The microfossil record of early land plants

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Dispersed microfossils (spores and phytodebris) provide the earliest evidence for land plants. They are first reported from the Llanvirn (Mid-Ordovician). More or less identical assemblages occur from the Llanvirn (Mid-Ordovician) to the late Llandovery (Early Silurian), suggesting a period of relative stasis some 40 Myr in duration. Various lines of evidence suggest that these early dispersed microfossils derive from parent plants that were bryophyte-like if not in fact bryophytes. In the late Llandovery (late Early Silurian) there was a major change in the nature of dispersed spore assemblages as the separated products of dyads (hilate monads) and tetrads (trilete spores) became relatively abundant. The inception of trilete spores probably represents the appearance of vascular plants or their immediate progenitors. A little later in time, in the Wenlock (early Late Silurian), the earliest unequivocal land plant megafossils occur. They are represented by rhyniophytoids. It is only from the Late Silurian onwards that the microfossil/ megafossil record can be integrated and utilized in interpretation of the flora. Dispersed microfossils are preserved in vast numbers, in a variety of environments, and have a reasonable spatial and temporal fossil record. The fossil record of plant megafossils by comparison is poor and biased, with only a dozen or so known pre-Devonian assemblages. In this paper, the early land plant microfossil record, and its interpretation, are reviewed. New discoveries, novel techniques and fresh lines of inquiry are outlined and discussed.

Keywords: early land plants; early embryophytes; bryophytes; tracheophytes; spores; phytodebris

1. INTRODUCTION

The earliest fossil evidence for embryophytes consists entirely of dispersed microfossils. These oldest generally accepted microfossils are from the Llanvirn (Mid-Ordovician), but it is not until the Wenlock (Late Silurian), some 40 Myr later, that the oldest unequivocal land plant megafossils occur. The early land plant microfossil record consists of dispersed spores and phytodebris (fragments of cuticles and tubes). Such remains are preserved in large numbers in a variety of environments (continental and marine) because: (i) they were composed of recalcitrant material and readily fossilized; (ii) they were produced in vast numbers; and (iii) they had the potential for long-distance dispersal by wind and water due to their small size. Consequently they have an excellent fossil record with good spatial and temporal representation. However, the dispersed microfossils are difficult to interpret because they represent discrete parts of whole organisms and phytodebris is fragmentary. Nonetheless, comparisons with purportedly homologous structures in extant plants, and to a certain extent younger fossil plants, provide compelling evidence that they derive from land plants. As the earliest evidence for land plants, they are utilized in interpretation of the nature and affinities of the plants from which they derive. Furthermore, their excellent fossil record documents the early evolution and diversification of land plants, and provides information on the composition and distribution of early terrestrial vegetation. In this review, the microfossil record for early embryophytes is documented, and interpretation of these remains discussed.

2. DISPERSED SPORES

(a) *The fossil record*

The earliest dispersed embryophyte spores that appear creditable are reported from the early Llanvirn (Vavrdova 1984) of Bohemia (i.e. Perunica, the palaeogeographic term applied to the Cambro-Devonian of Central Bohemia; A. J. Boucot, personal communication) and from the mid-Llanvirn of Saudi Arabia (Strother *et al.* 1996), well-separated palaeogeographically from Perunica. Apart from Vavrdova's limited material (she only reports spore tetrads) more or less identical spore assemblages have been reported from the Llanvirn (Mid-Ordovician) to Llandovery (Early Silurian) (Gray 1985, 1991; Richardson 1988; Strother 1991; Wellman 1996; Steemans 1999). These early spores have unusual configurations/ morphology in comparison with mature spores of extant embryophytes (figures 2 and 3), and are sometimes termed 'cryptospores', a name originally used to reflect their unfamiliar appearance and lack of knowledge regarding the nature of their producers (see Richardson 1996a and references therein). Cryptospores comprise monads and permanently united dyads and tetrads, that are either naked or enclosed within a thin, laevigate or variously ornamented envelope. The nature of cohesion between spores in permanently united dyads and tetrads is unclear (Wellman 1996). They are termed unfused if
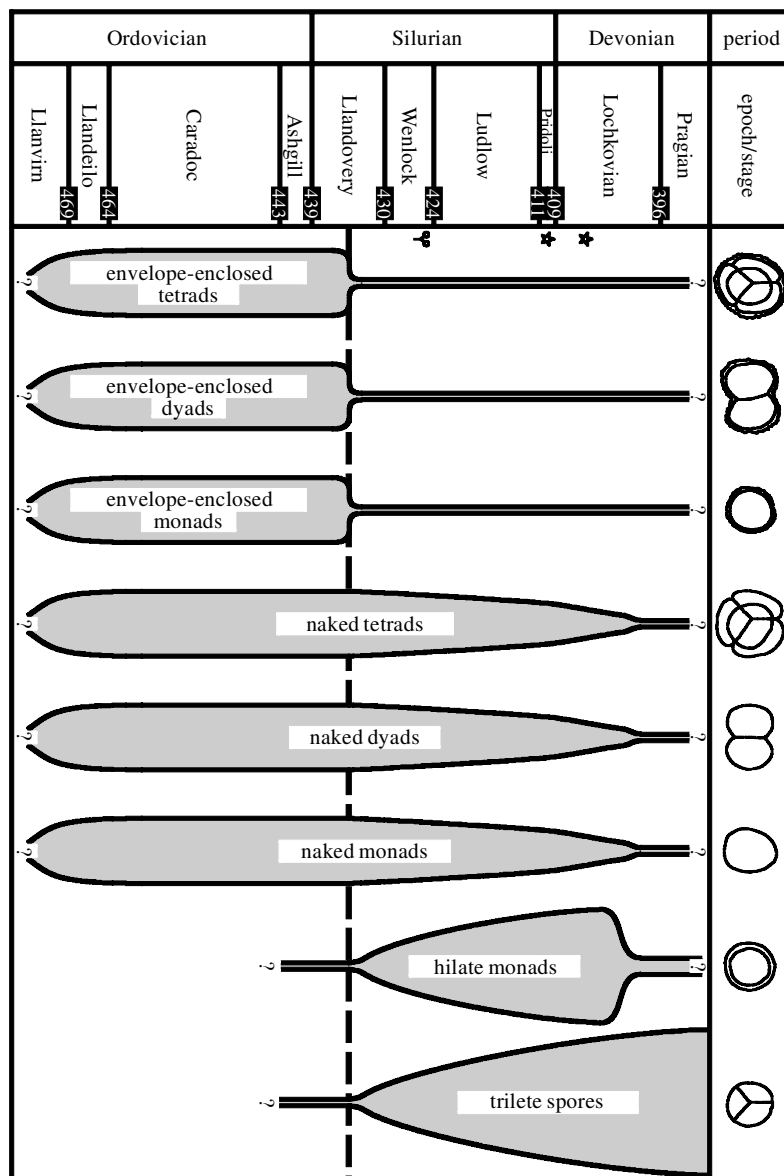
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Figure 1. Stratigraphical range chart for early land plant spore morphotypes. Time-scale from Harland *et al.* (1989). Regarding annotation adjacent to the stratigraphic column: the small '*Cooksonia*' indicates the age of the earliest unequivocal land plant megafossils, the asterisks indicate the age of important plant mesofossil assemblages (i.e. Ludford Lane-Pridoli; North Brown Clee Hill-Lochkovian). The dashed time-line indicates the position of the major change in the nature of dispersed spore assemblages in the Llandovery. The width of range bars provides a very basic indication of relative abundance to illustrate gross changes in abundance through time. Note that range bar width has no quantitative implications. The taper and question marks at the base of range bars extending into the Llanvirn indicate the age of the earliest known spore assemblages and do not necessarily coincide with their first appearance, nor necessarily with changes in abundance.

