reveal fair to fine anatomical details with little compression. Most tissues are strongly stained by mineral or organic coatings and some lumens are infilled by opaque residues. Thin-walled parenchymatous tissues and epidermal cells tend to be more strongly degraded and, in some cases, moderately to heavily crushed.

The abundance of detrital organic material, saprotrophs and detritivore coprolites suggest that aerobic conditions existed at least episodically within the peat profile. Some woody remains show transitional phases of cellular degradation from the exterior to interior, suggesting a combination of saprotrophic and oxidative attrition of the peat mass. The main phase of organic matter degradation occurred before permineralization. Entombment by silica was then rapid, encasing even delicate parenchyma cell walls and fungal remains but not to the extent of preserving fragile membrane-bound organelles (e.g. Bomfleur et al. 2014).

Biotic diversity and phytogeography

The peat-forming community was apparently of low diversity. Gymnosperms are represented by abundant autochthonous roots, fragmentary wood, and sparse dispersed leaves, seeds and pollen of Bennettitales, together with very scarce bisaccate pollen of probable coniferous or pteridospermous affinity. Ferns and bryophytes are represented by sparse sporangia and dispersed spores. Herbaceous lycophytes are represented by rare diminutive axes, moderate concentrations of dispersed cavate microspores and scattered megaspores. Saprotrophs and detritivores are evident in the peat body either as cryptic body fossils (fungal hyphae and reproductive structures) or traces (putative galls,
coprolites and excavated chambers within plant tissues).

The Svalbard archipelago flora, situated at around 55–65° N in the Late Triassic (Scotese 1997; Feist-Burkhardt et al. 2008), is the northernmost expression of the Euramerican flora at that time and falls within the 'Greenland–Japan belt' of the 'European–Sinian palaeofloral area' of Dobruskina (1994). The floras of Skåne (southern Sweden) and Scoresby Sound (Greenland), preserved at approximately 40–45° N palaeolatitude, were prime representatives of this floristic belt based on their shared occurrence of Dipteridaceae, Czekanowskiales and Ginkgoales. However, these two regions share such a broad range of distinctive taxa and richness in Bennettitales (Harris 1932b; Pott & McLoughlin 2009) that they appear to constitute a distinct North Atlantic subprovince, at least during the Rhaetian (Pott & McLoughlin 2011). The Hopen permineralized flora may represent a slightly higher latitude, specialized ecological expression of that subprovince’s flora in the Late Triassic. The Swedish and Greenlandic deposits contain a much more diverse range of gymnosperm, fern, sphenophyte and lycophyte families (Harris 1932a, b; Lundblad 1950) than the permineralized flora of Hopen (Strullu-Derrien et al. 2012; this study).

However, the adhesion floras from Hopen (Pott 2014b) indicate a moderate array of marratiacean, dipteridacean, matoniacean and osmundaceous ferns, equisetaleans, Peltaspermales, Ptilozamites, Bennettitales, Caytoniales, and Ginkgoales. This diversity probably reflects contributions from a broader array of habitats within the floodplain community. Vigran et al. (2014) recorded at least 40 spore–pollen taxa from the DGF on Hopen, including a range of bisaccate gymnosperm pollen, polylicate, striate, asaccate and monosaccate pollen, tri- and monolette spores, and sparse algal cysts. They noted a monotonous association of fern, equisetalean, bryophyte and lycophyte spores from the coal-bearing beds of this formation, suggesting that the mire-forming communities were of relatively low diversity.

No animal body fossils have been detected in the permineralized biota, adhesion assemblages or palynological suites from the DGF of Hopen. Beyond the coprolites and excavations identified in the permineralized peat, the only trace of animals are rare waxy cocoons (Dictyothylakos sp.) identified within palynological residues (Vigran et al. 2014). Waxy cocoons attributable to Dictyothylakos are common in flood-basin sediments of mesic environments globally from the Late Triassic onwards (Manum et al. 1991; Jansson et al. 2008) and attest not only to the existence of obligate parasitic leeches, but also the presence of larger animal hosts in the immediate environment.

