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Early land plant phytodebris

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Abstract: Historically, phytodebris (often considered a type of non-pollen palynomorph – NPP) has played a prominent role in research into the fossil record of early land plants. This phytodebris consists of cuticles and cuticle-like sheets, various tubular structures (including tracheids and tracheid-like tubes) and sundry other enigmatic fragments. Initial research focused on elucidating their morphology, attempts to identify them *in situ* in plant megafossils and comparisons with potentially homologous structures in extant plants. The fragmentary nature of these remains, and associated difficulties in positively identifying their presence in fossil/extant plants, resulted in vigorous debate regarding what many of these microfossils actually represented and their relevance to early land plant studies. More recently a wider array of analytical techniques has been applied (e.g. ultrastructural analysis, geochemistry and taphonomic experiments). However, positive identification of the affinities of at least some of these enigmatic fossils remained elusive. Ongoing investigations based on exceptionally preserved material from Lagerstätten (charcoalified and silicified) seem to have finally demonstrated that the more enigmatic of these remains derive from nematophytes that probably represent fungi and possibly also lichenized fungi.

Land plants (embryophytes) produce potentially fossilizable parts both throughout their lives and upon their death. During life, they naturally shed (including abscission) organs such as roots, branches and leaves, and propagules such as seeds and spores/pollen. Upon death they begin to disintegrate, whereupon all of their structures become potential fossils. Many plant parts have a high fossilization potential because they are composed of, or at least contain, highly resistant organic macromolecules (for example, the lignin of woody tissues, the cutan of cuticles and the sporopollenin of spore and pollen walls).

Palaeobotanists generally study fossils of relatively large plant organs (that may or may not be preserved in organic connection with other plant organs). Typically, these have been little transported and rapidly buried, except in the cases of leaves and seeds that can undergo considerable transportation before being incorporated into sediment relatively intact. Plant megafossils are most commonly preserved as standard coalified compressions or sediment casts. Less often they may be better preserved by permineralization or even charcoalification following natural burning. General reviews of the taphonomy of fossil plants are provided by Cleal and Thomas (2009) and Taylor *et al.* (2009).

The palynologist, on the other hand, chiefly studies dispersed plant microfossils, liberated from the host sediment by palynological acid-maceration techniques. These fossils may have experienced vast transportation distances, usually by wind and water, prior to deposition. These either represent essentially complete organs (spores, megaspores, pollen or seeds) or disarticulated fragments (including cuticle fragments and bundles of tracheids). These palynomorphs and disarticulated fragments are essentially preserved as coalified compressions, although they can be charcoalified. General reviews of the taphonomy of fossil palynomorphs are provided in Jansonius and McGregor (1996) and Traverse (2007).

The terminology used to describe dispersed fragments of land plants is somewhat confused. Here we use the term phytodebris (*sensu* Gensel *et al.* 1991). But other terms have been utilized, such as palynodebris (particularly in palynofacies classifications) and nematoclasts (when referring specifically to fragments derived from an enigmatic group of ‘plants’ called nematophytes). However, when excluding dispersed spores and pollen and considering only dispersed fragments, we are dealing with what is often considered to be a discrete group of non-pollen palynomorphs (NPP). This paper is concerned solely with phytodebris and is confined to that produced by the earliest land plants. Consequently, it is stratigraphically circumscribed between the Middle Ordovician and Early Devonian (Fig. 1).

