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Reconstructing the Lower Devonian (Lochkovian) vegetation from the Anglo-Welsh Basin: Two spore masses containing *Emphanisporites* McGregor spores

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ABSTRACT

In situ spores have gone some way towards harmonising the prominent disparity between the Early Devonian dispersed spore and megafossil records, greatly advancing but often challenging our understanding of early vegetation. Here, we investigate an elongate and a discoidal spore mass, yielding *Emphanisporites epicautus* Richardson and Lister and *Emphanisporites* sp. respectively from the early (not earliest) Lochkovian (Lower *micrornatus-newportensis* spore assemblage biozone) of the Ross-Tewkesbury Spur (M50) motorway section in the Anglo-Welsh Basin, UK. We explore their morphology and spore wall ultrastructure using SEM and TEM. A paucity of useful phylogenetic characters precludes formal identification or description of the parent plants but a relationship to the rhyniophytes is hypothesised. A dearth of vascular tissues, however, necessitates their placement amongst the rhyniophytoids. Both the sporangial morphology and spore wall ultrastructure differs between the specimens, distancing them from each other and from other *Emphanisporites* species. While similarities exist, no unequivocal relationships with contemporaneous or extant taxa, or indeed lineages, can be made using sporangial morphology or spore wall architecture. These differences lend further support to deliberations that the 'emphanoid' condition was a consequence of convergent evolution. Using the dispersed spore record we explore the paleoecology of the plants, which points towards them being minor components of the vegetation, restricted to areas away from river catchment. This interpretation is redolent of the middle Lochkovian cf. *Horneophyton* sp. (*E.* cf. *micrornatus* parent plant) from North Brown Clee Hill, but that plant may have been restricted to a more specialised niche. What characterised the niches of these plants is uncertain, but they may have been ephemerally water stressed, perhaps hinting at a moisture sensing function for the 'emphanoid' spore structure.

1. Introduction

Over the last 80 years a considerable amount of research has shed light on the late Silurian - Lower Devonian vegetation of the Anglo-Welsh Basin (e.g. Richardson and Lister, 1969; Wellman et al., 2000; Edwards and Richardson, 2004; Edwards et al., 2014, 2021a, b; Morris et al., 2011a, b, 2012a, b). Essentially, research points towards a major floral turnover near the Siluro-Devonian boundary, in which primitive cryptospore-bearing plants gave way to apparently rapidly diversifying tracheophytes and their immediate progenitors via an adaptive radiation and later competitive replacement amongst the latter group (Wellman et al., 2000; Edwards and Richardson, 2004; Edwards and Morris, 2014).

Palynomorph assemblages from the basin are particularly well preserved and provide a nearly ubiquitous insight into floral diversity and development through time. The excellent preservation and diversity of dispersed spores mean they have been used to construct regionally and internationally important spore assemblage biozones (e.g. Richardson, 1974; Richardson and McGregor, 1986; Richardson, 1996a), although these remain problematic in the late Silurian and Earliest Devonian of the basin (Edwards and Richardson, 2004). In contrast to the spore record, the plant macrofossil record, whilst informative and diverse (e.g. Morris et al., 2011a), provides less insight in terms of taxonomic richness, mainly due to preservational bias. Caveats also exist in the dispersed spore record, however, principally when attempting to relate dispersed spores to parent plants.

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Minute, charcoalified sporangia and spore masses have been instrumental for reconciling the macrofossil and dispersed spore records. These often provide information for which, individually, neither can offer (e.g. Fanning et al., 1988; Fanning et al., 1990; Fanning et al., 1991a, b; Edwards et al., 1999; Morris et al., 2012b; Edwards et al., 2014), although they are far from a panacea (e.g. Morris et al., 2018). The sporangia and spore masses contain *in situ* spores often comparable to dispersed spore species, and extensive work demonstrates that a given sporangium or spore mass contains a single, or complex of, spore species (e.g. Wellman, 1999; Morris et al., 2012a, b; Edwards et al., 2014). Thus, they are useful for: (1) demonstrating a biological link between the dispersed and macrofossil records, often allowing reconstruction of vegetation using dispersed spores without macrofossils (although complications exist, e.g. Wellman et al., 1998b); (2) understanding aspects of anatomy and physiology of the plants, and; (3) adding morphological characters which aid investigations into the wider phylogenetic affinities of the plant and associated dispersed spore species (Morris et al., 2018).

One prominent trilete spore genus in late Silurian and Early Devonian assemblages is *Emphanisporites* McGregor. This diverse genus, characterised by proximal, 'spoke-like' interadial ('emphanoid') muri, reaches peak diversity in the Early Devonian. The genus is used extensively in biostratigraphy but despite being widely reported, is consistently rare in assemblages, typically comprising <6% of palynofloras (Edwards and Richardson, 2000). The phylogenetic affinities of *Emphanisporites* have been explored through ultrastructural analysis of dispersed specimens (Taylor et al., 2011), and other workers have reported a limited number of species *in situ* from the Pragian Rhynie Chert (Wellman et al., 2004) and middle *micrornatus-newportensis* (MN) spore biozone of the Anglo-Welsh Basin (Edwards and Richardson, 2000; Morris et al., 2012b) (Fig. 1). Understanding of affinities and phylogenetic relationships remains clouded, however, with studies pointing to at least two separate lineages producing the *Emphanisporites* genus (Taylor et al., 2011; Morris et al., 2012b), leading workers to posit that the structural, emphanoid features characterising the genus is probably a result of convergent evolution.

Here, we present *in situ Emphanisporites epicautus* Richardson and Lister and *E.* sp. from the lower MN spore biozone (early, but not earliest, Lochkovian) of the Ross-Tewkesbury Spur (M50) motorway section in the Anglo-Welsh Basin. We use SEM and TEM to investigate the morphology and ultrastructure of the specimens and deliberate their affinities and wider phylogenetic relationships. We also explore spore wall development in these *Emphanisporites* species and use the dispersed spore record to deliberate on the palaeoecology of the parent plants.

2. Geological setting

The mesofossils were isolated from a fine beige siltstone, collected by D. Edwards in 1986 from the Freshwater West formation (*sensu* Barclay et al., 2015), 2 m above the Chapel Point Limestone member, just south-west of Junction 3 on the northern side of the Ross–Tewkesbury Spur (M50) motorway (near the 29.5-furlong marker post, fig. 2, Allen and Dineley, 1976) (Fig. 2). The lower Freshwater West formation was deposited in a seasonally semi-arid, terrestrial-fluvial setting by variously meandering perennial and ephemeral sandy streams and rivers (e.g. Allen and Dineley, 1976; Morris et al., 2012c).

Analysis of the dispersed spore assemblage from the sample identified *Streelispora newportensis* Richardson and Lister, *Emphanisporites* cf. *micrornatus* Richardson and Lister and *Chelinospora vermiculata* Chaloner and Streel, alongside an absence of *E. micrornatus* Richardson and Lister. This assemblage is indicative of the lower *micrornatus-newportensis* subzone, with *E. micrornatus* proper not appearing until the middle subzone of the MN biozone. The location of the assemblage in the lower MN subzone indicates an early, but not earliest, Lochkovian age (Early Devonian) for the specimens described herein (Fig. 1).

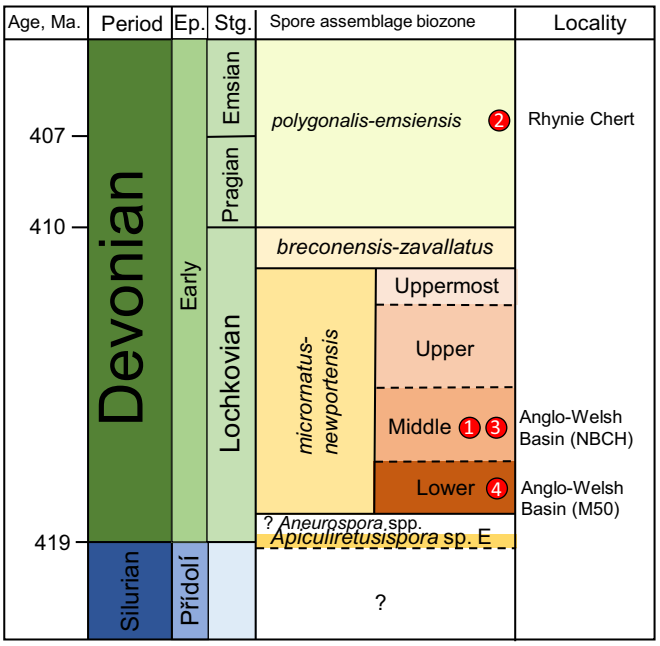

Fig. 1. Stratigraphy and spore assemblage biozones of the upper Silurian and Lower Devonian of Great Britain from which specimens containing *in situ Emphanisporites* spores have been described – numeration is in order of publication. **(1)** cf. *Horneophyton* sp. and numerous fragmentary *Salopella*-esque sporangia in Edwards and Richardson, 2000 **(2)**; *Horneophyton lignieri* in Wellman et al., 2004; **(3)** Discoidal spore mass in Morris et al., 2012b; **(4)** Elongate? and discoidal spore masses, this study. Figure modified from Edwards and Richardson (2000). Age constraints from GSA Geologic timescale v. 5.0 (2018). Constraints on stratigraphic positions of *in situ Emphanisporites*: (1) Edwards and Richardson (2000); (2) Wellman et al., 2004 (approximate); (3) Morris et al. (2012b); (4) Edwards et al. (1994), Allen and Dineley (1976).

In terms of other Anglo-Welsh Basin mesofossil localities, the lower MN subzone placement means that the M50 assemblage predates the North Brown Clee Hill (NBCH) locality (middle MN subzone, Lochkovian) (e.g. Morris et al., 2012a, b; Edwards et al., 2014) (Fig. 1) but is younger than the Ludford Lane locality (*tripapillatus-spicula* biozone, earliest Přidólí)(Jeram et al., 1990; Edwards, 1996).

3. Material and methods

3.1. Bulk maceration

100 g of 15–50 mm sized fragments from sample 19M50-26 were selected for bulk maceration. The samples were not ground down or otherwise processed before bulk acid maceration. 200 ml of concentrated hydrochloric acid (HCl) was added to the samples, which were then left for five days, allowing time for carbonate digestion. The HCl-sample mixture was then diluted with water seven times. The diluted mixture was then poured off as far as possible, waiting twenty-four hours between individual dilutions to allow settling. 100 ml of 40% concentrated hydrofluoric acid (HF) was then added to digest silicates that were adhering to the mesofossils and left for two days. The HF solution was then diluted eight times with water, again leaving twenty-four hours between each dilution to allow for settling. The diluted solution was then sieved through an 80 μm nylon mesh. Organic matter >80 μm was collected for picking.