there is a superficial line of attachment between the spores and cohesion probably results from localized exospore links or bridges rather than large-scale fusion. They are termed fused if there is no discernible line of attachment and cohesion probably results from fusion over most or all of the contact area. Cohesion may also result from enclosure within a tight-fitting envelope. The composition of cryptospores (wall and envelope) is unknown, but their preservation in ancient deposits suggests they constitute sporopollenin or a sporopollenin-type macromolecule. Since there seems little question that these structures are spores, the term cryptospore has no taxonomic usefulness, but we retain the term here for descriptive convenience.

Reports of Ordovician–Early Silurian dispersed spores are relatively few, but are stratigraphically and geographically widespread, and indicate that cryptospore assemblages are remarkably constant in composition (both temporally and spatially) throughout this interval (Gray 1985, 1988, 1991; Richardson 1996a; Strother *et al.* 1996; Wellman 1996; Steemans 1999). These data suggest that the vegetation was widespread, but of limited diversity, with little evolutionary change (at least in the spores) during an interval some 40 Myr in duration.

Over much of the globe, a major change in the nature of spore assemblages is reported in the late Llandovery (late Early Silurian) (Gray 1985, 1991; Gray *et al.* 1986; Richardson 1988, 1996a; Burgess 1991; Wellman 1996; Steemans 1999) (figure 1). While naked monads, dyads and tetrads continued to dominate spore assemblages, the abundance of envelope-enclosed forms is seriously reduced, and in places they appear to virtually disappear. At the same time, hilate monads and trilete spores first became widespread and occur in relative abundance. Hilate monads comprise single spores with a circular contact area on their proximal surface, and clearly
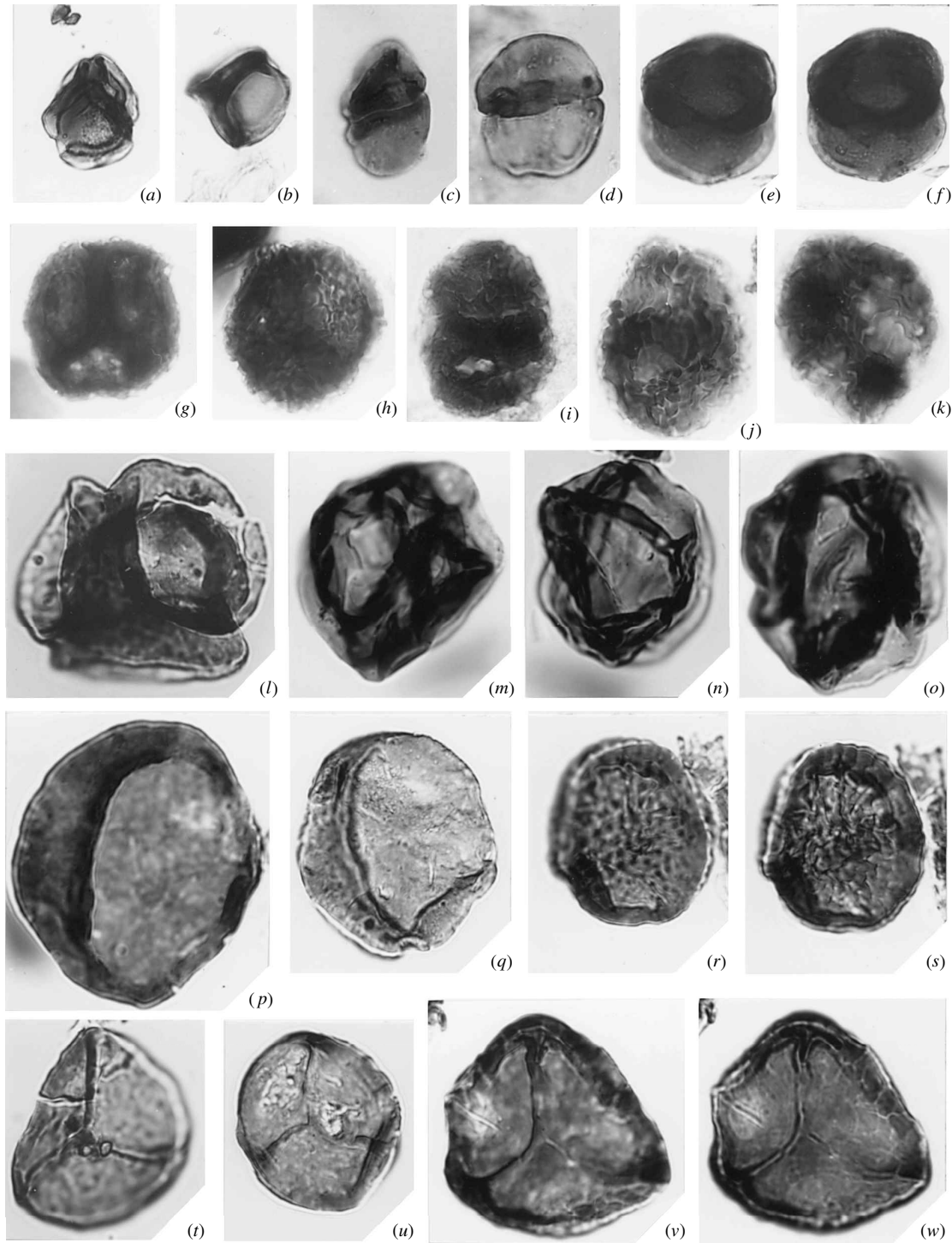