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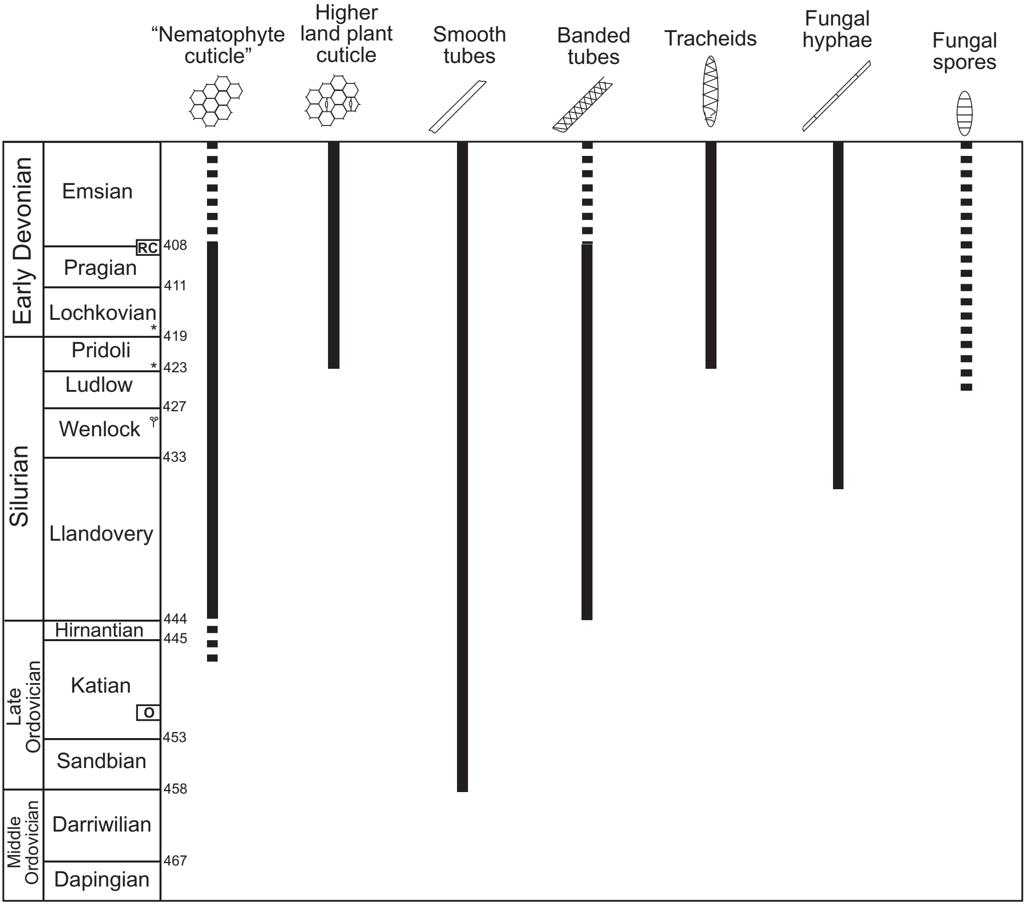

Fig. 1. Stratigraphical distribution of phytodebris. The stratigraphical column is based on *A Geologic Timescale* v. 5 (Walker *et al.* 2018). Dashed lines represent uncertain distribution. The small fossil rhyniophytoid plant illustrated in the Wenlock represents the earliest generally accepted land plant megafossils. The asterisks in the Pridoli and Lochkovian represent the Ludford Lane and Hudwick Dingle charcoalified plant assemblages, respectively. RC in the Pragian–?earliest Emsian represents the Rhynie chert. O in the Katian represents the earliest evidence for cryptosporophyte sporangia from Oman (Wellman *et al.* 2003).

Examples of early land plant phytodebris are illustrated in Figures 2 & 3.

The origin and early evolution of land plants

The origin of land plants was one of the most important events in the history of life on Earth. From a biological perspective land plants (embryophytes) represent one of the main kingdoms of multicellular life. Ecologically, their colonization of the land opened up the continents and subaerial world for the aquatic animals that followed the plants on to the land, be that from the saline oceans or freshwater bodies such as lakes, rivers and marshes (Shear and Selden 2001). Furthermore, they had enormous effects on the actual environment of planet Earth due to their actions involving: (i) weathering and soil formation; and (ii) photosynthetic carbon-capture, resulting in biomass accumulation and carbon burial. This not only created soils and affected sedimentation patterns in many other ways, but also changed atmospheric composition leading to, *inter alia*, climate change.

As a consequence of the above, much research activity has been dedicated to exploring the origin and early evolution of land plants. Whilst numerous lines of scientific enquiry have been explored, the fossil record of early land plants has, of course, always featured prominently. Initially this concentrated on early land plant megafossils recovered from late Silurian–Early Devonian deposits (e.g.