3.2. SEM

Mesofossils were picked from macerated material using a single-bristled paintbrush under a Vickers dissection microscope and individually mounted on SEM stubs with mounted graphite discs. Samples

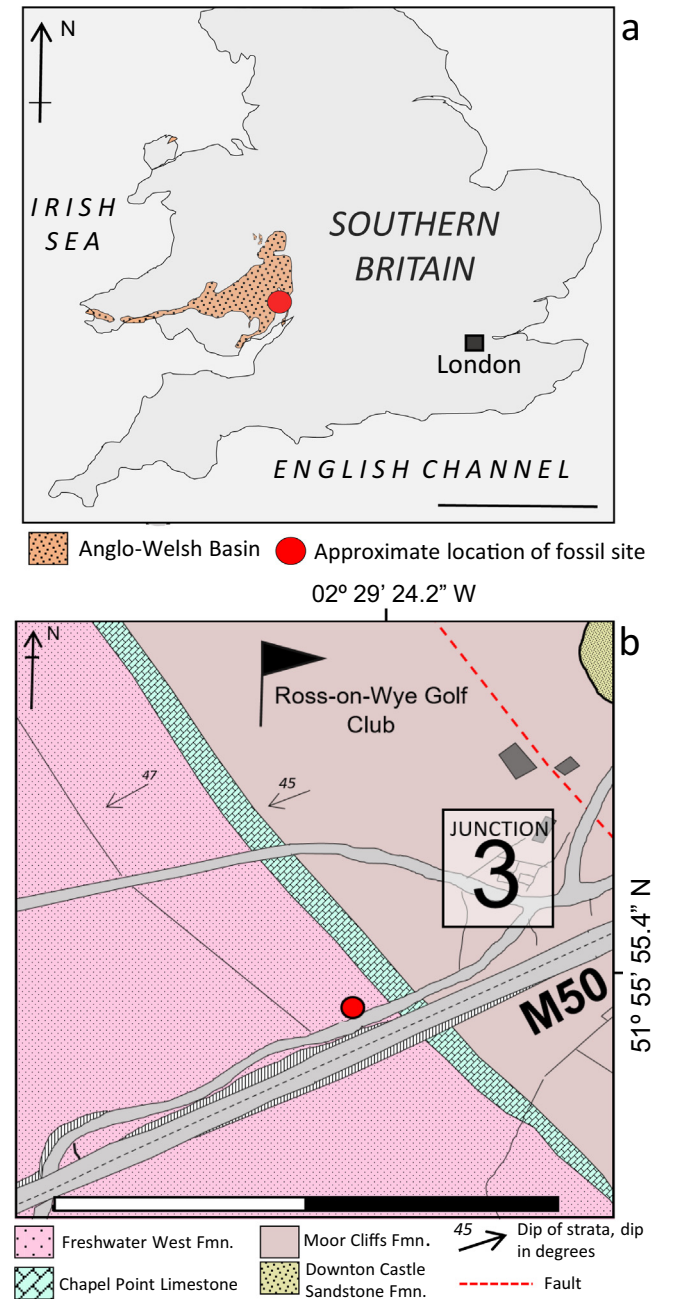

Fig. 2. a: Extent of the Anglo-Welsh Basin in South Wales and the Welsh Borderlands, scale bar 200 km. b: Geological map of the Ross-Tewkesbury Spur M50 motorway. Red circle indicates approximate site of mesofossil horizon. Scale bar: 500 m. Map based on Ordnance Survey and British Geological Survey Data, modified from Digimap ®. British National Grid projection lines.

were then covered and left to dry. Following drying, samples were gold coated using an Edwards S105B sputter coater for three minutes, prior to imaging with a Tescan Vega-3 Scanning Electron Microscope at 15–20 KV. Following initial examination and photography, samples were recoated with gold for a further three minutes to reduce any charge and rephotographed where necessary.

3.3. TEM

Once examined under SEM, a fragment (approximately half) of each spore mass was prised from the carbon tab using a steel razor blade and placed in a solution of pure ethanol. Samples were then sent to the University of Wisconsin Eau-Claire for TEM analysis by WAT. The spore masses were not oxidised or stained prior to imaging. The specimens were sectioned using a diamond knife before imaging with a JEOL-2010 Transmission Electron Microscope.

3.4. Curation

All SEM stubs and 19M50-26 sample and light microscope slides are housed at the Centre for Palynology at the University of Sheffield, Western Bank, Sheffield, S10 2TN, UK. All other light microscope slides are housed in the Micropalaeontology Unit at the Natural History Museum, London, SW7 5BD, UK. All TEM blocks and sections are curated in the Department of Biology of the University of Wisconsin-Eau Claire, Eau-Claire, WI, 53706, USA.

4. Results

Two specimens bearing *in situ Emphanisporites* spores were recovered (Table 1) alongside abundant spore masses, sterile axes and other 'phytodebris'. Both show varying degrees of completeness and different morphologies (Fig. 3). No sporangial cell walls or subtending axes have been observed in either of the specimens, but some acellular material is preserved. The occurrence of single or closely similar spore types, the absence of interspersed cuticular sheets, plant debris or tubes and the morphology of the specimens indicates that they are not coprolites. Sporangia and spore masses differ as the former exhibit enclosing sporangial wall layers, and while both specimens exhibit some remnants of an acellular wall layer, we refer to them here as spore masses given their largely incomplete nature. Both of the specimens were examined under SEM and then TEM. Light microscopy was attempted, but this was unsuccessful for both specimens. Whilst fragmentary, no saprotrophic encrustations or other evidence of decay, such as tubules, were observed.

4.1. Specimen ABM5015-001: Emphanisporites epicautus Richardson and Lister in an elongate spore mass (Plate I, a–d)

4.1.1. SEM observations

4.1.1.1. Spore mass. A large, incomplete spore mass appearing to be elongated, possibly originally being cylindrical (Plate I). A distinctive 'lump' is developed on one edge and the specimen appears to bend slightly to one side, away from the 'lump' (Plate I, fig. a, arrow). No subtending axis or sporangial wall cells are preserved. The mass is compressed and flattened with little three-dimensional shape retained. The spore mass has a total length of 1540 μm and is 725 μm at its widest point. A small amount of acellular material adheres to the specimen, but no sporangial wall cells are preserved which leaves numerous *in situ* spores readily observable. A small amount of amorphous material adheres to some of the spore mass and *in situ* spores and appears to form an intersporal matrix.

4.1.1.2. In situ spores. The spores are relatively well preserved with limited damage, despite the fragmentary and compressed nature of the spore mass. Some pitting, folding and pyrite growth is present, alongside common extraneous material which is present across most of the spores – this material does not obscure spore structure, however. This extraneous material is angular to approximately spherical in habit, up to 1 μm wide. Spores have circular ambs, 26 μm to 38 μm (10 measured), mean size 33 μm. Proximally, the spores exhibit an emphanoid ornament of 8–12 very fine interadial muri, typically 0.7 μm wide, in each interadial area. The trilete mark has lips but is relatively indistinct and there is an apical thickening. The triradiate mark extends approximately 2/3rds of the spore radius before diverging into fine curvaturae perfectae which are not greatly invaginated at the radial points. Distally

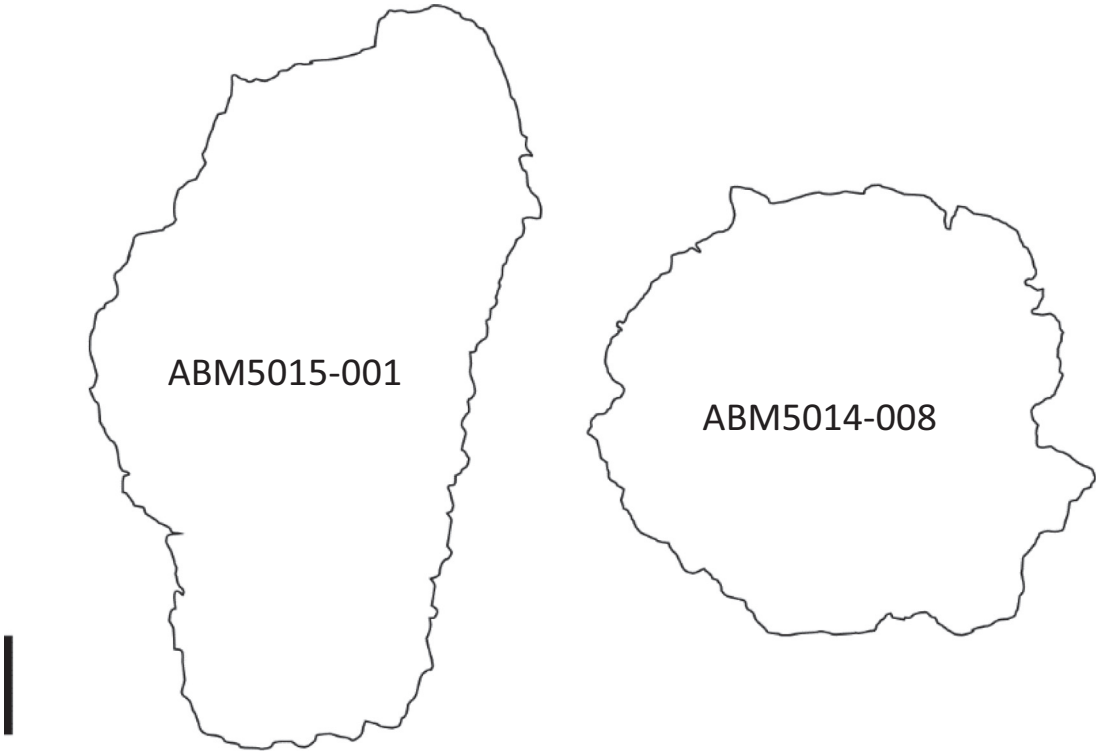

Fig. 3. Outlines of the spore masses described in this paper(Table 1). Scale bar 200 μm.

and equatorially the spores are laevigate. *In situ* spores show some variation in the apical thickening and interadial muri.

4.1.1.3. Comparisons with the megafossil and dispersed spore record. The incomplete nature of this spore mass makes it difficult to relate it to a megafossil genus, given the absence of complete morphology and key anatomical features. The gross shape may suggest the sporangium was elongate, perhaps cylindrical, in life, rather than discoidal or reniform, but the shape may result from fortuitous breakage. Elongate sporangia are common in compressed megafossils, variously seen in *Salopella*, *Tortilicaulis* (Edwards et al., 1994) and other unnamed compressed mesofossils (e.g. Morris et al., 2011a). The spore mass does not appear to have been bivalved, there is no indication of tapering and the presence of *Emphanisporites* species rather than *Apiculiretusispora* species precludes assignment to *Salopella*. Similarly, *inter alia*, the rounded tips and tapering apices of *Tortilicaulis* are not observed, precluding assignment to that genus. The lump on one side of the spore mass may suggest that the sporangium was bifurcating in life, perhaps reminiscent of *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah sporangia, or cf. *Horneophyton* sp., although this is tenuous; perhaps less speculatively it is a result of breakage. Ultimately, the lack of specimens and morphological characters exhibited on the spore mass precludes us from making a formal description or placement of the spore mass.

The size range and mean size of spores, character and number of interadial muri, excellent curvaturae perfectae and probable apical thickening on most of the in situ spores corresponds well with the description of *E. epicautus* Richardson and Lister. Those that differ (Plate I, fig. d) are reminiscent of *E.* cf. *epicautus sensu* Richardson and Lister, having the apical 'bald' region where interadial muri fail to reach the proximal pole, and a similar extent, number and robustness of the interadial muri and distinct curvaturae perfectae.

4.1.2. TEM observations

The specimen is heavily compressed and brittle, offering suboptimal preservation but examination of the ultrastructure remains possible. 'Chattering' occurs across the spore wall (vertical lines across entirety of specimen), which is a methodological artefact derived from the specimen being brittle (described in Taylor, 2002). Fig. 4a illustrates the wall ultrastructure of an *E. epicautus* spore, as sectioned through the equator, Fig. 4b is a schematic diagram of the ultrastructure. The internal wall ultrastructure is entirely homogenous with no lamellae or differentiation of the exine. Because of the angle of sectioning of the spore, it is difficult to ascertain which is the proximal and distal hemisphere; regardless, both are similar in thickness of *c.* 1 μm. Compression makes the lumen unclear across much of the specimen, but a part is visible near the centre of the spore (Fig. 4b, arrow 2).

Table 1
Specimens described in this paper. Dimensions describe the widest and longest portions of the spore masses. * ten in situ spores measured: smallest (mean) largest; † estimated number of spores in each spore mass (nearest 100), calculated by (0.74 x Volume of spore mass($\pi r^2 h$)/ Volume of mean spores ($4\pi r^3/3$), assuming (1) spores are perfect spheres giving rhombohedral packing to give a porosity of 26%, and (2) that sporangia are cylindrical, following Wellman (1999).