Figure 2. LM images of dispersed early land plant spores. (*a–k*) from the type area for the Caradoc, Shropshire, England (Caradoc, Late Ordovician) (Wellman 1996); (*l–w*) from the Stonehaven Group of the north-east Midland Valley of Scotland (late Wenlock, Late Silurian) (Wellman 1993*b*). (*a,b*) Naked, unfused, permanent tetrad (×1500); (*c,d*) naked, unfused, permanent dyad (×1500); (*e,f*) naked, fused, permanent dyad (×1500); (*g,h*) envelope-enclosed permanent tetrad (×1500); (*i,j*) envelope-enclosed permanent dyad (×1500); (*k*) envelope-enclosed monad (×1500); (*l*) naked, fused, permanent tetrad (×1000); (*m–o*) naked monad (×1000); (*p,q*) laevigate hilate monad (×1000); (*r,s*) ornamented hilate monad (×1000); (*t,u*) laevigate trilete spore (×1000); (*v,w*) ornamented trilete spore (×1000).
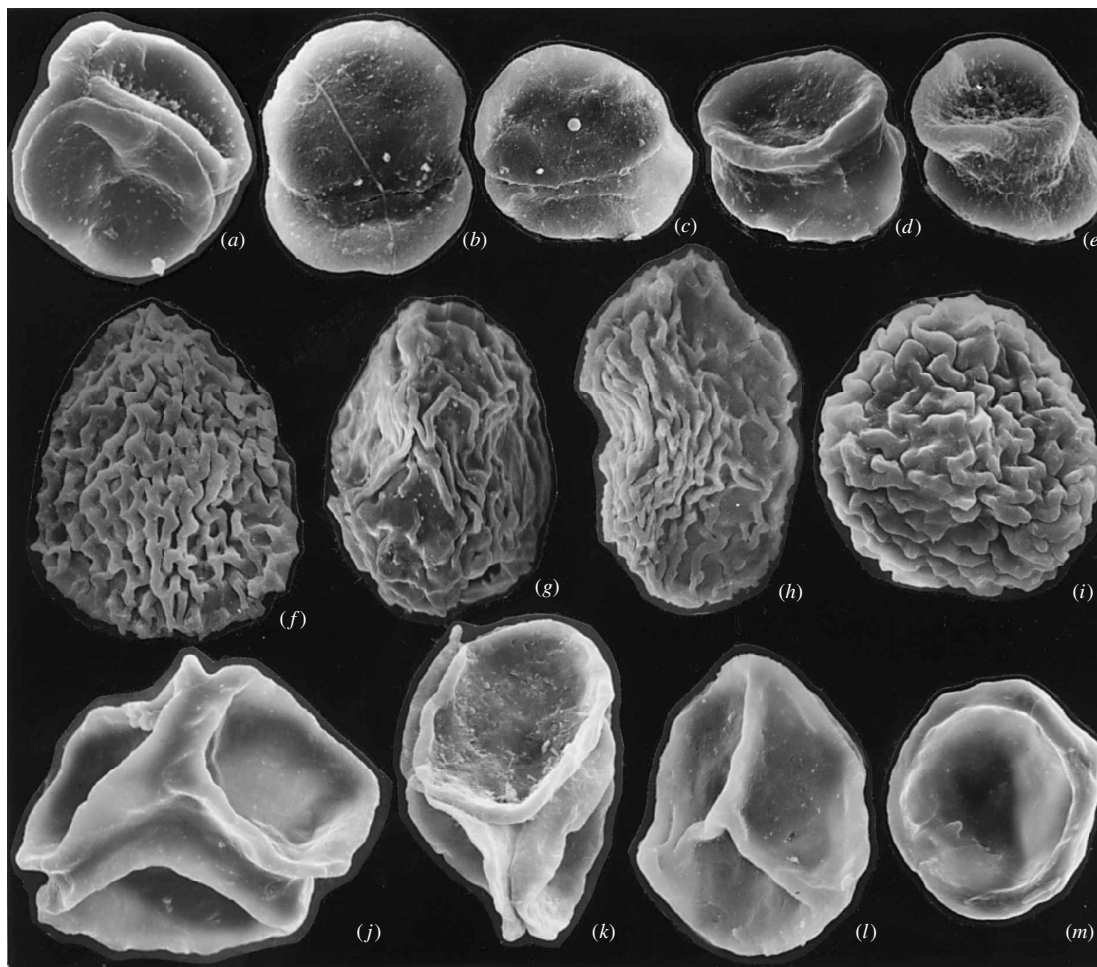
Figure 3. SEM images of dispersed early land plant spores. (*a–i*) From the type area for the Caradoc, Shropshire, England (Caradoc, Late Ordovician) (Wellman 1996); (*j–m*) from the Silurian inliers along the southern margin of the Midland Valley of Scotland (early Wenlock, Late Silurian) (Wellman & Richardson 1993). (*a*) Naked, unfused, permanent tetrad (×2000); (*b,c*) naked, unfused, permanent dyad (×1500); (*d,e*) naked, fused, permanent dyad (×1500); (*f–h*) envelope-enclosed permanent ?dyad (×1500); (*i*) envelope-enclosed permanent ?monad (×1500); (*j*) naked, fused, permanent tetrad (×1210); (*k*) loose tetrad (×1070); (*l*) laevigate trilete spore (×1380); (*m*) laevigate hilate monad (×1230).

formed in dyads that dissociated prior to dispersal (figures 2 and 3). Similarly, trilete spores comprise single spores with a distinct trilete scar and three contact areas on their proximal surface, and clearly formed in tetrads that dissociated prior to dispersal (figures 2 and 3). Dissociation of the products of (presumably) meiosis suggests a major change in plant reproductive strategy (see Gray 1985; Wellman *et al*. 1998*a*; Edwards *et al*. 1999).