Quantitative composition of the peat

Quantitative evaluation of the peat content involved recording constituents at precisely 0.5 mm intervals across the slides held in the collections of the Swedish Museum of Natural History. One thousand counts revealed that the greatest constituent of the peat is pith and cortex tissues of Bennettitalean axes (mainly roots). Pith and cortical parenchyma are difficult to differentiate in all cases and collectively constitute about 40% of the peat volume (Figs 8 & 9). Nearly 24% of the peat volume is represented by voids between plant material. True original porosity was substantially greater than 24% because intracellular voids (lumens) were counted as part of the host tissue. All voids are now filled by cryptocrystalline silica cement. Bennettitalean axial xylem (both primary and secondary) constitutes approximately 11% of the peat volume. A similar proportion is represented by unidentifiable plant detritus forming the peat matrix. Opaque resinous material, gels, bacterial globules and fungal remains collectively constitute just less 10% of the peat volume (Fig. 9). Coprolites, leaf tissues and other remnants make up less than 5% of the peat mass.

Vegetation stature

The plant community contributing to the peat appears to have been an almost monospecific stand of Bennettitales. Most of the axes are no more than a few millimetres in diameter and are consistent with previous interpretations of a small (shrub-like) stature for williamsoniaceous bennettitaleans. Williamsoniaceae, which had slender, profusely branching stems (Nathorst 1902; Pott 2014a; Pott & McLoughlin 2014), are dominant in some of the geographically closest Late Triassic coal-forming floras to Hopen: that is, those of southern Sweden (Lundblad 1950; Pott & McLoughlin 2009) and Greenland (Harris 1932a, b). The architecture of this family contrasts with that of the other major clade of Bennettitales, Cycadeoideaceae, which had stocky cycad-like stems (Delevoryas 1971).

The occurrence of bisaccate pollen in the peat, together with the associated adhesion fossil assemblage documented by Pott (2014b), attest to the regional presence of sphenophytes, ferns, caytonialeans, putative peltaspermalean, conifers and ginkgoophytes. Many of the gymnospermous components may have grown on sites away from the immediate vicinity of deposition. Sparse bryophytes, ferns and diminutive heterosporous lycophytes probably occupied the understorey of the mire vegetation. Since none of the dominant components in the plant assemblage has a growth habit greater than shrub-size, we interpret the parent vegetation to have constituted a low-diversity, low-stature, more...
community that hosted a range of saprotrophs and detritivores within the peat substrate.

The dominance of bennettitalean roots is consistent with this deposit being classified as a fibric (fine root-dominated) peat (Wüst et al. 2003). The low-diversity flora, high levels of fine organic detritus, high initial porosity, a significant representation of saprotrophs and abundant arthropod detritivore traces suggest that the peat profile was at least periodically exposed to aerobic conditions. Low-diversity peats in modern microthermal climates that are depleted in siliciclastic grains commonly develop in nutrient-deficient, rainwater-fed mires (Moore 1987, 1989, 1995; Cameron et al. 1989) but, based on the small sample size, accumulation in other types of mire settings (e.g. eutrophic–mesotrophic mires) cannot be excluded.

Peat trophic levels

Integration of the fossil biota, biotic interactions, taphonomic characters and inorganic constituents of permineralized peats enables reconstruction of the palaeoecology of ancient mire ecosystems (Slater et al. 2015). The Hopen peat preserves a very specialized community low in plant diversity with few trophic levels (Fig. 10). Only five major autotrophic groups are identified in the peat flora: upper storey conifers or pteridosperms; mid-storey bennettitales; and lower storey bryophytes, lycophytes and ferns. The dispersed leaf and sporomorph...
assemblages identified from the DGF by Pott (2014b) and Vigran et al. (2014) indicate a substantially more diverse hinterland vegetation containing, in particular, a richer representation of sphenophytes, ferns and gymnosperms.