Specimen	Description	In situ spore	Dimensions	Spore size*	*c.* Number of spores†
ABM5015-001	Elongate spore mass	*E. epicautus*	1540 × 725 μm	26 (33) 38	*c.* 6200
ABM5014-008	Discoidal spore mass	*E.* sp.	909 × 969 μm	28(32) 40	*c.* 5500

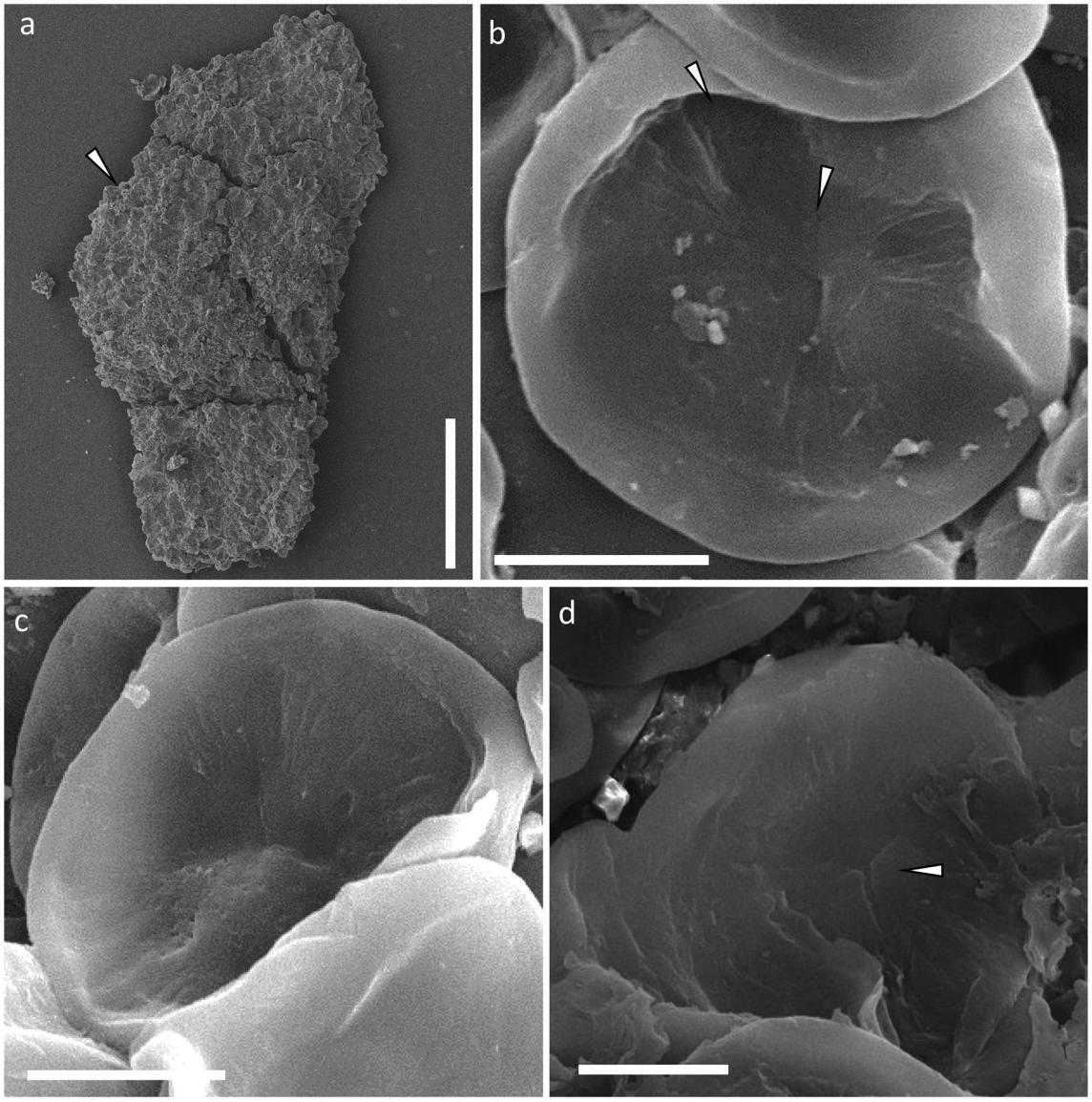

Plate I. SEM micrographs of spore mass yielding *in situ Emphanisporites epicautus*, ABM5015-001. **A**: Spore mass. Note apparently elongate slightly bent structure with distinctive 'lump' about the middle-upper margin (arrow), scale bar: 500 μm. **b:** *In situ E. epicautus*, note the apical thickening and thickened Y ray terminations (arrows). Consider also the well-defined curvaturae perfectae, fine inter-radial muri and concave proximal face. This specimen also shows the rare cubic to spherical excess mineralisation; **c:** Subcircular *E. epicautus*, note again the thickening at the proximal pole and fine interadial muri; **d:** an *in situ* spore redolent of *E.* cf. *epicautus*, exhibiting the much larger apical thickening (apical 'bald patch', arrow) on the proximal face and slightly coarser interadial muri relative to *E. epicautus* proper; this specimen also shows the amorphous material found across the spore mass adhering to the spore. Scale bars 10 μm.

4.2. Specimen ABM5014-008: Emphanisporites sp. in a discoidal spore mass (Plate II, a–g)

4.2.1. SEM observations

4.2.1.1. Spore mass. Approximately discoidal in plan, it is compressed but retains some three-dimensional shape. The spore mass has a length of *c.* 909 μm and a width of *c.*969 μm. The gross morphology of the spore mass is visible, although some cracking is observed and portions have been cleaved off. The edges of the mass are damaged, and no subtending axis is present. Limiting material is present across some areas of the spore mass but is largely lost. This material is acellular, variously adherent and largely unstructured aside from small, randomly orientated folds. Areas without limiting material expose numerous in situ spores. No evidence of saprotrophy is observed.

4.2.1.2. In situ spores. The spores are reasonably well preserved although folding, pitting and proximal face loss affect them. Apparent extraneous material is present and variously coats the spores, although never significantly so. Spores have a subtriangular to circular amb, 27–38 μm, mean 32 μm (nine measured). The proximal face is distinctly concave, and interadial areas are ornamented by 8–10 robust, straight, tapering interadial muri which are 2 μm at their widest point at the inner crassitude. Muri become more distinct towards the equator and show some tapering towards the proximal pole, petering out before they reach it. A thickening is present, extending approximately ¼ of the length of the triradiate mark at the proximal apex. The triradiate mark is distinct, accompanied by well developed, tall lips up to 2 μm wide which rise above the interadial muri. Rays extend ⅔ to ¾ of the radius of the spore before reaching the inner crassitude. The robust equatorial region is 3–4 μm wide and is sometimes laevigate but chiefly exhibits small

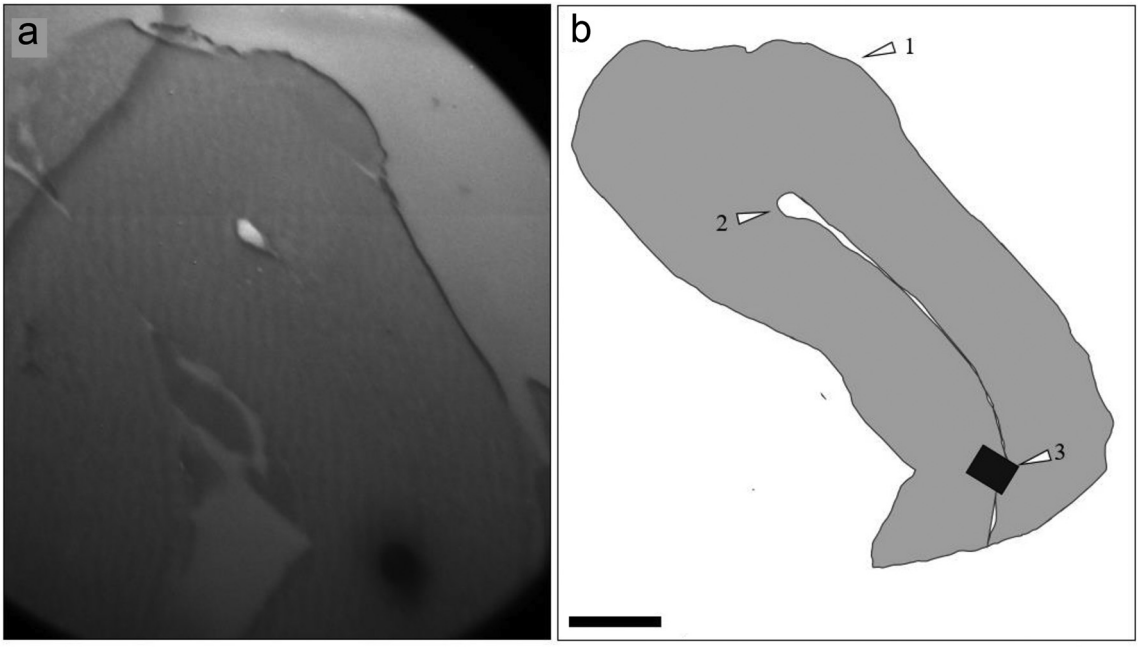

Fig. 4. TEM micrograph showing the ultrastructure of in situ *Emphanisporites epicautus*. Note the 'chattering' occurring as vertical lines across the specimen. The black line along the 'top' margin of the specimen is remnant gold coating from SEM analysis. **b**: schematic of *E. epicautus* ultrastructure. Note homogenous wall. **1:**?Equator; **2:** spore lumen; **3**: Pyrite grain.

folds and 'hummocks'. The distal exine is robust with an irregular 'hummocky' sculpture (Plate II, d–f). Given the irregularity and failure to identify comparative features in the dispersed record, this may be a result of decay rather than sculpture, but this is not certain.

4.2.1.3. Comparisons with the megafossil and dispersed record. Spheroidal sporangia and spore masses are common in the compressed record and the latter have already yielded *in situ Emphanisporites* spores (Morris et al., 2011b). The discoidal spore mass may be comparable to various *Cooksonia*, *Paracooksonia* or *Lenticulitheca* species (e.g. Edwards, 1979; Edwards et al., 2014; Morris et al., 2011b); however, in all instances *in situ* spores from these plants (where known) differ from the *E.* sp. described here, with the former two yielding crassitate, apiculate trilete spores of the *Aneurospora-Streelispora* complex (e.g. Morris et al., 2011b) and the latter yielding cryptospore species belonging to *Cymbohilates* (Morris et al., 2011b). The difference between *in situ* spores and the unclear nature of the subtending axis and overall anatomy distances this specimen from those genera mentioned above. The *in situ Emphanisporites* spores in the discoidal sporangium described in Morris et al. (2012b) differ from this specimen, with the former being comparable to *E.* sp. A *sensu* Richardson and Lister. In terms of gross morphology the two spore masses are quite similar, being discoidal with a roughly circular outline although ABM5014-008 is slightly more oblate. Both exhibit an acellular, cracked surface which may represent remnants of the sporangial wall or a cuticular layer (Morris et al., 2012b). If the morphology reflects the sporangial shape, it is plausible that, if these spore masses were found as megafossils, they would be classified as the same morphospecies. Because of a lack of specimens and morphological characters, we do not formally describe this *Emphanisporites* yielding spore mass.

The *Emphanisporites* species from ABM5014-008 does not appear to have a direct published counterpart in the palynological record, and *in situ* and dispersed spore size comparisons are complicated by shrinkage of the former during burning. Of similar dispersed species, the *in situ* spores have some similarities with *Emphanisporites rotatus* McGregor and *Emphanisporites neglectus* Vigran, although significantly differs from both in terms robustness of the spore and the nature of the distal hemisphere. Neither *E. neglectus* nor *E. rotatus*, or indeed any other published *Emphanisporites* species, fully satisfies the features exhibited by this *Emphanisporites* species. Given the robust nature of the equatorial and distal exine this spore might be considered patinate. TEM analysis, however, (below) indicates that the spore wall is not considerably thicker than other *Emphanisporites* spores (Taylor et al., 2011) and is distinctly thinner than other sectioned patinate spores (*Cymbosporites echinautus* in Johnson and Taylor, 2005).

Analysis of the dispersed spore assemblage from 19M50-26 did not yield comparable spores and attempts to extract *in situ* spores from the spore mass to observe under light microscope failed. A single example of a reasonably comparable *Emphanisporites* sp. spore was identified from the dispersed record of the M50 (Plate II, g). This spore exhibits a roundly subtriangular amb (29 μm), robust equator, distinct triradiate mark accompanied by narrow lips extending to the inner edge of the equator and interadial areas populated by *c.* 10 robust, tapering interadial muri which do not reach the proximal apex; although an apical thickening may be present it is not certain. Equatorially and distally, the spore is sculptured with angular micro-?verrucae. This differs from the distal hemisphere on *in situ E.* sp., which appears more chaotic. Interestingly, this spore was identified from the pre-MN?Earliest Lochkovian *Apiculiretusispora* sp. E spore biozone (−35.3 m relative to the Chapel Point limestone).