Fig. 2. Phytodebris recovered from Late Silurian–Early Devonian 'Lower Old Red Sandstone' sediments from the Ross-Spur M50 motorway succession of the Anglo-Welsh Basin (for details see Edwards 1986). Scale bar (top right-hand corner) is 75 µm. (**a**) Banded tube. Freshwater West Formation, Sample 19M5001.1, Specimen (M22). (**b**) Banded tube. Moor Cliffs Formation, Sample 19M5009.1, Specimen (U30/2). (**c**) *Constrictitubulus*. Freshwater West Formation, Sample 19M5001.3, Specimen (G36/2). (**d**) Banded tube. Freshwater West Formation, Sample

Lang 1937). The advent of palynological techniques through the 1950s–60s saw new evidence become available in the form of dispersed palynomorphs and phytodebris. Indeed, it is clear that dispersed land plant microfossils began to play an increasingly prominent role in research into the earliest land plants from this time. Early reviews of the palynological evidence include those of Chaloner (1960, 1970) and, more recently, reviews of both the microfossil and megafossil evidence include those of Wellman and Gray (2000), Edwards and Wellman (2001), Gensel (2008), Kenrick *et al.* (2012), Wellman *et al.* (2013) and Meyer-Berthaud *et al.* (2016*a*, *b*).

By the 1970s Jane Gray and colleagues (Gray and Boucot 1971; Gray *et al.* 1974) had proposed a critical role for early land plant phytodebris, revealing an early hidden history of land plant evolution not represented in the megafossil record. Fierce debate ensued as to the authenticity and relevance of this dispersed microfossil record (Banks 1975*a*, *b*; Gray and Boucot 1977). By the 1980s many of these debates had essentially been resolved. It became widely accepted that by the Middle Ordovician a rather cryptic period of early land plant evolution was represented by dispersed microfossils (including phytodebris) (Pratt *et al.* 1978; Strother and Traverse 1979; Gray 1985; Johnson 1985) which existed prior to, and later complemented, the late Silurian appearance of plant megafossils (Edwards *et al.* 1979; Libertín *et al.* 2018; Morris *et al.* 2018).

Early land plant spores

Initial research on land plant dispersed microfossils concentrated on their dispersed spores/pollen and, over the succeeding decades, a vast literature emerged on the subject (reviewed in Jansonius and McGregor 1996; Traverse 2007). It was soon realized that the land plant (embryophyte) megafossil record is rather poor compared to the rich dispersed spore record. This is because the latter are produced in vast numbers, readily transported long distances by wind and water and have high fossilization potential. Research into early land plants also relied heavily on the dispersed spore record, particularly as megafossils are so rare. To date less than 25 megafossil localities are known worldwide from the entire Silurian and these are almost exclusively of allochthonous plant remains transported into marine environments (Edwards and Wellman 2001; Wellman *et al.* 2013). Furthermore, the dispersed spore record appears to extend back further in time than the plant megafossil record. This almost certainly reflects the facts that: (i) dispersed spores have higher preservation potential than plant megafossils; and (ii) the earliest land plants may have been very small and lacking in preservable resistant tissues and consequently lost to the fossil record.

Early land plant phytodebris

Somewhat lagging behind the study of land plant dispersed spores/pollen was the study of the phytodebris they produce. However, due to the paucity of early land plant megafossils, studies of phytodebris became increasingly important for research into these earliest plants (e.g. Gray and Boucot 1977). These other ‘bits-and-pieces’ (rather endearingly termed ‘Hooker’s “Waifs and strays”’ by Gensel *et al.* 1991) began to feature prominently because it was considered that they may represent disarticulated fragments of the earliest land plants that lacked a megafossil record. However, interpretation of early land plant dispersed phytodebris (Figs 1 & 2) was often problematic, owing to: (i) multiple organisms producing similar, morphologically simple structures, of which the original biological affinities are difficult to trace; and (ii) difficulties in reconciling these fragmentary structures with equivalent material produced by extant land plants.