Both trilete spore and hilate monad abundance and diversity increased throughout the Late Silurian. It was previously considered that their first appearance in abundance, and associated changes in dispersed spore assemblages, was near-contemporaneous on a global scale. However, recent reports from Ashgill (Upper Ordovician)–Lower Llandovery (Early Silurian) deposits from Turkey and Saudi Arabia support an early appearance of both hilate monads and trilete spores in this region of northeast Gondwana (Steemans *et al*. 1996, 2000; Wellman *et al*. 2000*a*). However, the hilate monads and trilete spores occur in low numbers, and do not

coincide with a decrease in the abundance of envelope-enclosed cryptospores, which in this region persist in relative abundance at least into the Late Silurian.

Sculptured forms of both hilate monads and trilete spores (figure 2) appear in the late Wenlock (Late Silurian) and structural–sculptural innovations ensued as both groups proliferated throughout the remainder of the Silurian and earliest Devonian (e.g. Richardson & McGregor 1986; Burgess & Richardson 1995; Steemans 1999). Again, the appearance of sculptured hilate monads and trilete spores was believed to be near-contemporaneous on a global scale, but recent reports from Saudi Arabia indicate that ornamented hilate monads may occur earlier (in the Llandovery) in this region (Steemans *et al*. 2000). Other morphotypes (naked dyads and tetrads) persisted in the hilate monad/trilete spore-dominated assemblages, but as an increasingly insignificant element. In the earliest Devonian, hilate monad numbers began to decline (possibly rapidly), until cryptospores became a minor component of spore assemblages that were

dominated by a bewildering variety of trilete spores (e.g. Richardson & McGregor 1986). Cryptospores persist in spore assemblages at least until the end of the Lochkovian (Early Devonian). Their upper stratigraphic range is poorly documented, but they are seldom reported from post-Lochkovian strata.

For the Late Silurian–Early Devonian interval there is considerable variation in the calibre of reporting for the dispersed spore record, with different time intervals exhibiting substantial differences in the number and quality of reports, and the extent of their palaeogeographical coverage. This creates problems when attempting to identify palaeophytogeographical variations, which are further enhanced by difficulties associated with recognizing the effects of small-scale variation dependent on local environmental control (e.g. substrate, altitude, etc.), subtle facies effects and non-contemporaneity due to incorrect correlation of strata. Nonetheless, certain patterns are beginning to emerge, and are summarized below. Recent detailed reviews are provided by Richardson (1996*a*), Steemans (1999) and Edwards & Wellman (2000).

For the Late Silurian there is acceptable reporting of spore assemblages from the palaeocontinents Laurentia, Avalonia and Baltica, which were closely associated and constituted part of a large cluster of land that straddled the Equator, and from northern Gondwana, which lay further to the south and was separated by a relatively large ocean. Reporting from elsewhere is sparse. Sequences of spore assemblages from Laurentia, Avalonia and Baltica are notably similar in composition, suggesting that this land mass contained a flora representing a single palaeophytogeographical realm, and subtle differences probably reflect small-scale variation related to localized variations in environmental conditions. However, sequences of spore assemblages from northern Gondwana (e.g. Spain, north Africa and Brazil; J. Gray, unpublished data), although sharing many elements in common with those from Laurentia, Avalonia and Baltica, also exhibit marked differences, suggesting they belong to a different palaeophytogeographical realm (Richardson & Ioannides 1973; Rodriguez 1983; Tekbali & Wood 1991).

By earliest Devonian times, Laurentia, Avalonia and Baltica were all essentially part of the same large continent (the 'Old Red Sandstone continent'), which was now not far removed from Gondwana, the distance between them having diminished through the Late Silurian. The vast majority of spore assemblages known from the Lochkovian (Early Devonian) is from the 'Old Red Sandstone continent' and northern Gondwana, with few reported assemblages from elsewhere. One might expect differences between the sequences of spore assemblages from these two regions to become less apparent as the two palaeophytogeographical realms moved closer together and permitted interaction between their biota, and preliminary research seems to indicate that this was the case. However, comparisons between Lochkovian spore assemblages are difficult because localized variation appears to have become more prevalent by this time, hampering the identification of larger-scale variation. The small-scale variation probably reflects a combination of effects, including variation due to localized differences in environmental conditions and facies effects, which are difficult to disentangle. For example, in the 'Old Red Sandstone continent' there are differences between coeval spore assemblages from upland intermontane and lowland floodplain deposits (Richardson *et al*. 1984; Wellman 1993*a*; Edwards 1996; Wellman & Richardson 1996; Wellman *et al*. 2000*b*). It is unclear to what extent these reflect subtle facies effects or variation (small- or large-scale) in the distribution of flora due to variation in environment (altitude, climate, substrate, etc.). However, it is clear that cryptospores are far more abundant in the lowland floodplain deposits than in the upland intermontane deposits, possibly because the former were a damper environment more suited to the cryptospore-producing plants (e.g. Wellman & Richardson 1996; Wellman *et al*. 2000*b*).