4.2.2. TEM observations

A partial montage exhibiting *c.* 60% of the spore and schematic are illustrated in Fig. 5. The specimen has been heavily compressed and folded but ultrastructural architecture remains. Part of the distal and possibly proximal wall is partially obscured by a fold in the plastic (black region along the lower right of the spore, Fig. 5). Proximally, the spore wall thickness is *c.* 0.7 μm. The proximal face is folded, but the aperture may be exhibited (Fig. 5, arrow IV); no variation in spore wall architecture is observed about this region. The distal spore wall is up to 1.5 μm thick. It appears to be divisible into two parts: (1) an inner, possibly faintly lamellate layer up to 0.5 μm thick, with a (2) wider, faintly spongy surface layer comprised of a series of knobs, which are variously connected to the laminate layer, up to 1 μm thick.

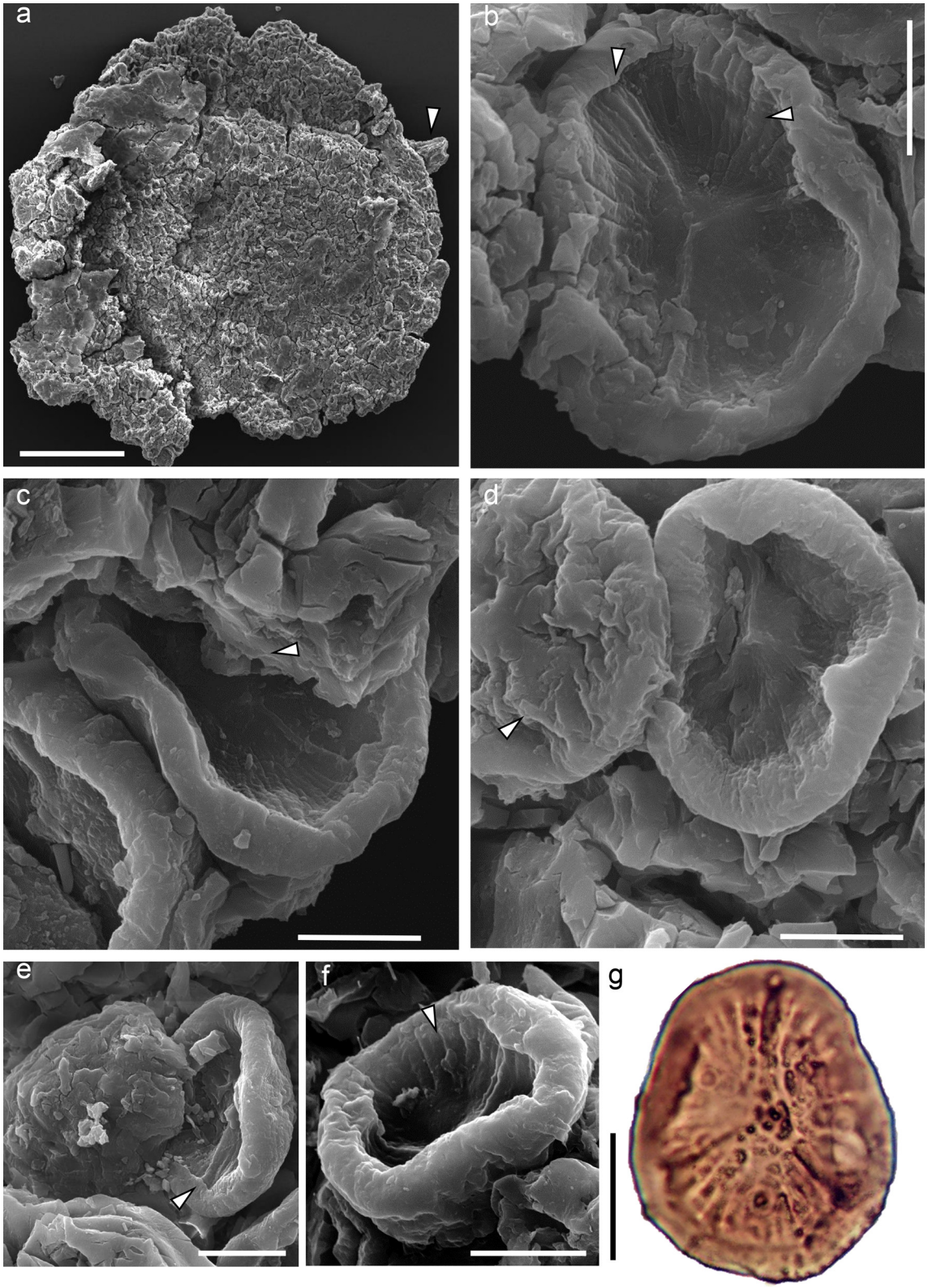

Plate II. SEM micrographs of the discoidalspore mass yielding *in situ Emphanisporites* sp., ABM5014-008. A: Spore mass. Note discoidal morphology with fractured outer edge: arrow indicates a section of the sporangium which has been fortuitously preserved; this is not a subtending axis, scale bar: 200 μm. b: *in situ* spore, proximal face. Arrows indicate robust inter-radial muri and distinctive lips. Note the robust equator and the distinctive apical thickening. c: Proximal face, note the concave habit and apical thickening (arrow) d: Proximal and distal hemispheres: note the chaotic, hummocky nature of the distal hemisphere. This may be compounded by shrinkage of the spore. Note also the highly robust equator of the specimen on the right. e: Proximal and distal view, note again the irregular nature of the distal hemisphere. f: Tipped spore, note how the distal 'sculpture' continues to a lesser extent onto the equator; b – f scale bars 10 μm. g: Light micrograph of the most comparable *Emphanisporites* sp. identified in the dispersed spore record, from the *Apiculiretusispora* sp. E biozone, Moor Cliffs formation. Note the robust tapering muri which are lost towards the proximal apex, the robust equator, and distal?sculpture. Ross-Tewkesbury Spur (M50) motorway section, slide M50-85-2C-1, E.F. no. U11. Scale bar 10 μm.

These are populated by occasional lacunae, which sometimes mark the separation between the layers. The distal sculpture is exhibited in cross section, having the same architecture as the homogenous outer layer, suggesting that this is a sculptural, rather than a decay, feature. No interadial muri are identified in the section.

4.3. Dispersed Emphanisporites species in sample 19M5026

A major analysis of the Siluro - Devonian dispersed spore record from the Lower 'Old Red Sandstone' of the basin building on Richardson and colleagues' work (e.g. Richardson, 1996, 2007; Wellman et al., 2000; Morris et al., 2011a; Richardson and Lister, 1969) is being carried out by ACB. The dispersed spores recovered from this sample are extremely well preserved with low thermal maturity. Some mild pyritisation and/or decay occurs in some specimens, but this is minimal. In quantitative counts of 250 spores the diverse assemblage briefly comprises species of *Aneurospora* (12%), *Ambitisporites* (26%) and *Laevolancis* (16%), with accessory ornamented hilate cryptospores including *Cymbohilates* (5%), cryptospore tetrads such as *Tetrahedraletes medinensis* (4%) and laevigate, apiculate and murornate crassitate and patinate trilete spore species of *Streelispora* (6%) and *Archaeozonotriletes* (9%), amongst others. Five species of *Emphanisporites* were identified in these samples with the spores comprising 2% of the overall assemblage or 114 *Emphanisporites* spores per gram of rock processed. Individual species of *Emphanisporites* all occur in low relative abundances and most are 'rare', that is, are identified during logging outside of spore counts.

5. Discussion

5.1. Spore mass maturity

The morphology of the ABM5015-001 *in situ* spores is comparable to the dispersed species *E. epicautus* and *E.* cf. *epicautus* which, on the assumption that spores are dispersed as individual monads at maturity suggests that the *in situ* spores must be close to maturity. The maturity

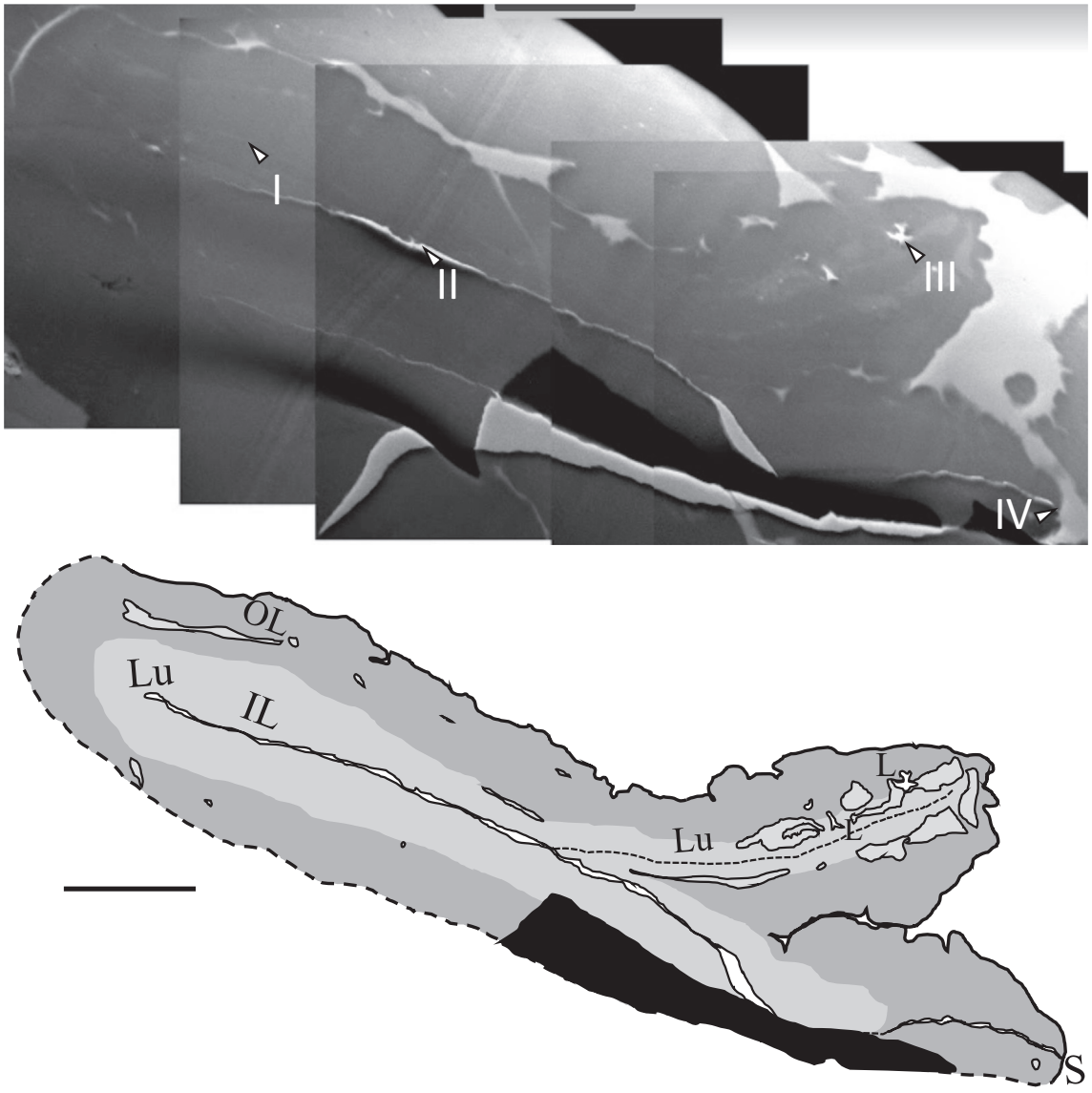

Fig. 5. (Top) TEM montage micrograph showing the ultrastructure of in situ *Emphanisporites* sp., with the spore outlined by black dashed lines. Arrow I:?inner lamellate layer; arrow II indicates part of the lumen. Note that due to folding, the lumen probably folds into the upper right extension of the wall but is not visible due to compression/ fusion; Arrow III: rare lacunae; Arrow IV indicates the suture. The black region along the bottom right of the spore is a fold in the plastic and is a preparative artefact. Scale bar 1 μm. Bottom: Schematic diagram showing the bilayered exine of *E.* sp. The dark layer is the homogenous outer layer, whilst the paler layer is the inner homogenous layer. OL: Outer layer, IL: inner layer, Lu: lumen, L: lacunae, S:suture. Scale bars 1 μm.

of the spores of *E.* sp. is less certain, as no unequivocal comparative dispersed species have been identified. Whilst this may be a function of the rarity of this *Emphanisporites* species, it may also suggest that the *in situ* spores had some morphological additions/ reductions to come in the latter stages of ontogeny. However, as with *E. epicautus*, no associated tetrads were found in the spore mass, indicating that the spores were mature or nearly so.