Dispersed cuticles and ‘cuticle-like sheets’

Some bryophytes (non-vascular plants) and the vast majority of tracheophytes (vascular plants) produce a cuticular covering composed primarily of cutan

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Fig. 2. *Continued.* 19M5001.1, Specimen (E44/3). (**e**) Banded tube. Freshwater West Formation, Sample 19M5001.1, Specimen (O34). (**f**) Banded tube. Freshwater West Formation, Sample 19M5001.3, Specimen (P50/4). (**g**) Laevigate tube. Freshwater West Formation, Sample 19M5001.3, Specimen (O42/1). (**h**) Banded tube. Freshwater West Formation, Sample 19M5002.3, Specimen (W44/1). (**i**) Banded tube. Freshwater West Formation, Sample 19M5002.1, Specimen (K43). (**j**) *Constrictitubulus*. Freshwater West Formation, Sample 19M5001.1, Specimen (O51/3). (**k**) Banded tube. Freshwater West Formation, Sample 19M5001.1, Specimen (N24). (**l**) Banded tube. Freshwater West Formation, Sample 19M5002.3, Specimen (M44). (**m**) Laevigate tube. Freshwater West Formation, Sample 19M5001.1, Specimen (M50/4). (**n**) Sporangial cuticle of ?cryptosporophytic origin. Freshwater West Formation, Sample 19M50026.3, Specimen (N45). (**o**) Embryophyte cuticle. Freshwater West Formation, Sample 19M5001.3, Specimen (E35/1). (**p**) Nematophyte cuticle. Freshwater West Formation, Sample 19M5001.3, Specimen (S30/3). (**q**) Nematophyte cuticle. Freshwater West Formation, Sample 19M5001.3, Specimen (N31). (**r**) Nematophyte cuticle. Freshwater West Formation, Sample 19M5001.1, Specimen (N42/3). (**s**) Nematophyte cuticle. Freshwater West Formation, Sample 19M5001.3, Specimen (E35/1).


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and waxes. As leaves, axes and other cuticle-covered structures decompose, the cuticle can be shed and fragment. The organic macromolecule cutan is highly resistant and readily fossilized. Thus, fragments of cuticle can undergo extensive transportation before finally being deposited and incorporated into sediment and, as such, these cuticle fragments frequently occur in palynological preparations. Cuticles preserve the patterning of the epidermal cells underlying the cuticle and often indicate from which part of the plant the cuticle is derived. For example, axial cuticles often have elongate cells whereas those from leaves may be more equidimensional (e.g. Edwards *et al.* 1981, 1996; Guo and Wang 2015). Cuticles are often also of taxonomic value, particularly when considered alongside characters of stomata that are preserved in the dispersed cuticles of stomatiferous plants (Edwards *et al.* 1998*b*). The distribution of these stomata can also be used to calculate the stomatal density/index, which can be used as proxies for past atmospheric CO_2 levels (e.g. McElwain and Chaloner 1995). The earliest unequivocal stomata reported from plant megafossils are from rhyniophytoid plants from the upper Silurian (Pridoli) of Ludford Lane in the Anglo-Welsh Basin (Jeram *et al.* 1990). The earliest dispersed cuticles with stomata have been reported from the Lower Devonian (Lochkovian) of the same basin (Edwards and Axe 1992; Edwards *et al.* 1996).

Early research highlighted the presence of ‘cuticle-like sheets’ that were very similar to the cuticles of land plants, although they differed from many in that they lacked stomata. Gray and Boucot (1977) argued that these were most likely cuticles of early land plants, and called them ‘cuticle-like remains’, although other workers urged caution (e.g. Banks 1975*a*, *b*). Detailed taxonomic studies were undertaken (Edwards 1982, 1986; Edwards and Rose 1984), and these authors interpreted many of the cuticles as representing the covering of nematophytes (see below), with Edwards (1986) including formal systematic naming of some of the cuticles.

Enigmatic megafossils that co-occurred with early land plants in Silurian–Devonian non-marine strata were called nematophytes by Lang (1937). These strange, so-called ‘plants’, had an anatomy based on various different forms and combinations of tubular structure with some, Lang believed, possessing a cuticular covering. The unfamiliar anatomy appeared to have no counterpart among the living world and Lang suggested that nematophytes may represent a new phylum that had experimented with life on land before going extinct. Subsequently much attention was paid to these enigmatic remains and other workers suggested affinities with algae, fungi, lichens and other groups represented in the living biota. As noted above, Dianne Edwards was firmly of the opinion that at least some of the dispersed cuticle-like sheets represented fragments of nematophyte coverings (Edwards 1982, 1986; Edwards and Rose 1984).