(b) *Affinities*
(i) *Introduction*

Evidence for the affinities of early higher land plant spores (cryptospores and trilete spores) is derived from four main sources: (i) occurrence (i.e. depositional environment) of the dispersed fossil spores; (ii) inferences based on comparison with the spores of extant land plants (size and morphology); (iii) studies of land plant fossils preserving *in situ* spores; (iv) analysis of spore wall ultrastructure. There is abundant evidence suggesting that trilete spores represent the reproductive propagules of land plants (see Gray 1985, 1991 and references therein). However, evidence of similar affinities for the cryptospores, particularly the earliest occurrences, has been more fiercely contested (e.g. Banks 1975). Nonetheless, recent findings provide convincing evidence for higher land plant affinities, and there are now few who disagree with such an origin (see Gray 1985, 1991; Strother 1991; Richardson 1992; Taylor 1996; Edwards *et al*. 1995*a*, 1998). The evidence for higher land plant/embryophyte affinities is summarized below.

(ii) *Occurrence of early land plant spores*

It has long been noted that early land plant spores are distributed in a similar range of depositional environments in which the spores/pollen of extant land plants occur and with similar abundances. Their occurrence in continental and nearshore marine deposits (with abundances usually decreasing offshore) is wholly consistent with their representing the subaerially released spores of land plants, which were transported to their sites of deposition through the actions of wind and water. However, while there are numerous examples of spore assemblages derived from continental deposits from the Late Silurian and Early Devonian, few examples exist for the Ordovician–Early Silurian interval. These findings are almost certainly an artefact of the stratigraphical record: the Ordovician–Early Silurian was a time of persistently high sea levels and fewer continental deposits are known, and those that do exist possess geological characteristics unsuitable for the preservation of organic-walled microfossils (e.g. unsuitable lithologies and/or high thermal maturity). The earliest known spore assemblages preserved in continental deposits are from the Ashgill (Gray 1988), Llandovery (Pratt *et al*. 1978; Johnson 1985; Gray 1988) and Wenlock (Strother & Traverse 1979; Wellman 1993*b*; Wellman & Richardson 1993). All of these reported assemblages include cryptospores and trilete spores, except those from

the Ashgill palaeokarst on Manitoulin Island, Ontario (Gray 1988), the early Llandovery Tuscarora Formation in the Millerstown section, Pennsylvania (Gray 1988) and the early Llandovery Tuscarora Formation at the Mill Hall locality, Pennsylvania (Johnson 1985), which are the oldest and appear to contains only cryptospores.

(iii) *Comparisons with extant embryophyte spores*

Early higher land plant/embryophyte spores are similar to the reproductive propagules of extant land plants in terms of size, gross morphology and possession of a thick sporopollenin spore wall (regarded as a synapomorphy for embryophytes). Sporopollenin walls may have multiple functions (Graham & Gray 2000), one being to protect propagules during transport following subaerial release (e.g. Blackmore & Barnes 1987). Thus the possession of such walls in early higher land plant spores provides excellent evidence that they were functionally similar to their modern counterparts. Furthermore, the small size of early land plant spores is within the range of subaerially dispersed spores produced by extant free-sporing plants. Based largely on analogy with the reproductive propagules of extant embryophytes, Gray (1985, 1991 and references therein) has argued persuasively that the obligate spore tetrad of the fossil record is an ancestral character in embryophytes and that such tetrads derive from land plants at a bryophyte, most likely hepatic, grade of organization. She notes that among extant free-sporing embryophytes only hepatics regularly produce permanent tetrads as mature spores, some of which are contained within an envelope similar to those enclosing certain fossil spore tetrads, but that a tetrad regularly occurs in the spore ontogeny of embryophytes. The affinities of hilate monads and dyads are more equivocal, primarily because such morphologies do not have an obvious modern counterpart (Wellman *et al.* 1998*a*) either in mature spores or in spore ontogeny. Dyads rarely occur in extant (non-angiosperm) embryophytes, and only through meiotic abnormalities (Fanning *et al.* 1991; Gray 1993; Richardson 1996*b*; Wellman *et al.* 1998*a,b*). The abundance of dyads in early land plant spore assemblages indicates that they were commonly produced and are therefore probably not the products of meiotic abnormalities. Their occurrence is most comfortably explained by invoking successive meiosis, with separation occurring following the first meiotic division and sporopollenin deposition on the products of the second division. It has been noted that monads, dyads and tetrads often have identical envelopes, and some authors have suggested that they are closely related, perhaps even deriving from a single species (Johnson 1985; Richardson 1988, 1992; Strother 1991; Hemsley 1994). However, fixing affinity on the basis of a single character is problematic. Trilete spores dissociated from juvenile tetrads have a clear counterpart among extant embryophytes, where their production is widespread among free-sporing tracheophytes and also occurs sporadically among bryophytes (e.g. Gray 1985).

(iv) *Fossil plants preserving* in situ *spores*

Studies of *in situ* spores supply the only direct link between the dispersed spore and plant megafossil records, and are critical to our understanding of the affinities of dispersed spore types. Unfortunately, however, the plant megafossil record for the Ordovician–Early Devonian is relatively poor (see Edwards 1990; Edwards & Wellman 2000). Plant megafossils are practically unknown until the Late Silurian, probably because the vast majority of plants, believed to be at a bryophyte-like grade of organization, lacked the appropriate recalcitrant tissues suitable for preservation. Hence there are no *in situ* spore records for the first 50 million or so years of higher land plant evolution. When they eventually appear, land plant megafossils are initially very rare, becoming progressively more common in younger sediments (Edwards & Wellman 2000). They are usually preserved as coalified compressions, and in this mode of preservation *in situ* spores are generally absent or, when present, too poorly preserved to permit comparisons with better-preserved dispersed spores. Occasionally, however, exceptional preservation of plant megafossils preserves *in situ* spores in sufficient detail to enable such comparisons (Allen 1980; Gensel 1980). Suitable preservation occurs at the Ludford Lane (Late Silurian-Pridoli) and North Brown Clee Hill (Early Devonian-Lochkovian) localities from the Welsh Borderland, and the record of *in situ* early land plant spores is based primarily on material from these localities (see reviews by Fanning *et al.* 1991; Edwards 1996, this issue; Edwards & Richardson 1996). At both localities extremely small plant fragments (sometimes referred to as mesofossils sensu Hughes (1994)) are preserved as relatively uncompressed coalifications that preserve exquisite cellular detail (Edwards 1996).