5.2. Comments on spore wall development

Detailed commentary of the spore wall development of *E. epicautus* is problematic given the homogenous architecture of the exine which obscures the original method of sporopollenin deposition. Most embryophytes utilise white line centred laminations (WLCL) to accumulate sporopollenin during sporogenesis (Wellman, 2004), so the lack of lamellations in the mature spore wall does not exclude their presence in initial stages of sporopollenin deposition; they may have been heavily compressed and subsequently obliterated or obscured by later deposition of sporopollenin. The apparent occurrence of *E. epicautus* and *E.* cf. *epicautus* in the same sporangium is evidence that they are both derived from the same plant, rather than a complex of similar plants as has been previously suggested (e.g. Edwards and Richardson, 2000). They could represent different developmental stages (with *E.* cf. *epicautus* perhaps representing some ontogenetic failure), or indicate some failure or disruption in sporopollenin deposition as the interadial muri were forming, or may be a result of some genetic disruption leading to malformation. The common occurrence of *E. epicautus* and *E.* cf. *epicautus* together in the dispersed record (see 5.4) may suggest that, if they are indeed derived from the same plant, that this malformation was either common or the production of spores with slightly different morphologies was a deliberate strategy of the plant. It is important to note that these dispersed species are not always contemporaneous, however (Higgs, 2004; Morris et al., 2011a).

The bilayered architecture of *E.* sp. spores suggest a different mode of development. The partially separated bilayered wall structure suggests that the lamellate and homogenous layer formed by different mechanisms, although the timing of formation is not certain. Given the faint laminations, the inner layer probably formed by WLCL, as lamellae were laid down on the spore plasma membrane, followed by sporopollenin accumulation on either side. Sporopollenin deposition may have been quite significant, largely obscuring the initially formed lamellae. Formation of the outer layer is less clear. A possible mechanism for the formation of the outer layer might be found in the extant moss *Andreaea*, where the spongy exospore develops via the accumulation of discrete globules of sporopollenin (Brown and Lemmon, 1984) secreted onto the sporocyte, an ontogenetic pathway peculiar to these plants. In this case, the lamellar layer would develop underneath the previously deposited layer, i.e. centripetally (Blackmore et al., 2000). Alternatively, it may have formed by the secretion of sporopollenin from a tapetum, such as in *Rhabdosporites langii* (Wellman, 2009), onto the lamellar layer, i.e. centrifugally. We cannot rule out either of these mechanisms, or other mechanisms of formation, but note that no evidence of a tapetum is observed in this specimen. The entire wall may have developed by WLCL, with lamellations in the 'outer' layer being obscured later on in ontogeny. Alternativley, given the highly folded nature of the spore wall, it may also be possible that intense folding lead to partial delamination of layers along weak horizons.

5.3. Affinities and phylogenetic considerations

5.3.1. Broad affinities

The wider coeval mega-, mesofossil and dispersed spore record indicates that in life these plants shared their environment with herbaceous, diminutive rhyniophytes, rhyniophytoids, primitive cryptospore-bearing plants and eophytes alongside larger zosterophylls, this being a plant community typical of the Early Lochkovian of the Anglo-Welsh Basin (e.g. Wellman et al., 2000; Edwards and Richardson, 2004; Morris et al., 2011a; Edwards et al., 2021a).

Of these, their production of trilete spores excludes them from the cryptospore producing eophytes and other primitive cryptospore-bearing plants. Likewise, a zosterophyll affinity can be excluded based on the shape of the spore mass and the fact that *Emphanisporites* species have not been identified *in situ* from zosterophyll sporangia (e.g. Edwards, 1969; Allen, 1980). We conclude that these *Emphanisporites* producers probably belong amongst the rhyniophytes. However, given the absence of vascular tissue we must refer to them as rhyniophytoids. It is possible that these plants closely resembled the rhyniophytic body plan, being diminutive with terminal sporangia - but features such as sporophytic branching or stomata are unknown. The rhyniophytoids comprise a particularly diverse complex of plants from a variety of lineages (Steemans et al., 2012), and thus it is interesting to explore how closely related to one another *E. epicautus* and *E.* sp. are. Due to a lack of morphological characters, this is largely unclear from SEM studies. The apparently different morphologies of the spore masses (and indeed, the *in situ* spores) indicate that the parent plants were at least generically distinct, but ultrastructural features of the *in situ* spores provide the firmest evidence that they were in fact derived from quite different taxa.

5.3.2. Comparisons with other Emphanisporites spp.

This is the first TEM study of *in situ Emphanisporites* spores, but comparisons can be made with three dispersed species from Gaspé Bay in Canada (*E. rotatus, E. schultzii* and *E. annulatus*: Taylor et al., 2011). Broadly, Taylor et al. (2011) found that *Emphanisporites* generally exhibit (1) a single layered exospore ranging from laminated to spongy in structure, and (2) proximal radial ribs that were compositionally confluent with the outer part of the exospore. Both *in situ Emphanisporites* spores described here differ significantly (Table 2).

It is possible that the ultrastructure of the spore walls was obliterated or altered during diagenesis, especially in the case of *E. epicautus*. However, the ultrastructure of *E.* sp. appears to be well preserved and, considering the two masses were recovered from within at most a few centimetres of each other, they are unlikely to have had different diagenetic histories. Similarly, both of the spore masses were exposed to the same treatment; HF + HCl maceration and were not oxidised or stained. There is a possibility that more subtle structures such as fine lamellations have not been identified because the spore masses were not stained. Whilst this remains possible even very subtle structures would be hinted at under the TEM (as they are in *E.* sp.). We conclude that the ultrastructure exhibited by these *in situ* spores is natural.

The most striking difference between *E. epicautus* and other *Emphanisporites* spore wall ultrastructures is the lack of lamellations in the exospore, a common feature amongst all but one *Emphanisporites* specimen (*E. rotatus* II) in Taylor et al. (2011).Those workers found that lamellations range from very subtle to distinctive across the examined *Emphanisporites* spores, leading them to suggest that the homogeneity of *E. rotatus* II may be derived from diagenetic or preparative influence, but note that all of the specimens again have similar diagenetic and preparative histories. Furthermore, the sectioning of the *E. epicautus* spore mass was not comprehensive across several specimens; it could be that this specimen simply exhibits no lamellations, whilst others of the same species do, or that they were largely obliterated during ontogeny and only remain in isolated sections of the spore, which were not seen under TEM (as hypothesised for *Chelinospora vermiculata*, Johnson and Taylor, 2005). Similarly at odds with the findings of Taylor et al. (2011) is the dearth of a spongy layer or larger lacunae in the exospore. Finally, the thickness of the spore wall is slightly less than in other *Emphanisporites* species. While differentiating the proximal and distal hemispheres is problematic, the areas towards the poles are no thicker than 0.7 μm, thickening to 1 μm at the equator. Ultimately, if the homogenous spore wall in *E. epicautus* is indeed natural, then (1) the ultrastructure distances it

from other species of *Emphanisporites*, including *E.* sp. and (2) there may be some relationship with *E. rotatus* II (Taylor et al., 2011) in terms of the mature wall ultrastructure, ontogenetic developmental pathways aside (discussed in 5.3.3).

Morris et al. (2012b) described a discoidal spore masses yielding *in situ Emphanisporites* sp. A *sensu* Richardson and Lister from the middle MN spore biozone NBCH site. While no TEM imaging of the spore wall of *E.* sp. A was carried out, it is of interest that they noted that the fractured surfaces of the spore walls were homogenous to faintly granular, hinting at a similarity between *E.* sp. A and *E. epicautus*.

Considering *E.* sp., initial congruence with most of the other *Emphanisporites* species is found with regard to the inner lamellate layer, setting the ultrastructure of *E.* sp. at odds with *E. epicautus*. The thickness of the spore wall is also comparable to other *Emphanisporites* specimens. On the other hand, a distinctive feature which sets *E.* sp. apart from the other *Emphanisporites* ultrastructures is the bilayered exine. The outer, semi-detachable surface layer appears to be peculiar to *E* sp. and is not seen in other species of *Emphanisporites*. It is worth noting, however, that some *Emphanisporites* species do exhibit some differentiation in the single layered exospore, such as *E. rotatus* I, but it is difficult to gauge how far this feature differs from the bilayering seen in *E. sp.*

5.3.3. Comparisons with contemporaneous fossil taxa

Many fossil spores exhibit some element of a homogenous wall in their ultrastructure but this is normally associated with other features such as lamellae (e.g. in *Scylaspora* sp., Wellman, 1999) or a combination of features (e.g. in *Cymbohilates horridus* var. *splendidus*, Edwards et al., 2012a). Mature spore walls that are fully homogeneous are less common and are mainly found in the spore walls of cryptospores such as *Tetrahedraletes medinensis* (variant #1; Taylor, 2002) but also in some trilete spores. Alongside the dispersed *E. rotatus* II spore, Pre-Silurian (lower Wenlock to lower Ludlow) *Ambitisporites* spores have homogenous walls (Taylor, 2003), but this could be diagenetic. Most interestingly, two spore masses from NBCH yielded emphanoid spores probably belonging to *Ibereospora* which exhibited entirely homogenous spore wall architecture (Morris et al., 2012b).

Given the similarities between the mature spore walls of *E. epicautus* and the above taxa, perhaps the homogenous spore wall is a homologous feature between them? The amount, composition and timing of sporopollenin deposition during ontogeny of the spore wall is probably under genetic control (Wellman, 2004) and an entirely homogenous wall is considered to be a derived condition, with the primitive condition being lamellate walls (Taylor et al., 2017):could the loss and/ or obliteration of lamellae during ontogeny have occurred in a common ancestor between these homogenously walled taxa? Cryptospore tetrads such as *T. medinensis* persist, and are contemporaneous, with *E. epicautus*, but they are probably representatives of more ancient (and cryptically diverse) lineages, some of which are possibly ancestral to more derived trilete spores. However, ultrastructural analysis on older and contemporaneous material is required to trace such lineages.

The question of a close relationship between these taxa not only depends on the nature of the mature spore wall, however, but the ontogenetic pathway by which the spore wall develops. Wellman (2004) notes that because of the variety of methods by which any given spore wall type can form, it is desirable to study the ontogenetic pathway. There is certainly more than one ontogenetic pathway that can lead to the formation of homogenous spore walls, including the obliteration of lamellations formed in the early stages of ontogeny by latterly deposited sporopollenin. Furthermore, given the nature of the wall it is particularly difficult to unpack the mode of formation, which is not necessarily comparable to extant processes. A focused study of fossil spores inside sporangia at different developmental stages could shed light on spore wall ontogeny, but this would be extremely difficult.

Considering the ultrastructure of *E.* sp., bilayered spore walls are common in late Silurian–Early Devonian spores (e.g. Edwards et al., 1995a, b; Wellman, 1999; Johnson and Taylor, 2005). *Ambitisporites–Synorisporites–Streelispora/Aneurospora* and *Scylaspora* all exhibit a bilayered exine. Some cryptospores, too, exhibit bilayered ultrastructure (e.g. *Laevolancis divellomedium* type 2 Wellman et al., 1998b). Interestingly, the combination of a bilayered exine and discoidal spore mass could ally *E.* sp. with the *Lenticulitheca–Paracooksonia–Cooksonia* complex (Morris et al., 2011b; Edwards et al., 2014). However, the presence of the separating outer layer in the ultrastructure of *E.* sp. sets it at odds with the spore wall architecture from the *in situ* spores in those plants, and the lack of key morphological characters exhibited by the *E.* sp. spore mass precludes assignment to any of the constituents of that complex, not to mention the differences in spore morphology. An inner lamellate layer with an outer homogenous layer has been identified in *in situ Scylaspora* (Wellman, 1999). However, *E.* sp. differs considerably due to the separation of the outer layer, and additionally, no lacunae are exhibited in *Scylaspora* spore walls. Indeed, few spore ultrastructures exhibit such a separation of layers. One example, however, is *Dyadospora murusattenuata* type I from the Ordovician (Taylor, 1997), which has varying degrees of separation between an inner lamellate

Table 2
Current data for *Emphanisporites* ultrastructure.