Herbivores (folivores) may be represented by sparse millimetre-sized coprolites that appear to incorporate leaf debris. Sapro-xylophagous detritivores are represented only by their traces (excavations and coprolites) but most probably included oribatid mites. Although invertebrate eggs, cocoons, carapace fragments and even whole exoskeletons are commonly recovered from palynological sampling of modern peats (van Geel 1978, 2001), exhaustive examination of the Hopen thin sections failed to yield evidence of invertebrate herbivore (first-level heterotroph) or carnivore (second-level heterotroph) invertebrate body fossils within the Triassic peat profile. The putative plant galls documented by Strullu-Derrien et al. (2012) cannot be attributed confidently to any agent but, if correctly interpreted, they add an additional parasitic trophic level to the peat community. Alternatively, these structures may represent fungal sporocarps.

The only other evidence for terrestrial animals in the local biota is of leeches (Dictyothylakos sp.: Vigran et al. 2014), which by inference means that larger animal hosts of these obligate parasites existed in the local environment. Animals as large as several-metre-tall theropods are known from the regional northern European Late Triassic on the basis of trackways (Vajda et al. 2013).

Fungal remains (hyphae and reproductive structures) are intimately associated with plant tissues, finely degraded plant detritus and arthropod coprolites. Although many fungal remains in the Hopen peat are unidentifiable, some have features typical of chytrids, and these are significant in revealing their infestation of bennettitalean parenchymatous root cells, most probably as saprotrophs as there is no evidence of plant-cell reaction.

Filaments resembling Cashhickia acuminata (Taylor et al., 2012) in the Hopen material lack any obvious host response. The only response identified by Taylor et al. (2015) of cortical cell walls of the calamite root Astromyelon infected by Cashhickia was the presence of a delicate sheath of new wall (?) material around some hyphae. This suggests an endophytic or parasitic role for this fungus. Despite their morphological similarities,
the role of the Hopen filaments remains ambiguous; they may even represent filamentous inorganic precipitates formed as part of the fossilization process.

Other fungal remains, fungi-like structures and bacteria are generally associated with dead tissues and finely degraded plant detritus. Many of the plant cells infected by such microorganisms show no evidence of response to the invasion. Consequently, fungal/bacterial penetration and growth may have occurred entirely in dead plant tissues (saprotrophy).

A few spherical fungal bodies occur within individual coprolites (Fig. 7c). We found no extensive hyphal masses within or surrounding these coprolites, thus we infer that these fungi were consumed (mycophagy) by the predominantly detritivorous mites.

Such a low-complexity food web (Fig. 10) may be characteristic of the particular microenvironment of deposition – a locally wet, temperate, root mat. However, taphonomic factors (e.g. preferential degradation of chitinous tissues) and the small size of the studied sample may also have contributed to the apparent low biotic diversity.

Silicification

The source of the silica involved in permineralization of the peat remains uncertain. Numerous examples of silicified peat or in situ plants are known from diverse localities of various ages around the world. Silicification in those deposits tends to be associated with hydrothermal springs (e.g. the Rhynie Chert in the UK: Trewin 2003; and the San Agustín deposit in Argentina: Channing et al. 2007; Guido et al. 2010) or the release of silica from the decay of volcanic glass and unstable silicates in volcanlastic sediments (e.g. the Permian Homevale and Sydney Basin peats of eastern Australia: Gould & Delevoryas 1977; Pigg & McLoughlin 1997; the Permian Skaar and Collinson ridge peats of the Transantarctic Mountains: Taylor et al. 1989; McManus et al. 2002; the Eocene Princeton Chert of British Columbia: Basinger & Rothwell 1977; and the Upper Pennsylvanian Grand-Croix chert from France: Galtier 2008; Strullu-Derrien et al. 2009). Other silicified peats have no obvious connection to hydrothermal springs or volcanicogenic sediments, and their silicification may relate to deep leaching of silica from adjacent felspar-rich crystalline rocks and strongly fluctuating groundwater levels (e.g. the silcrete/opaline-entombed floras of SW Australia: Wilde & Backhouse 1977; McLoughlin & Hill 1996), fluctuating lake or coastal lagoon pH levels (e.g. the Coorong Lagoon organic mats, South Australia: Peterson & Von Der Borch 1965; Yachi peat, Japan: Umeda 2003; Olorgesailie Basin rhizolith masses, Kenya: Owen et al. 2009; and the Permian Toploje Member peat of East Antarctica: McLoughlin & Drinnan 1997; Holdgate et al. 2005). The Hopen peat block, being recovered ex situ, cannot be placed in precise sedimentary context to evaluate the source of the silica. However, the upper part of the DGF reportedly hosts rhyolitic pyroclastic material (Chlebowksi & Wierzbowski 1983). The unit also contains widely dispersed silicified wood elsewhere in Svalbard (Smith et al. 1975), thus favouring a source of silica from the early breakdown of unstable volcanogenic silicate minerals and glass within the host formation.