The record of early land plants with *in situ* spores has most recently been reviewed by Edwards (1996, this issue), Edwards & Richardson (1996) and Edwards & Wellman (2000). It is noteworthy that most cryptospore morphotypes have been recovered *in situ* (naked and envelope-enclosed permanent tetrads and dyads, and hilate monads). However, it is unclear if the parent plants represent relict populations, and provide a true reflection of earlier cryptospore-producing plants, or if the cryptospores are plesiomorphic in more advanced plants, or perhaps even arose due to convergence (Gray 1991; Edwards, this issue). It must be borne in mind that the fossils occur some 65 Myr after the earliest reported cryptospores from the Llanvirn (Mid-Ordovician).

Interpretation of the parent plants is not always straightforward as the mesofossils are fragmentary. Usually only terminal parts of the axes (±sporangia) are preserved, and cellular detail is variable. Furthermore, many of the 'rhyniophytoid' plants preserve unusual character combinations, confusing considerations of affinities. However, trilete spores have been recovered from the rhyniophyte *Cooksonia pertoni* (Fanning *et al.* 1988), which is demonstrably a true tracheophyte (Edwards *et al.* 1992), and the vast majority of trilete spore-producers appear to have constituted plants with bifurcating axes, terminal sporangia and, often, stomata. Interestingly, some dyads and tetrads derive from plants with bifurcating axes/sporangia (Edwards *et al.* 1995*a*, 1999; Wellman *et al.* 1998*a*), a character not represented among extant bryophytes (see Edwards, this issue). Another interesting observation is the presence of stomata on plants containing *in situ* hilate monads (Habgood 2000; Edwards, this issue). Stomata

are absent from liverworts, but present in hornworts, mosses and vascular plants (although losses are not uncommon in these groups, and are generally considered to be related to ecological factors and functional requirements) (see review in Kenrick & Crane 1997).

Consideration of dispersed spore assemblages from Ludford Lane and North Brown Clee Hill allows us to gauge the extent to which the *in situ* record reflects the dispersed record. Permanent tetrads and dyads (including envelope-enclosed forms) were relatively minor components of dispersed spore assemblages dominated by hilate monads and trilete spores. Studies of *in situ* spores reflect this situation in that specimens with tetrads and dyads are extremely rare but those containing hilate monads and trilete spores are abundant. However, not all trilete spore morphotypes have been discovered *in situ*. *In situ* patinate spores and *in situ Emphanisporites*-type spores are extremely uncommon (Edwards & Richardson 2000), although both spore types are abundant in dispersed spore assemblages, and even coprolites, from the mesofossil-bearing horizons. These findings may be a consequence of: (i) preservational artefact (the missing spore types may derive from plants with low preservation potential); (ii) palaeogeographical effects (the missing spore types may derive from plants from outside of the depositional basin—an unlikely scenario as the spores are preserved in coprolites at this locality); (iii) facies effects (the missing spore types may derive from larger plants not represented among the assemblages of small, highly sorted mesofossils).

(v) *Spore wall ultrastructure*

It is well established that analysis of spore wall ultrastructure characters can be extremely profitable when attempting to ascertain the phylogenetic relationships of extant land plants, and similar research has been extrapolated back in time and is now routinely undertaken on fossil spores (e.g. Kurmann & Doyle 1994). Such research is also of paramount importance in studies of spore wall development. Recently there has been a surge of interest in wall ultrastructure in early higher land plant/embryophyte spores, and it is hoped that exploitation of this potentially extremely rich data source will provide characters useful in ascertaining the affinities of these ancient plants, and shed light on the nature of spore wall development.

To date, studies of wall ultrastructure in early land plant spores are in their infancy, and two principal lines of inquiry have been explored. Some of the earlier cryptospores have been studied based on analysis of isolated dispersed spores from the Late Ordovician (Ashgill)–Early Silurian (Llandovery) of Ohio, USA (Taylor 1995*a*,*b*, 1996, 1997). Later cryptospores and trilete spores have been studied based on analysis of *in situ* spores exceptionally preserved in mesofossils from the latest Silurian (Ludford Lane) and earliest Devonian (North Brown Clee Hill) localities in the Welsh Borderland (Rogerson *et al.* 1993; Edwards *et al.* 1995*b*, 1996*a*, 1999; Wellman 1999; Wellman *et al.* 1998*a*,*b*). Studies on Late Silurian–Early Devonian dispersed spores remains an unexploited, but potentially extremely useful, data source. Nonetheless, many early land plant spore morphotypes have now been ultrastructurally examined. Taylor has studied early

examples of naked and envelope-enclosed tetrads (Taylor 1995*b*, 1996, 1997) and naked and envelope-enclosed dyads (Taylor 1995*a*, 1996, 1997). Later tetrads (Edwards *et al.* 1999), dyads (Wellman *et al.* 1998*a*) and hilate monads (Wellman *et al.* 1998*b*) have also been examined, as has a variety of trilete spore taxa (Rogerson *et al.* 1993; Edwards *et al.* 1995*b*, 1996*a*; Wellman 1999).

In terms of ascertaining phylogenetic relationships, findings to date are rather difficult to interpret, with no clear patterns emerging regarding the relationships between different mesofossil taxa, *in situ* spore morphology and wall ultrastructure. This is most likely a consequence of the frailty of the database, as studies are extremely limited to date, and there are major gaps in our knowledge. However, interpretation of wall ultrastructure in early embryophyte spores is also problematical due to a number of technical and theoretical factors. These include: (i) different workers employ slightly differing techniques, each with its associated artefacts, which may be difficult to recognize; (ii) diagenetic effects may vary, rendering comparisons problematical, particularly when comparing extant with fossil plants or fossils from different localities with differing diagenetic histories; (iii) unlike extant plants where complete ontogenetic sequences can be studied, fossils usually preserve only a particular ontogenetic state, and although they usually represent mature forms, the exact stage of maturation may be unclear; (iv) it is difficult to detect convergence resulting from similarities in developmental processes; (v) it is uncertain to what extent the spore wall ultrastructure characters of extant plants differ from such distant ancestors. Nonetheless, these problems are not insurmountable. If the database continues to improve at its current rate, 'noise' created by the above-mentioned problems will probably be filtered out by an abundance of reliable data. It is likely that in the future, spore wall ultrastructural studies will play an increasingly important role in phylogenetic analysis of early land plants. Taylor (1997) recently summarized his findings and proposed a tentative hypothesis for evolutionary relationships among early cryptospore producers. He suggests that at least two separate lineages occur, but goes on to say that 'the phylogenetic relationship between these groups and to more recent land plants remains uncertain', although he has suggested possible hepatic affinities for some of the dyads (e.g. Taylor 1995*a*). The question of lineages among permanent tetrads has been discussed by Gray (1991) based on envelope characters.