Species	Gross wall ultrastructure	Laminations?	Wall thickness (μm)	Reference
E. rotatus I*	• Inner: laminated • Outer: spongy with lacunae	Yes	4 P. & D.	Taylor et al., 2011
E. rotatus II*	• Homogenous	No	2 D. 1.5 P.	Taylor et al., 2011
E. rotatus III*	• Faint laminations • Inner wall has large lacunae	Yes	3 D. 2.5 P.	Taylor et al., 2011
E. rotatus IV*	• Faintly laminar	Yes	2.5 D. 1.5 P.	Taylor et al., 2011
E. rotatus V*	• Faintly laminar • ?Pseudosture • Thick laminar surface layer	Yes	1.5 P. & D.	Taylor et al., 2011
E. schultzii I*	• Distal wall laminated throughout • Spongy innermost exospore	Yes	5 D. 2 P.	Taylor et al., 2011
E. schultzii II*	• Distal wall laminated • Lacunae in proximal wall • Pseudosuture	Yes	3–4 P. & D.	Taylor et al., 2011
*E. annulatus**	• Inner laminations • Outer coarse sponginess	Yes	1–2.5 P. & D.	Taylor et al., 2011
E. epicautus† *E.* sp. †	• Homogenous • Inner laminations • Outer homogenous, partially detachable surface layer	No Yes	0.7 1.5	This paper This paper

layer and outer homogenous layer, but the spore wall ultrastructures are otherwise quite different. Considering this, a contemporaneous spore wall architecture to *E.* sp. is yet to be identified.

5.3.4. Affinities to extant taxa

A possible relationship between some *Emphanisporites* spores and hornworts was posited by Taylor et al. (2011), based on (1) ultrastructural features reminiscent of some characteristic features of extant hornworts, (2) the phylogeny of Qiu et al. (2006) which posited that hornworts were the sister group to tracheophytes, and (3) the occurrence of a columella, a characteristic feature of extant hornworts, in *H. lignieri*, the parent plant of *E. decoratus* (Wellman et al., 2004). Recent land-plant phylogenies by Puttick et al. (2018) and the recent placement of *Horneophyton lignieri* into the tracheophytes (Cascales-Miñana et al., 2019) cast some doubt on the hornwort – *Emphanisporites* association. Whilst hornwort placement remains equivocal in Puttick et al. (2018), the most significantly supported result was for hornworts as a sister group to the 'setaphyta' (mosses + liverworts) and being the most basal of the Bryophyta, distancing them from the tracheophytes. Puttick et al. (2018) suggest that the simplistic nature of the putative plesiomorphic liverwort body plan was in fact derived from a loss of ancestral characters, such as stomata, rather than simply an absence of derived embryophytic characters. Instead, the basal embryophyte may have had body plan more congruent with stem-tracheophytes than previously thought. The results of Puttick et al. (2018) may go some way towards explaining the hornwort associations of some of the *Emphanisporites* spores found by Taylor et al. (2011). Tentatively, the presence of characteristic features of extant hornworts in the ultrastructure of certain dispersed *Emphanisporites* spores (pseudosuture +/− external laminar layer) and some tracheophytic *Emphanisporites* producers (the columella in *H. lignieri*) are not indicative of hornwort association *per se* in these fossil plants and spores, but instead perhaps the retention of primitive features from some enigmatic, possibly relatively complex, basal embryophyte (Puttick et al., 2018) or may be a further example of evolutionary convergence amongst these plants.

Regarding the affinities of *E. epicautus*, the homogenous ultrastructure may indicate an association to Anthocerotopsida, where the mature trilete spores exhibit homogenous spore wall architectures (Brown and Lemmon, 1990). However, these plants also exhibit a number of key features including pseudoelaters, columellae and sequential spore maturation. Whilst the incomplete nature of the spore mass means we cannot rule these features out, their presence remains equivocal. In other hornworts, although little studied, the ultrastructure is highly diverse (Taylor, 2003) and, *inter alia*, some may exhibit a 'pseudosuture' and external laminar layers (e.g. Renzaglia et al., 2008) alongside often subdivided walls with two or more wall layers and an inner granular layer about the suture and sometimes beyond, as seen in the specimens in Taylor et al. (2011). The spore wall ultrastructure of *E. epicautus* exhibits none of these features (with granular features about the suture equivocal), undermining any strong associations with other members of the hornworts. Whilst some taxa outside of the hornworts do exhibit a homogenous ultrastructure, other features distance them from *E. epicautus*. Members of bryopsida often exhibit homogenous spore walls but are generally not trilete and also have an additional perine. In the case of leptosporangiate ferns which exhibit a homogenous exospore at maturity, an outer perispore is also observed which is not seen in *E. epicautus*. As such, there is little indication of a direct extant counterpart to *E. epicautus*. Additionally, the problem of comparative ontogenetic pathways persists.

In terms of *Emphanisporites* sp., several extant taxa have significant involvement of lamellae in some or all of their spore wall ultrastructure, including hepatics (Brown and Lemmon, 1990), Sphagnidae mosses, ferns and lycophytes. Liverworts typically exhibit lamellations in at least some part of the spore wall (Blackmore and Barnes, 1987), but spores derived from these plants lack trilete sutures and typically lack a homogenous outer layer or bilayering. In Sphagnidae mosses, an inner lamellate layer is overlain by a homogeneous outer layer, as in *E.* sp., but the former wall is highly derived, comprising five layers (Wellman, 2004). Lycopsids exhibit a laminar layer and an outer homogenous layer in the spore wall but they also exhibit a granular region (e.g. Lugardon, 1990) beneath the spore aperture, a feature not exhibited in *E.* sp., which is further distinguished from Lycopsids by the detachable surface layer. Extant, homosporous Filicopsida also exhibit an inner lamellate layer and an outer homogeneous layer (e.g. Tryon and Lugardon, 1991), but always exhibit a perine and the layers do not partially separate. Thus, no extant direct comparisons are yet known. Taylor et al. (2011) found that the ultrastructure of some *Emphanisporites* species exhibited lamellae and spongy areas reminiscent of extant lycophyte spores - offering tentative support for a basal-tracheophytic affinity of some species of *Emphanisporites*. Furthermore, the bilayered construction of the spore walls from taxa in the *Lenticulitheca-Paracooksonia-Cooksonia* complex was used to tentatively suggest the association of the complex to the stem-tracheophytes (Edwards et al., 2014), although as discussed, *E.* sp. is different to those spores. *E.* sp. does exhibit lamellae, but the outer spongy areas are not seen. Whilst the combination of an inner lamellate and outer homogenous layer might hint at a tracheophytic affinity, the strongest link to lineage is the triradiate mark which has long been attributed to vascular plants (e.g. Gray, 1985). However, authors (Kenrick et al., 2012; Edwards et al., 2014; Salamon et al., 2018) have noted that trilete marks are not peculiar to tracheophyte-derived spores, as they occur in several living bryophytes, also. Some extant hornworts even produce triradiate spores with a superficial resemblance to *Emphanisporites* (e.g. Boros and Jarai-Komlodi, 1975; Tryon and Lugardon, 1991; but see Taylor et al., 2011), although this may not have been true of fossil hornworts also. With extant trilete spores occupying a broader grouping outside of tracheophytes, it is probable that the same is true of fossil trilete spores (e.g. Edwards et al., 2014), and this complicates their relationships to any lineage which is compounded a lack of key morphological characters such as associated vascular tissue.

It is difficult to explore the phylogenetic relationships of *Emphanisporites* producers with such fragmentary fossils and limited data, but it may be that some of the producers lie outside of the tracheophytes proper, despite having a fully formed and functioning triradiate mark. What does seem clear is that the varied, although still largely enigmatic, lineages of *Emphanisporites* parent plants, evidenced by *H. lignieri*, dispersed *Emphanisporites* and the specimens described here, strongly support previous hypotheses that the emphanoid condition is an example of convergent evolution (e.g. Taylor et al., 2011; Morris et al., 2012b). Emphanoid muri are not peculiar to *Emphanisporites*, being identified in other trilete spore taxa (Morris et al., 2012b) and some hilate cryptospores such as *Artemopyra* (Burgess and Richardson) Richardson and some species of *Cymbohilates* Richardson. The reason for this convergence remains uncertain, but as previously hypothesised (e.g. Taylor et al., 2011) it is possible that, with so many taxa selecting for the emphanoid muri, it conferred some advantage to a reasonably common environmental or ecological pressure.

5.4. Broad palaeoecology – Inferences from the dispersed record

The parent plants of *Emphanisporites* remain poorly represented in the mesofossil record. They are largely outnumbered in charcoalified mesofossil assemblages by sporangia and spore masses yielding laevigate hilate cryptospores such as *Laevolancis* or crassitate trilete spores such as *Ambitisporites* and *Aneurospora*/ *Streelispora* (e.g. Morris et al., 2012b). This is reflected in the dispersed spore record. When considering the dearth of cf. *Horneophyton* sp. and other *Emphanisporites* producers in the megafossil record, Edwards and Richardson (2000) assessed the implications of taphonomy and palaeoecology on the likelihood of the plants being fossilised (Table 3).

Table 3
Palaeoecological and taphonomic effects on the dispersed spore record, after Edwards and Richardson (2000).

Possible cause of under representation	Effect on dispersed spore record
Plants living outside of river catchment areas and hence rarely entrained in deposited sediment.	Dispersed spores would be represented in the spore rain but would be swamped out by local plants.
Plants occupied restricted ecological niches and were hence rare in local vegetation.	Sporadic to no representation of dispersed spores from assemblages in local geographical areas.
The plants lacked recalcitrant biopolymers in their vegetative tissues, prohibiting fossilisation.	The plants would be represented in the dispersed spore record dependent on local numbers and proximity to depositional environments.

Here, we apply the rationale of Edwards and Richardson (2000) to the two *Emphanisporites* plants to assess the impact of taphonomy on their presence in the fossil record and explore their broad palaeoecologies.

Examination of the sample from which the specimens were isolated did not yield any dispersed spores directly comparable to *E.* sp. Extensive logging of material from the latest Silurian/earliest Lochkovian to the middle Lochkovian of the M50, Ammons Hill and NBCH found few comparatives, with only one relatively convincing specimen (Plate II, g) identified from the earliest Lochkovian of the M50 (−34.3 m below Chapel Point Limestone; *Apiculiretusispora* sp. E spore biozone, Fig. 1). The absence of the spore in the horizon from which the spore mass was uncovered suggests that the plant was either extremely rare or not growing in the M50 at that time, but the possible occurrence in the Moor Cliffs formation may indicate that it was growing near the area in the earliest Lochkovian – although the single occurrence necessitates caution. The lack of published records of *E.* sp. and paucity across the Anglo-Welsh assemblages suggests that the plant was not a common constituent of this Lochkovian vegetation, perhaps growing far from the present-day sample sites, with spores very rarely being incorporated into these assemblages. In this scenario the spore mass may have been transported a considerable distance, which is a plausible hypothesis for charcoalified remains.

Deciphering the exact relationship between all dispersed *E. epicautus* and *E.* cf. *epicautus* spores is not possible from the single occurrence recorded here and requires further ultrastructural study to confirm a consistent relationship, especially in dispersed specimens. As such, we will consider dispersed *E. epicautus* and *E.* cf. *epicautus* separately. Logging by ACB and previous work (Richardson and Lister, 1969; Edwards and Richardson, 2000; Higgs, 2004; Morris et al., 2011a) indicates that *E. epicautus* and *E.* cf. epicautus are widespread but rare constituents of the Anglo-Welsh basin palynoflora (Fig. 6). In the *Apiculiretusispora* sp. E zone (earliest Lochkovian) both *E. epicautus* and *E.* cf. *epicautus* are 'rare' in the M50 assemblage (cf. Edwards and Richardson, 2000), with *E.* cf. epicautus sometimes comprising up to 0.4% of the 250 spore count. A similar pattern is seen at Ammons Hill and NBCH (*E. epicautus* being rare and *E.* cf. *epicautus* comprising up to 0.4%). In the Lower MN zone of the M50, *E. epicautus* is sometimes rare, but more frequently comprises between 0.4 - 1.6% of the assemblage. *E.* cf. *epicautus* is found in lower proportions, at around 0.4%. Both are rare constituents in Ammons Hill, while only *E.* cf. e*picautus* is present, but rare, at NBCH. At Gardeners Bank (lower MN only), both comprise up to 0.4% of the assemblage. Finally, in the middle MN of the M50, *E. epicautus* is sometimes rare, but generally comprises between 0.4 – 0.8% of counts, while *E.* cf. *epicautus* comprises up to 0.4%. At Ammons Hill, *E. epicautus* comprises up to 0.4% of the assemblage, whilst *E.* cf. *epicautus* comprises up to 0.8%. At NBCH, *E. epicautus* is rare, whilst *E.* cf. *epicautus* is rare, or comprises up to 0.4%.