One line of enquiry that has been pursued regarding the affinities of the cuticles is their geochemistry. Various techniques have been utilized, such as flash pyrolysis–gas chromatography–mass spectrometry (Ewbank *et al.* 1996), Fourier transform IR (FTIR; e.g. Abbott *et al.* 1998) and ^{13}C solid-state nuclear magnetic resonance (NMR; e.g. Edwards *et al.* 1997), on both dispersed cuticles, fragments of vascular land plant and nematophyte megafossils. These authors reported the presence of cutan in some early vascular land plants, which presumably derived from their cuticle covering (reviewed in Edwards *et al.* 1996, 1998*a*). Furthermore, it was shown that cuticles of *Nematothallus* had a distinctly different geochemical profile than those from vascular plants (Edwards *et al.* 1998*a*). As geochemical techniques improve and new technique emerge this line of enquiry has the potential to be explored further. However, limitations due to taphonomic effects, including thermal maturity, need to be fully appreciated.

In the 1990s Linda Graham and co-workers began reporting on a series of taphonomic experiments relevant to the debate regarding the affinities

Fig. 3. Phytodebris recovered from sediments hosting the Early Devonian (late Pragian–?earliest Emsian) Rhynie cherts from Scotland (for details of palynological investigation see Wellman 2006). Scale bar (top right-hand corner) is 60 µm (a–j), 125 µm (k–m), 80 µm (n–o) and 140 µm (p). (**a**) Tracheid. Sample 97/2 (39.0)/4. (**b**) Tracheid. Sample 97/2 (39.0)/4. (**c**) Tracheid. Sample 97/2 (39.0)/4. (**d**) Two attached tracheids. Sample 97/2 (39.0)/4. (**e**) Banded tube associated with a cluster of narrow laevigate tubes. Sample 97/2 (32.5)/2, Specimen (N39.1). (**f**) Wide laevigate tube in association with narrow laevigate tubes (?*Prototaxites* spp.). Sample 97/9 (24.0)/2, Specimen (W44.4). (**g**) Two ?attached banded tubes. Sample 97/2 (34.8)/2, Specimen (G38). (**h**) Fungal hypha. Sample 97/2 (94.0)/2, Specimen (V29.2). (**i**) H-shaped branching in a laevigate tube. Sample 97/8 (14.5)/2, Specimen (W28.4). (**j**) Fungal hypha. Sample 97/2 (39.0)/4, Specimen (H29). (**k**) Cuticle-like sheet (*Nematothallus*). Sample 97/2 (36.2)/3, Specimen (S41). (**l**) Cuticle of a stomatous plant (note the hole where a stoma was situated). Sample 97/9 (24.0)/2, Specimen (Q44.2). (**m**) Cuticle of a stomatous plant (note the stoma with the guard cells in place). Sample 97/2 (36.2)/3, Specimen (F35.2). (**n**) Fragment of arthropod cuticle. Sample 97/2 (89.0)/6, Specimen (O29). (**o**) Fragment of arthropod cuticle. Sample 97/2 (94.0)/2, Specimen (E35). (**p**) Spiny ?tube of unknown affinity. Sample 97/2 (34.8)/2, Specimen (Q43).

of early land plant phytodebris. They selected representatives of living plants considered to be basal (phylogenetically early diverging) and acetolysed them. The process of acetolysis mimics the results of natural rotting, stripping out labile components and leaving only those composed of or containing resistant parts (i.e. those parts that are most likely to survive in the fossil record). When acetolysing various bryophytes they recovered fragments reminiscent of Middle Ordovician–Early Devonian cuticle-like sheets and suggested that some may derive from ancient bryophytes (Kroken *et al.* 1996; Cook and Graham 1998; Graham *et al.* 2004). However, it has been suggested that some of these resemblances are only superficial with such basic morphological structures produced by a variety of organisms (e.g. Edwards *et al.* 1998*a*).