In terms of understanding spore wall development in early land plants, studies of spore wall ultrastructure have resulted in a number of important findings. Lamellae have been recognized in trilete spores (Wellman 1999), dyads (Taylor 1995*a*) and hilate monads (Wellman *et al.* 1998*b*), including the presence of typical white-line-centred lamellae in the latter. Such findings provide the earliest fossil evidence for the antiquity of such structures, and provide further evidence that sporopollenin deposition on these structures is the most primitive mode of sporopollenin deposition among land plants (e.g. Blackmore & Barnes 1987). Important information has also been provided on the nature of cryptospore envelopes (Taylor 1996, 1997; Wellman *et al.* 1998*a*; Edwards *et al.* 1999) and junctions between units in permanent tetrads and dyads

(Taylor 1995*a*, 1996, 1997; Wellman *et al*. 1998*a*; Edwards *et al*. 1999). For example, Edwards *et al*. (1999) and Habgood (2000) have recently suggested, based on evidence derived from ultrastructural studies of fossil material, that cryptospore envelopes may have been tapetally derived, a possibility previously discussed by Gray (1991).

(vi) *Conclusions*

Studies on early land plant spores are providing an important source of information in attempts to understand the affinities and phylogenetic relationships of early higher land plants. This is particularly true for the earliest land plants, which left no megafossil record, as we are dependent on the dispersed microfossil record as our only source of information. Analysis of these earliest land plant spores suggests that the producers were bryophyte-like if not bryophytes (Gray 1985, 1991). It is anticipated that our understanding of early land plant spores will continue to improve as further localities are discovered, and more work is undertaken on these and pre-existing localities, particularly if these searches should turn up body fossils of the spore producers. Additionally, it is probable that some of the identified gaps in knowledge will be filled following further research on *in situ* spores and spore wall ultrastructure, which may shed further light on the evolutionary relationships of early land plants. Researchers are also utilizing different methods of phylogenetic analysis on the primary data set. For example, Kenrick & Crane (1997) have recently undertaken a detailed cladistic analysis of early land plants, which incorporates some of the data derived from studies of early land plant spores. At this juncture it is interesting to note that certain recent cladistic analyses (based on morphological and/or molecular data) indicate that the 'bryophytes' are paraphyletic with respect to the tracheophytes, but the three major lineages of 'bryophytes' (liverworts, hornworts and mosses) are all monophyletic, and occupy basal positions within the embryophytes, with one of these lineages (probably the mosses) sister group to the tracheophytes (see Mishler *et al*. 1994; Kenrick & Crane (1997) and references therein). Thus it might be anticipated as previously suggested (Gray 1985, 1991 and other references) that the earliest land plants were bryophyte-like (?cryptospore-producers), with tracheophytes (?trilete spore-producers) appearing somewhat later. However, it must be borne in mind that early land plant classification and phylogenetic interpretation are in a state of flux, and the biological integrity and evolutionary relationships of many higher taxa are uncertain (e.g. Kenrick & Crane 1997). Furthermore, many early fossil plants, such as the rhyniophytoids, are of unknown affinity, and it is possible that the diversity of higher taxa is masked.

(c) *Observations on the dispersed spore fossil record*
(i) *Completeness and integrity*

The early land plant dispersed record varies in terms of the quantity and quality of reports and their palaeogeographical coverage for different stratigraphical levels. Two generalizations can be made: (i) as one moves up column the dispersed spore record becomes better known; (ii) there is an overrepresentation of reports from eastern North America (Laurentia), western Europe (Laurentia, Avalonia and Baltica) and North Africa–Arabia (northern

Gondwana), with other areas either under-represented or simply not represented at all. Obviously this creates problems for interpretation of the dispersed spore record, particularly when attempting to identify patterns of evolution and palaeophytogeographical variation on a global scale.

(ii) *Patterns of evolution and palaeophytogeography*

Comments about evolutionary and palaeophytogeographical patterns are necessarily highly speculative. In part this is due to gaps and probable biases associated with the dispersed spore record, and in part it is due to the state of flux in palaeogeographical models. Palaeophytogeographical speculations here and elsewhere in this paper are based on the Scotese & McKerrow (1990) model. It should be realized that observations based on any one model, including this one, will probably be subject to major revision in the future.

Their first known appearance in the Llanvirn (Mid-Ordovician) appears to have been followed over much of the globe by an extended period of stasis of *ca*. 40 Myr, with little evolutionary development until the late Llandovery (Early Silurian). During this period the vast majority of dispersed spore assemblages consist entirely of cryptospores, believed to derive from plants at a bryophyte-like (hepatic) grade of organization, if not in fact bryophytes. A notable exception is the early occurrence of trilete spores in northern Gondwana (see p. 4).

Gray *et al*. (1992) suggest that variation in the palaeogeographical distribution of envelope-enclosed permanent tetrads (manifested in type of envelope ornament), provides the first evidence for phytogeographical differentiation among early land plants during the Ordovician–Early Silurian. They suggest that a cool Malvinokaffric Realm and a warmer extra-Malvinokaffric Realm existed. However, certain reported data apparently conflict with their findings (see discussion in Wellman 1996, p. 130 and Steemans *et al*. 2000). More palaeogeographically extensive reporting is required to clarify this matter.