It is interesting to note here that *E.* cf. *epicautus* is ubiquitous, in varying proportions, across the investigated sites and biozones. Meanwhile, *E. epicautus* is observed in all of the sites and across all of the biozones except NBCH in the lower MN biozone, where only *E.* cf. *epicautus* is observed. If ABM5015-001 is representative of all *E. epicautus* and *E.* cf. *epicautus* parent plants (that is, that both spores are derived from the same plant) then the absence of the former in the lower MN of NBCH could be a result of taphonomy. Alternatively, it may suggest that the plant was not present in NBCH, and the observation of *E.* cf. *epicautus* in the assemblage results from fortuitous transport of that spore from some distance away. This is supported as only a single *E.* cf. *epicautus* specimen was found throughout extensive logging of these lower MN NBCH samples. Whether or not the plant was present in NBCH at this time, the plant was probably not restricted to a specialised niche given how widespread and consistent its occurrence is in the rest of the basin through time. However, the plants probably comprised a small proportion of the flora and seem to have been restricted to areas outside

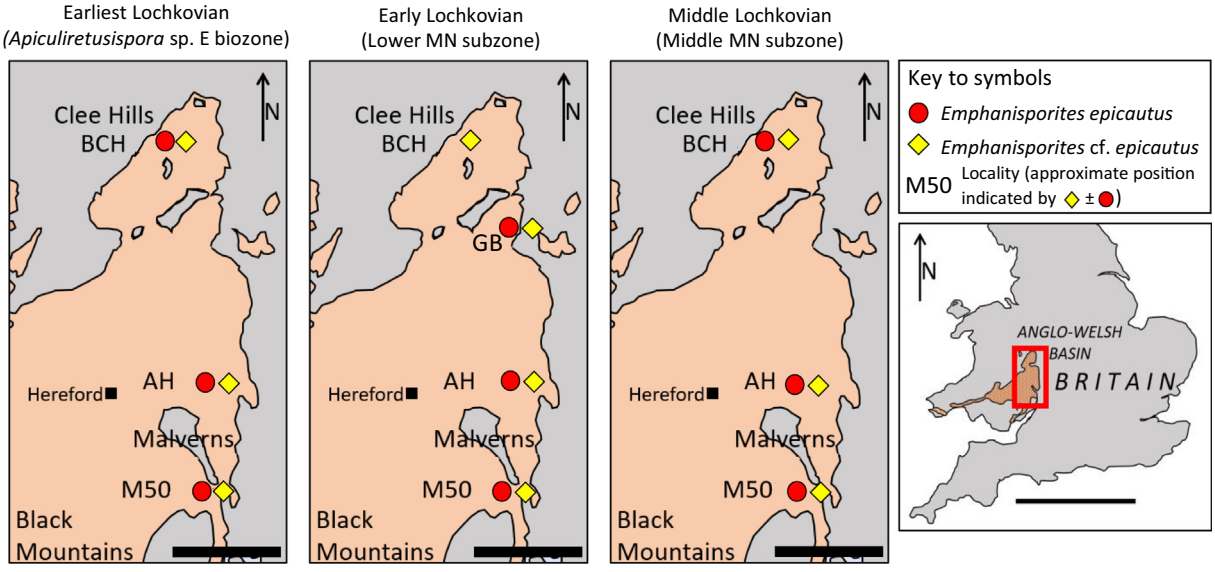

Fig. 6. Spatial and temporal distribution of E. epicautus and E. cf. epicautus across sites in the Welsh Borderlands. **BCH** = Brown Clee Hills area (including NBCH); **GB** = Gardeners bank (only present in the lower MN; **AH** = Ammons Hill; **M50** = M50 motorway. Locations approximate. Scale bar 20km. Bottom right, map: Outcrop of Anglo-Welsh Basin in South Wales and the Welsh Borderlands, red box

of river catchment. Because a single source plant for these spores cannot be confidently ascertained at present, an alternative hypothesis could be that the *E. epicautus* parent plant was not growing in NBCH during the lower MN, while the parent plant of *E.* cf. *epicautus* was, but both remained otherwise widespread in low proportions. As such, regardless of whether ABM5015-001 is representative of the *E. epicautus* and *E.* cf. *epicautus* producers, it is probable that the plant or plants, whilst not restricted to a specialised niche, were restricted to areas outside of river catchment and comprised a small proportion of the flora. As such, the spore mass found here was likely transported some distance to the depocenter, but was more local than the *E.* sp. mass.

Whilst the occurrence of *E. epicautus* and *E.* cf. *epicautus* spores across the basin supports a widespread, somewhat restricted niche, the possibility remains that this was located proximally rather than distally to rivers, with the *Emphanisporites* source plants simply being rare amongst the riparian vegetation or being lost to preservational biases. The chief support for the plants growing outside of the catchment area of rivers is the paucity of their spores in the dispersed record in these riparian deposits. Had they grown near depositional settings such as rivers, it seems plausible that despite their rarity a higher incidence might be expected. Sorting of spores is a possible explanation, however the size range of dispersed spores in the assemblages ranges between 16 and 52 μm, with a mean size of 27 μm. Dispersed and *in situ E. epicautus* and *E.* cf. *epicautus* from the Lochkovian measure between 26 and 38 μm, and *in situ* E. sp. measure between 28 and 40 μm, suggesting that these spores were unlikely to have been removed from the assemblage due to sorting, supporting the hypothesis that these plants inhabited niches outside of river catchment, but does not discount a taphonomic explanation altogether.

If the largely palaeoecological hypothesis holds, then, the paleoecology of the *E. epicautus* and *E.* cf. *epicautus* parent plant (or plants) is somewhat similar to that posited for cf. *Horneophyton* sp. by Edwards and Richardson (2000), except that the latter seems to have been more restricted and absent in marine influenced settings at Ammons Hill during lower MN times.Both appear to have been growing away from the catchment areas of rivers, but cf. *Horneophyton* may have inhabited more specialised niches, only occurring sporadically. Growth in presumably less equable settings away from moist depocenters would have necessitated adaptations to cope with physiologically stressful conditions. It follows that fine moisture sensing capabilities of dispersed spores would be particularly important for such plants, perhaps suggesting a function for the 'emphanoid' condition.

6. Conclusions

We present the oldest-yet published examples of *in situ Emphanisporites* and add to the growing diversity of sporangial morphologies found amongst rare *Emphanisporites* producers. *E. epicautus* and *E.* sp. are most comparable to the rhyniophytes, although a lack of unequivocal vascular tissue necessitates their grouping amongst the rhyniophytoids. We have uncovered enough morphological and ultrastructural information to confidently ascertain that they belonged to quite different, although equivocal, lineages. They differ significantly from other *Emphanisporites* species, especially *E. epicautus*, and do not have any directly comparable contemporaneous fossil or extant taxa. While the homogenous exospore of *E. epicautus* makes comparisons difficult, the bilayered exine comprising an inner lamellate layer and outer homogenous layer of *E.* sp. may relate it to some modern tracheophytes, but this remains problematic. Investigation of sporocyte development for *E. epicautus* is difficult given the homogenous architecture of the spore wall, but *E.* sp. on the other hand may have formed by a variety of means. Whilst the Andreaea mode of formation for the outer homogenous layer is plausible in the absence of evidence for a tapetum and rare lacunae, the overall spore wall development remains clouded. Given the paucity of *E.* sp. in the dispersed record, we cannot currently explore the palaeoecology of this plant. The dispersed spore record of *E. epicautus* and *E.* cf. *epicautus* indicates that the parent plant/ plants inhabited widespread ecological niches away from the catchment areas of rivers, but these do not appear to have been as restrcted as the niche of cf. *Horneophyton* sp. It is possible that the emphanoid muri conferred some advantage to propagation in water stressed environments, as the diversity of *Emphanisporites* producers, and other emphanoid muri bearing taxa, strongly indicates that the emphanoid condition is convergent (Edwards and Richardson, 2000; Taylor et al., 2011; Morris et al., 2012b) and may have offered some selective advantage due to some environmental and/ or evolutionary pressure.

Author contributions

ACB conceived the study, performed SEM and light microscopy work and wrote the manuscript. WAT performed TEM sectioning and photography and reviewed the manuscript.

Declaration of Competing Interest

The authors declare that there are no conflicts of interest.

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References

Allen, K.C., 1980. A review of in situ Late Silurian and Devonian spores. Rev. Palaeobot. Palynol. 29, 253–269.
Allen, J.R.L., Dineley, D.L., 1976. The succession of the Lower Old Red Sandstone (Siluro-Devonian) along the Ross-Tewkesbury Spur Motorway (M50), Hereford and Worcester. Geol. J. 11, 1–14.
Barclay, W.J., Davies, J.R., Hillier, R.D., Waters, R.A., 2015. Lithostratigraphy of the Old Red Sandstone successions of the Anglo-Welsh Basin. British Geological Survey Research Report, RR/14/02, p. 96.
Barghoorn, E.S., Darrah, W.C., 1938. *Horneophyton*, a necessary change of name for *Hornea*. Harvard University Botanical Museum Leaflet 6, 142–144.
Blackmore, S., Barnes, S.H., 1987. Pollen wall morphogenesis in *Tragopogon porrifolius* L. (Compositae: Lactuceae) and its taxonomic significance. Rev. Palaeobot. Palynol. 52 (2–3), 233–246.
Blackmore, S., Takahashi, M., Uehara, K., 2000. A preliminary phylogenetic analysis of sporogenesis in pteridophytes. In: Harley, M.M., Morton, C.M., Blackmore, S. (Eds.), Pollen and Spores: Morphology and Biology. London, Kew, Royal Botanic Gardens, pp. 109–124.
Boros, A., Jarai-Komlodi, M., 1975. An Atlas of Recent European Moss Spores. *Akademiai Kiado*. Publishing House of the Hungarian Academy of Sciences, Budapest.
Brown, R.C., Lemmon, B.E., 1984. Spore wall development in Andreaea (Musci: Andreaeopsida). Am. J. Bot. 71 (3), 412–420.
Brown, R.C., Lemmon, B.E., 1990. Sporogenesis in bryophytes. In: Blackmore, S., Knox, R.B. (Eds.), Microspores: Evolution and Ontogeny. Academic Press, London, UK, pp. 55–94.
Burgess, N.D., Richardson, J.B., 1991. Silurian cryptospores and miospores from the type Wenlock area, Shropshire, England. Palaeontology 34, 601–628.
Cascales-Miñana, B., Steemans, P., Servais, T., Lepot, K., Gerrienne, P., 2019. An alternative model for the earliest evolution of vascular plants. Lethaia 52 (4), 445–453.
Chaloner, W.G., Streel, M., 1968. Lower Devonian spores from South Wales. Argum. Palaeobot. 1, 87–101.
Edwards, D., 1969. Zosterophyllum from the Lower Old Red Sandstone of South Wales. New Phytol. 68 (4), 923–931.
Edwards, D., 1979. A late Silurian flora from the Lower Old Red Sandstone of south-west Dyfed. Palaeontology 22, 23–52.
Edwards, D., 1996. New insights into early land ecosystems: a glimpse of a Lilliputian world. Rev. Palaeobot. Palynol. 90 (3–4), 159–174.
Edwards, D., Richardson, J.B., 2000. Progress in reconstructing vegetation on the Old Red Sandstone Continent: two *Emphanisporites* producers from the Lochkovian sequence of the Welsh Borderland. Geol. Soc. Lond., Spec. Publ. 180 (1), 355–370.