The debate around the origin of the cuticle-like sheets seemingly found a solution in the exquisitely preserved charcoalified plants from the late Silurian–Early Devonian of the Anglo-Welsh Basin (Edwards 1996). These contained spectacularly preserved nematophytes described in detail by Edwards *et al.* (2013, 2018). Some of these have a clear 'cuticular' covering associated with their internal tubular anatomy. The superior preservation of the charcoalified forms, compared to those preserved as coalified compressions, revealed structures that Edwards and co-workers interpreted as of fungal and lichen affinities (Edwards and Axe 2012; Edwards *et al.* 2013, 2018; Honegger *et al.* 2013, 2017).

Dispersed 'tubular structures'

Co-occurring with the 'cuticle-like sheets' in palynological preparations are usually a variety of tubular structures existing either as individual tubes of varying morphology, or as associations of tubes, either of one or a mixture of morphologies. The conducting tissues of tracheophytes comprise xylem (tracheids and their equivalents) and phloem. Tracheids themselves are lignified and, as such, have a high preservation potential. When a plant disintegrates after death, individual tracheids (or more usually bundles of tracheids) may be extensively transported prior to deposition as phytodebris. The earliest reported *in situ* tracheids in plant megafossils are found in rhyniophytoid plants from the upper Silurian (Ludlow) (Edwards and Davis 1976) and Lower Devonian (Lochkovian) (Edwards *et al.* 1992) of the Anglo-Welsh Basin. Meanwhile, dispersed tracheids are first reported from the Lower Devonian (Pragian) (e.g. Gensel *et al.* 1991).

Gray and Boucot (1977) postulated that many of the tubes that could not be positively identified as tracheids of vascular plants were derived from early land plants. Although these were clearly not genuine tracheids they argued that they represented conducting tissues and called them 'tracheid-like tubes' noting that those with internal annular and spiral thickenings bore a resemblance to the tracheids of vascular plants. Banks and others again urged caution (e.g. Banks 1975*a*, *b*; Schopf 1978). Clearly, many of the tubular structures resembled those known *in situ* from nematophytes (Lang 1937; Høeg 1942; Lyon 1962) and both parties agreed that at least some of these tubular structures may derive from the nematophytes (Gray and Boucot 1977; Gray 1985). Subsequently, Burgess and Edwards (1991) erected a formal taxonomic system for naming and classifying the dispersed tubular structures (see also Wellman 1995).

The taphonomic acetolysis experiments undertaken by Graham and co-workers (see above) also produced various structures that they related to the dispersed tubular structures. For example, Kodner and Graham (2001) reported on tubes produced by acetolysis of bryophytes. However, it has been suggested that these resemblances are also in this case only superficial (e.g. Edwards *et al.* 1998*a*).

Again, the exquisitely preserved charcoalified megafossils from the upper Silurian–Lower Devonian of the Anglo-Welsh Basin appear to have provided a partial solution to this problem. It is clear that the types of tubular structure forming the anatomy of the different nematophytes are very similar to dispersed forms that occur in palynological preparations from the same, and other coeval, deposits (see discussion below). Thus, it seems that many of the tubular structures are of nematophyte (i.e. probable fungal and possibly also lichen) origin.

It is highly likely, however, that not all of the tubes derive from nematophytes and some probably have entirely different sources. Strother (2010) noted that where we have plant megafossil remains in continental deposits of Middle Ordovician–Early Devonian age thalloid forms often dominate over axial forms. These thalloid forms are difficult to interpret due to a paucity of recognizable characters, but it is plausible that many may represent the remains of nematophytes. On the other hand, it has been suggested that others may represent cyanobacterial mats (Tomescu and Rothwell 2006; Tomescu *et al.* 2006, 2008, 2009). These authors showed that cyanobacterial mats did indeed form a component of these embryonic terrestrial biotas, as they are preserved in early Silurian (Llandovery) non-marine deposits such as the Massanutten Sandstone of Virginia, USA. These mat remains occur as flattened coalified thalloid structures on bedding planes and are run through with simple tubular structures that probably represent the sheaths of cyanobacteria. At least some of the simple laevigate tubes that occur dispersed in non-marine deposits of this age are thus likely derived from disintegrated cyanobacterial mats. These are equivalent to the simple tubes common in Precambrian palynological preparations that represent the sheaths of cyanobacteria, such as those described from one-billion-year-old non-marine deposits from the Torridonian of Scotland (Strother *et al.* 2011). Tomescu *et al.* (2010) reported on taphonomic simulation experiments on various modern taxa, including cyanobacteria that demonstrated that similar structures might survive in the fossil record.