Conclusions

The chert block from Hopen, Svalbard archipelago, collected by T. Iversen in 1929, contains a low-diversity, root-dominated, plant assemblage typical of a fibric peat. Gymnosperm, bryophyte, lycophyte and fern disseminules, together with abundant bennettitalean vegetative and reproductive remains, and sparse lycophyte axes constitute the bulk of the recognizable peat components and reflect a low-diversity parent vegetation. Variable degrees of plant tissue degradation, abundant detritivores and saprotrophs, and a high proportion of fine organic detritus in the matrix suggest a peat profile periodically exposed to oxidation and experiencing biological degradation. A dearth of charcoal suggests that fire was not a frequent factor in the environment. Although abundant in lower-latitude floras of the time, this study confirms that bennettitaleans were important contributors to high middle-latitude (55–65° N) peat-forming communities of the European Late Triassic and were not necessarily diagnostic of mega- to mesothermal climates like the superficially similar but unrelated modern cycads.

Excavations and coprolites reveal that root tissues and surrounding fine detrital peat matrix were heavily attacked by detritivorous arthropods – most probably oribatid mites. Many of the fossil fungi and fungi-like organisms (hyphae and reproductive structures) lack features sufficiently distinctive to allow strict taxonomic assignment, an exception being our recognition of chytrids within bennettitalean root parenchyma. Gall-like structures in plant root tissues described by Strullu-Derrien et al. (2012) suggest the presence of parasitic organisms but may, alternatively, represent fungal sporocarps.

The low-diversity flora, scarcity of large woody components, presence of aerobic fungi and arthropod traces, and moderate degradation of the peat matrix suggest that the peat developed from vegetation of low stature (shrub size). This, together with the dearth of siliclastic grains, suggests that the peat developed away from clastic sediment sources.
and was of low nutrient status. The peat is dominated by fine roots but many of these well-preserved organs may have penetrated the organic mass at a late stage of peat accumulation. This specialized microenvironment, together with the probable differential preservation of tissues under rather low-pH conditions, probably accounts for the few trophic levels and low-complexity food web represented in the permineralized peat.

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References


Flood, B., Nagy, J. & Wisnes, T. S. 1971. The Triassic Succession on Barentsøya, Edgeøya and Hopen (Svalbard). Norsk Polarinstitt Meddelelser, **100**.


Iversen, T. 1941. *Ishavøya Hopen*. Fiskeridirektoratets skrifter, Serie Havundersøkelser, **6**.


from the upper Viséan (Carboniferous) of central France. Comptes Rendus Palevol, 6, 431–436.
Labandeira, C. C. 2006b. Silurian to Triassic plant and hexapod clades and their associations: new data, a review, and interpretations. Arthropod Systematics and Phylogeny, 64, 53–94.


permineralised peat biota of the Prince Charles Mountains, Antarctica. Gondwana Research, 27, 1474–1486.