Edwards, D., Richardson, J.B., 2004. Silurian and Lower Devonian plant assemblages from the Anglo-Welsh Basin: a palaeobotanical and palynological synthesis. Geol. J. 39 (3–4), 375–402.
Edwards, D., Fanning, U., Richardson, J.B., 1994. Lower Devonian coalified sporangia from Shropshire: *Salopella* Edwards & Richardson and *Tortilicaulis* Edwards. Bot. J. Linn. Soc. 116, 89–110.
Edwards, D., Davies, K.L., Richardson, J.B., Axe, L., 1995a. The ultrastructure of spores of *Cooksonia pertoni*. Palaeontology 38, 153–168.
Edwards, D., Duckett, J.G., Richardson, J.B., 1995b. Hepatic characters in the earliest land plants. Nature 374, 635–636.
Edwards, D., Richardson, J.B., Axe, L., Davies, K.L., 2012a. A new group of Early Devonian plants with valvate sporangia containing sculptured permanent dyads. Bot. J. Linn. Soc. 168 (3), 229–257.
Edwards, D., Wellman, C.H., Axe, L., 1999. Tetrads in sporangia and spore masses from the Upper Silurian and Lower Devonian of the Welsh Borderland. Bot. J. Linn. Soc. 130, 111–156.
Edwards, D., Morris, J.L., 2014. An analysis of vegetational change in the Lower Devonian: New data from the Lochkovian of the Welsh Borderland, U.K. Review of Palaeobotany and Palynology 211, 28–54. https://doi.org/10.1016/j.revpalbo.2014.09.006.
Edwards, D., Morris, J.L., Axe, L., Taylor, W., Duckett, J.G., Kenrick, P., Pressel, S., et al., 2021a. Piecing together the eophytes – a new group of ancient plants containing cryptospores. New Phytologist 233 (3), 1440–1455. https://doi.org/10.1111/nph.17703.
Edwards, D, Morris, J.L., Axe, L., Taylor, W.A., Duckett, J.G., Kenrick, P., Pressel, S., 2021b. Earliest record of transfer cells in Lower Devonian plants. New Phytologist 233 (3), 1456–1465. https://doi.org/10.1111/nph.17704.
Edwards, D., Morris, J.L., Richardson, J.B., Kenrick, P., 2014. Cryptospores and cryptophytes reveal hidden diversity in early land floras. New Phytol. 202 (1), 50–78.
Fanning, U., Richardson, J.B., Edwards, D., 1988. Cryptic evolution in an early land plant. Evol. Trends Plants (ETP) 2 (1), 13–24.
Fanning, U., Edwards, D., Richardson, J.B., 1990. Further evidence for diversity in late Silurian land vegetation. J. Geol. Soc. 147 (4), 725–728.
Fanning, U., Edwards, D., Richardson, J.B., 1991a. A new rhyniophytoid from the late Silurian of the Welsh Borderland. Neues Jahrb. Geol. Palaontol. Abh. 183, 37–47.
Fanning, U., Richardson, J.B., Edwards, D., 1991b. A review of in situ spores in Silurian land plants. In: Blackmore, S., Barnes, S.H. (Eds.), Systematics Association Special Volume. Pollen and Sporesvol. 44, pp. 25–47.
Gray, J., 1985. The microfossil record of early land plants; advances in understanding of early terrestrialization, 1970–1984. Phil. Trans. R. Soc. Lond. B 309, 167–195.
Higgs, K.T., 2004. An Early Devonian (Lochkovian) microflora fromthe Freshwater West Formation, Lower Old Red Sandstone,southwest Wales. Geological Journal 39, 359–374. https://doi.org/10.1002/gj.994.
Jeram, A.J., Selden, P.A., Edwards, D., 1990. Land animals in the Silurian: arachnids and myriapods from Shropshire, England. Science 250 (4981), 658–661.
Johnson, T.R., Taylor, W.A., 2005. Single grain analysis of the late Silurian spore Cymbosporites echinatus from the Welsh Borderland. Rev. Palaeobot. Palynol. 137 (3–4), 163–172.
Kenrick, P., Wellman, C.H., Schneider, H., Edgecombe, D., 2012. A timeline for terrestrialization: consequence for the carbon cycle in the Palaeozoic. Philos. Trans. R. Soc. Lond. B 367, 519–536.
Kidston, R., Lang, W.H., 1920. On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part II. Additional notes on *Rhynia gwynne-vaughani*, Kidston and Lang: with descriptions of *Rhynia major*, n. sp., and *Hornea lignieri*, n. g. n. sp. Trans. R. Soc. Edinb. 52, 603–627.
Lugardon, B., 1990. Pteridophyte sporogenesis: a survey of spore wall ontogeny and fine structure in a polyphyletic plant group. In: Blackmore, S., Knox, R.B. (Eds.), Microspores: Evolution and Ontogeny. London Academic Press, pp. 95–120.
McGregor, D.C., 1961. Spores with proximal radial pattern from the Devonian of Canada. Geol. Surv. Can. Bull. 76, 1–11.
Morris, J.L., Richardson, J.B., Edwards, D., 2011a. Lower Devonian plant and spore assemblages from Lower Old Red Sandstone strata of Tredomen Quarry, South Wales. Rev. Palaeobot. Palynol. 165 (3–4), 183–208.
Morris, J.L., Edwards, D., Richardson, J.B., Axe, L., Davies, K.L., 2011b. New plant taxa from the Lower Devonian (Lochkovian) of the Welsh Borderland, with a hypothesis on the relationship between hilate and trilete spore producers. Rev. Palaeobot. Palynol. 167, 51–81.
Morris, J.L., Edwards, D., Richardson, J.B., Axe, L., 2012a. New dyad-producing plants from the Lower Devonian (Lochkovian) of the Welsh Borderland. Bot. J. Linn. Soc. 169, 569–595.
Morris, J.L., Edwards, D., Richardson, J.B., Axe, L., Davies, K.L., 2012b. Further insights into trilete spore producers from the Early Devonian (Lochkovian) of the Welsh Borderland, U.K. Rev. Palaeobot. Palynol. 185, 35–63.
Morris, J.L., Wright, V.P., Edwards, D., 2012c. Siluro-Devonian landscapes of southern Britain: the stability and nature of early vascular plant habitats. J. Geol. Soc. Lond. 169, 173–190.
Morris, J.L., Edwards, D., Richardson, J.B., 2018. The advantages and frustrations of a plant Lagerstätte as illustrated by a new taxon from the Lower Devonian of the Welsh Borderland, UK. In: Krings, M., Harper, C.J., Rubén Cúneo, N., Rothwell, G.W. (Eds.), Transformative Paleobotany. Academic Press, pp. 49–67.
Puttick, M.N., Morris, J.L., Williams, T.A., Cox, C.J., Edwards, D., Kenrick, P., Pressel, S., Wellman, C.H., Schneider, H., Pisani, D., Donoghue, P.C., 2018. The interrelationships of land plants and the nature of the ancestral embryophyte. Curr. Biol. 28 (5), 733–745.
Qiu, Y.-L., Li, L., Bin, W., Chen, Z., Knoop, V., Growth-Malonek, M., Dombrovska, O., Lee, J., Kent, L., Rest, J., Estabrook, G.F., Hendry, T.A., Taylor, D.W., Testa, C.M., Ambros, M., Crandall-Stotler, B., Duff, R.J., Stech, M., Frey, W., Quandt, D., Davis, C.C., 2006. The deepest divergences in land plants inferred from phylogenomic evidence. Proc. Natl. Acad. Sci. 103, 15511–15516.
Renzaglia, K.S., Villarreal, J.C., Duff, R.J., 2008. New insights into morphology, anatomy, and systematics of hornworts. In: Goffinet, B., Shaw, A.J. (Eds.), Bryophyte Biology, 2nd edition Cambridge University Press, Cambridge, UK, pp. 139–172.
Richardson, J.B., 1974. The stratigraphic utilization of some Silurian and Devonian miospore species in the northern hemisphere: an attempt at a synthesis. Int. Symp. Belg. Micropaleontol. Limits, Publ. No. 9, pp. 1–13.
Richardson, J.B., 1996. Taxonomy and classification of some new Early Devonian cryptospores from England. Spec. Pap. Palaeontol. 55, 7–40.
Richardson, J.B., 2007. Cryptospores and miospores, their distribution patterns in the Lower Old Red Sandstone of the Anglo-Welsh Basin, and the habitat of their parent plants. Bull. Geosci. 82 (4), 355–364.
Richardson, J.B., Lister, T.R., 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. Palaeontology 12, 37–43.
Richardson, J.B., McGregor, D.K., 1986. Silurian and Devonian spore zones of the Old Red Sandstone Continent and adjacent regions. Geol. Surv. Can. Bull. 364, 1–79.
Salamon, S.A., Gerrienne, P., Steemans, P., Gorzelak, P., Fillipiak, P., Hérissé A, L.E., Paris, F., Cascales-Miñana, B., Brachaniec, T., Misz-Kennan, M., Niedzwiedzki, R., 2018. Putative late Ordovician land plants. New Phytol. 218, 1305–1309.
Steemans, P., Petus, E., Breuer, P., Mauller-Mendlowicz, P., Gerrienne, P., 2012. Palaeozoic innovations in the micro-and megafossil plant record: from the earliest plant spores to the earliest seeds. In: TALENT, J.A. (Ed.), Earth and Life, International Year of Planet Earth. Springer, Dordrecht, pp. 437–477.
Taylor, W.A., 1997. Ultrastructure of lower Paleozoic dyads from southern Ohio II: *Dy*adospora murusattenuata, functional and evolutionary considerations. Rev. Palaeobot. Palynol. 97, 1–8.
Taylor, W.A., 2002. Studies in cryptospore ultrastructure: variability in the tetrad genus Tetrahedraletes and type material of the dyad *Dyadospora murusattenuata*. Rev. Palaeobot. Palynol. 119 (3–4), 325–334.
Taylor, W.A., 2003. Ultrastructure of selected Silurian trilete spores and the putative Ordovician trilete spore Virgatasporites. Rev. Palaeobot. Palynol. 126 (3–4), 211–223.
Taylor, W.A., Gensel, P.G., Wellman, C.H., 2011. Wall ultrastructure in three species of the dispersed spore Emphanisporites from the Early Devonian. Rev. Palaeobot. Palynol. 163 (3–4), 264–280.
Taylor, W.A., Strother, P.K., Vecoli, M., 2017. Wall ultrastructure of the oldest embryophytic spores: implications for early land plant evolution. Rev. Micropaleontol. 60 (3), 281–288.
Tryon, A.F., Lugardon, B., 1991. Spores of the Pteridophyta. Surface, wall structure and diversity based on electron microscope studies. Springer, New York, NY, pp. 523–540.
Vigran, J.O., 1964. Spores from Devonian deposits, Mimerdalen, Spitsbergen. Skrifter Norsk Polarinstitutt 132, 1–30.
Wellman, C.H., 1999. Sporangia containing Scylaspora from the lower Devonian of the Welsh Borderland. Palaeontology 42 (1), 67–81.
Wellman, C.H., 2004. Origin, function and development of the spore wall in early land plants. In: Hemsley, A.R., Poole, I. (Eds.), The Evolution of Plant Physiology. Royal Botanic Gardens, Kew, pp. 43–63.
Wellman, C.H., 2009. Ultrastructure of dispersed and in situ specimens of the Devonian spore *Rhabdosporites langii*: evidence for the evolutionary relationships of progymnosperms. Palaeontology 52 (1), 139–167.
Wellman, C.H., Edwards, D., Axe, L., 1998b. Ultrastructure of laevigate hilate spores in sporangia and spore masses from the Upper Silurian and Lower Devonian of the Welsh Borderland. Phil. Trans. R. Soc. Lond. B 353, 1983–2004.
Wellman, C.H., Habgood, K., Jenkins, G., Richardson, J.B., 2000. A new plant assemblage (microfossil and megafossil) from the Lower Old Red Sandstone of the Anglo–Welsh Basin: its implications for the palaeoecology of early terrestrial ecosystems. Rev. Palaeobot. Palynol. 109 (3–4), 161–196.
Wellman, C.H., Kerp, H., Hass, H., 2004. Spores of the Rhynie chert plants *Horneophyton lignieri* (Kidston & Lang) Barghoorn & Darrah, 1938. Trans. R. Soc. Edinb. Earth Sci. 95, 429–443.