Ultrastructural and geochemical analysis of dispersed tubular structures has also been undertaken with a view to better understanding them. Taylor and Wellman (2009) reported on a transmission electron microscope (TEM) ultrastructural analysis of both banded tubes and early land plant dispersed tracheids. They noted marked differences between the two in terms of gross structure, concluding that the banded tubes most likely derived from nematophytes.

The geochemistry of various types of tubular structure and fragments of vascular plant and nematophyte megafossils has also been analysed. Edwards *et al.* (1997) reported the presence of a signal for degraded lignin from the xylem of early vascular land plants, but unequivocal evidence for lignin was not forthcoming (Edwards *et al.* 1998*a*). Boyce *et al.* (2003) analysed conducting tissues in silicified plants preserved in the Rhynie chert Lagerstätte; following this, they suggested that some Rhynie chert plants lacked lignin in their vascular thickenings. Associations of tracheid-like tubes were analysed by Niklas and Pratt (1980) who interpreted their results as indicating the presence of lignin-like constituents. Regarding nematophyte megafossils, Niklas (1976) reported cutin and suberin derivatives from *Prototaxites*. However, following their geochemical analyses, Abbott *et al.* (1998, p. 1416) concluded that *Prototaxites* might contain ‘an extinct polyphenolic structural biomacromolecule that was a failed experiment during terrestrialisation’. Overall the various geochemical investigations that have been undertaken, utilizing various techniques, have provided rather ambiguous and inconclusive results thus far. This is probably a consequence of taphonomy, with many of the coalified and permineralized remains being of rather high thermal maturity and the charcoalified remains certainly being of very high thermal maturity. Again, as geochemical techniques improve and new techniques are developed, this may prove a fruitful line of enquiry in the future.

The nematophyte story

We have previously encountered the nematophytes, an enigmatic group of so-called ‘plants’. Lang (1937) proposed the group Nematophytales based on his analysis of *Nematothallus* and *Prototaxites* recovered from the upper Silurian–Lower Devonian of the Anglo-Welsh Basin. Lang’s concept of *Nematothallus* was of a thalloid organism with tubular anatomy covered by a cuticle and with spores produced among the tubes. Subsequently Strother (1988) described further specimens from North America and reported on a re-examination of Lang’s material (Strother 1993). Also included in the nematophytes by Lang was *Prototaxites* that had long been known from Silurian–Devonian localities worldwide. *Prototaxites* occurred as ‘trunks’, and fragments thereof, composed of associations of tubes (Hueber 2001). Subsequently further nematophyte taxa were established by Lyon (1962) describing *Nematoplexus* and Burgess and Edwards (1988) later erecting a new genus, very similar to *Prototaxites*, called *Nematosketum*.

The nematophytes have a most peculiar anatomy, making comparisons with extant organisms difficult and, as such, a large literature debating their affinities has accumulated. When initially establishing the Nematophytales, Lang (1937, p. 287) noted that ‘[w]hat is required, however, is not discussion, but an increase in our knowledge of these plants, which appear to have had a very general distribution in Siluro-Devonian times’. Fortunately, new information on the anatomy of these plants became available following the discovery of material in three Lagerstätten: the Rhynie chert and the charcoalified plant assemblages from Ludford Lane and Hudwick Dingle. The charcoalified plant remains from the upper Silurian–Lower Devonian of the Welsh Borderland yielded nematophyte specimens with exquisitely preserved anatomical detail. Following anatomical examination of the specimens, Edwards and Axe (2012) concluded that *Nematosketum* was of fungal affinity. Edwards *et al.* (2013, 2018) reported that the anatomy of *Nematothallus* was indicative of lichenized fungi. Silicified specimens of *Prototaxites* from the Early Devonian Rhynie chert, alongside charcoalified specimens from the upper Silurian–Lower Devonian of the Anglo-Welsh Basin, demonstrated an anatomy indicative of fungal affinities. Subsequently, Honegger *et al.* (2013) also described cyanobacterial and algal lichens among the assemblages of charcoalified fossil plants.

Whilst some of the phytodebris recovered from Middle Ordovician–Lower Devonian terrestrial deposits may be derived from land plants, it seems likely that many of the tubular structures and cuticle-like sheets derive from nematophytes. The current picture that might be drawn of these embryonic terrestrial environments appears to be that the earliest land plants shared the terrestrial surface with fungi/?lichens belonging to the Nematophytales, the latter of which may have formed a significant component of the biota.

The fungal story

The remit of this review is early land plant phytodebris. However, it seems prudent to discuss fungal phytodebris because it has historically played a significant role in discussions of early land plant phytodebris and because the nematophytes, as discussed, have now been shown to be of probable fungal/lichen affinity. Often co-occurring with early land plant phytodebris in palynological preparations are fungal remains in the form of dispersed spores and fragments of hyphae. The spores and hyphae of most extant fungi are constructed of the resistant macromolecule chitin, and Graham *et al.* (2017) recently reported on taphonomic acetolysis experiments on extant fungi, confirming that some fungal structures are indeed resistant and likely to survive in the fossil record. The earliest reported dispersed fungal spores are from the upper Silurian (Ludlow) (Sherwood-Pike and Gray 1985), with fragmented hyphae being reported from the same deposits. However, older hyphae have been reported, for example, from the lower Silurian (Llandovery) (Pratt *et al.* 1978; Johnson 1985) and possibly uppermost Ordovician (e.g. Thusu *et al.* 2013). Some of these early fossil fungi are from unequivocal non-marine deposits (e.g. Pratt *et al.* 1978; Wellman 1995). These remains are generally accepted as fungal in origin, although more precise taxonomic assignments are problematic due to a lack of morphological characters (e.g. Auxier *et al.* 2016; Smith 2016). We know from phylogenetic analyses and molecular clock studies that fungi originated early in the Mesoproterozoic (e.g. Parfrey *et al.* 2011), but it is entirely unclear when they first appeared on the land and if this was before, during or after the invasion of the land by plants. However, it seems highly likely that symbiotic relationships between multicellular green algae and fungi were intimately related to the origin of land plants and their invasion of the land. An excellent review of our current understanding of the earliest terrestrial fungi is provided by Taylor *et al.* (2015).

Early terrestrial animals

The colonization of the land by plants paved the way for aquatic animals to invade subaerial habitats (reviewed by Shear and Selden 2001; Kenrick *et al.* 2012). Phylogenetic analysis reveals that many different animal groups invaded the land on many different occasions. In some cases, this may have been directly from marine environments and, in others, it may have been via 'half-way houses' such as estuaries or continental freshwater rivers, lakes and waterlogged land. Non-marine animal-derived palynodebris from the Middle Ordovician–Lower Devonian consists predominantly of fish scales (the organic component survives palynological preparation techniques) and fragments of the chitinous exoskeleton of arthropods (Shear and Selden 2001). Whilst the fish remains are clearly aquatic, it is difficult to know if the arthropod cuticle derives from aquatic or truly terrestrial forms, unless positive taxonomic assignments can be made. The earliest fragments of arthropod that are known to be of non-marine origin (because they derive from terrestrial deposits) are from the early Silurian (Llandovery) deposits of the Tuscarora Formation in North America (Gray and Boucot 1993) and the late Silurian (early Wenlock) deposits of the Silurian inliers of the Midland Valley of Scotland (Wellman and Richardson 1993; Wellman 1995). However, it is unclear if these represent animals that inhabited aquatic freshwater environments or the land.

Conclusions

It is clear that non-pollen palynomorphs (phytodebris) continue to play an important role in research into the earliest land plants and their co-inhabitants of the land. Whilst recent years have witnessed a dramatic increase in knowledge regarding the affinities and nature of many of their producers, particularly regarding the nematophytes, there is still much to learn concerning this 'smorgasbord' of fossil remains.

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Data availability All materials and datasets generated during the current study are housed in and available from the Centre for Palynology of the University of Sheffield repository.

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