It has been highlighted that many of the early occurrences of cryptospores are from high latitudes (Gray *et al*. 1992; Edwards 1998), in areas associated with ice caps for at least some of this time. As there is little variation in spore assemblages over this interval, it has been suggested that the cryptospore-producers were little affected by climate changes associated with the glaciation, and could rapidly reinvade previously glaciated areas (Richardson 1996*a*; Edwards 1998). Such findings are consistent with the interpretation of Gray (1984, 1985) that the cryptospores-producers were at a bryophyte-like grade of organization, with life history strategies that included an ecophysiological tolerance to desiccation and a short vegetative lifestyle, and thus could tolerate wide extremes of climate.

There was a major event in the late Llandovery that in many areas saw the near disappearance of envelope-enclosed cryptospores, which apparently coincided with the appearance of hilate monads and trilete spores in relative abundance (cf. Gray *et al*. 1986). It has been suggested that the inception of trilete spores may reflect the first appearance of tracheophytes (rhyniophytes) (e.g. Gray 1985; Edwards & Wellman 2000). The affinities of

hilate monads are more controversial. Some appear to derive from rhyniophytoids (a group erected for plants of uncertain affinities); some may represent tracheophytes, while others may represent non-vascular plants, perhaps including 'primitive' groups ancestral to the vascular plants. Other cryptospore morphotypes remained as persistent, although not abundant, elements of dispersed spore assemblages, attesting to the continuation of certain cryptospore-producing plants, although there was clearly a serious reduction in the importance of the forms producing envelope-enclosed spores. As more evidence becomes available, the possibility that trilete spores first appeared in northern Gondwana seems more likely, fuelling speculation that this may have been a 'centre of origin' for tracheophytes.

Following the turnover in the nature of dispersed spore assemblages noted above, trilete spores and hilate monads had a major diversification, which probably reflects a diversification in the early tracheophytes (and possibly also their putative 'ancestors' that may occur among the rhyniophytoids). At about this time (late Wenlock–early Ludlow) we find the first evidence for significant palaeophytogeographical differentiation (see p. 5), which is not surprising as this was a time when some of the larger land masses were widely separated. Eventually, towards the end of the Lochkovian, hilate monad abundance diminishes, leaving a flora dominated by trilete spore-producing plants, with cryptospore-producing plants being a minor component. It may be significant that this pattern—a reduction in palaeophytographical differentiation—has been documented in areas that indicate a reduction in continental separation, but that paradoxically show increased provincialism in marine invertebrates and vertebrates (A. J. Boucot, personal communication). The post-Lochkovian (Early Devonian) paucity of cryptospores attests to large-scale extinction among some of the 'lineages' at bryophyte level of organization and possibly some early tracheophytes and/or their putative ancestors included in the rhyniophytoids. It relates as well to tetrad dissociation within at least one 'lineage' of tetrad producers (see discussion in Gray 1985, 1991).

(iii) *Measures of diversity*

There is often a reluctance to use dispersed spore diversity as a proxy for land plants' diversity because of concerns that the former may not necessarily reflect the latter. It is frequently noted, based on observations of both extant and fossil plants, that: (i) the same taxon may produce a variety of different spore morphologies, leading to an overestimate in diversity; (ii) similar spores are produced by different plant groups, resulting in an underestimate of diversity.

There is no *in situ* record for the earliest cryptospore producers, and hence it is difficult to test whether or not dispersed spore diversity reflects true diversity. Moreover, several potential pitfalls have been noted. First, it is clear that many taxa are morphologically simple, and it is highly likely that such similar forms could have been produced by a number of plant types (i.e. homoplasy abounds), but it would be difficult or impossible to distinguish between their dispersed spores. Second, it has been noted that different morphotypes (monads, dyads and tetrads) possess identical envelopes, and it has been suggested that they might have been produced by the same parent plant taxon (Johnson 1985; Richardson 1988, 1992; Strother 1991). Third, envelope-enclosed cryptospores may potentially lose their envelopes during transportation or diagenesis, producing forms that are secondarily naked and cannot be distinguished from those that never had an envelope (Gray 1991).

The occurrence of early land plants containing *in situ* spores from the latest Silurian–earliest Devonian allows us to examine critically the relationship between the dispersed spore and plant megafossil record at this time (e.g. Fanning *et al.* 1991). Findings suggest that spore formation was usually simultaneous within a single sporangium, producing spores of only one type (see summaries in Fanning *et al.* 1991; Edwards 1996; Edwards & Richardson 1996). However, Fanning *et al.* (1988) found that morphologically identical plant megafossils may produce different spore types, and suggested that this reflected reticulate evolution where evolution of spore morphology was rapid compared with that in the morphologically (although not necessarily anatomically) simple plants. Furthermore, Wellman *et al.* (1998b) found that superficially morphologically similar spores were produced by different plant types. Both of these findings could lead to discrepancies in diversity data derived from counts of dispersed spore 'species'. However, it is clear that the supposedly morphologically similar megafossils/spores can usually be distinguished if analysed in adequate detail.

There have been few sufficiently detailed investigations of early land plant dispersed spore diversity published to date. Counts based on spore genera are totally inadequate due to the ad hoc methods utilized in the creation of taxa of this taxonomic rank. Counts based on species are almost certainly more reliable. Steemans (1999) provides counts of genera and species for both cryptospores and trilete spores, for the interval Caradoc (Late Ordovician)–Lochkovian (Early Devonian), based on selected publications from geographically dispersed localities. His findings seem to confirm the general diversity changes noted in the synthesis of the early land plant spore record provided above. Similarly, preliminary counts based on species abundances in geographically isolated sequences (the 'Old Red Sandstone continent' and northern Gondwana) (C. H. Wellman, unpublished data) confirm these general trends. However, one must bear in mind: (i) potential distorting effects, as noted above, particularly for the older records (Ordovician–Early Silurian) where there are no *in situ* records available to test dispersed spore/parent plant relationships; (ii) variable spatial and/or temporal coverage due to differences in the availability and/or integrity of data.

3. DISPERSED PHYTODEBRIS

Enigmatic dispersed fragments (phytodebris) believed to derive from embryophytes and/or fungi, have long been known from the Ordovician/Early Devonian, and have provided an important contribution to our understanding of early land plants and terrestrial ecosystems (e.g. Gray 1985; Sherwood-Pike & Gray 1985; Gensel *et al.* 1991; Edwards & Wellman 1996). They consist
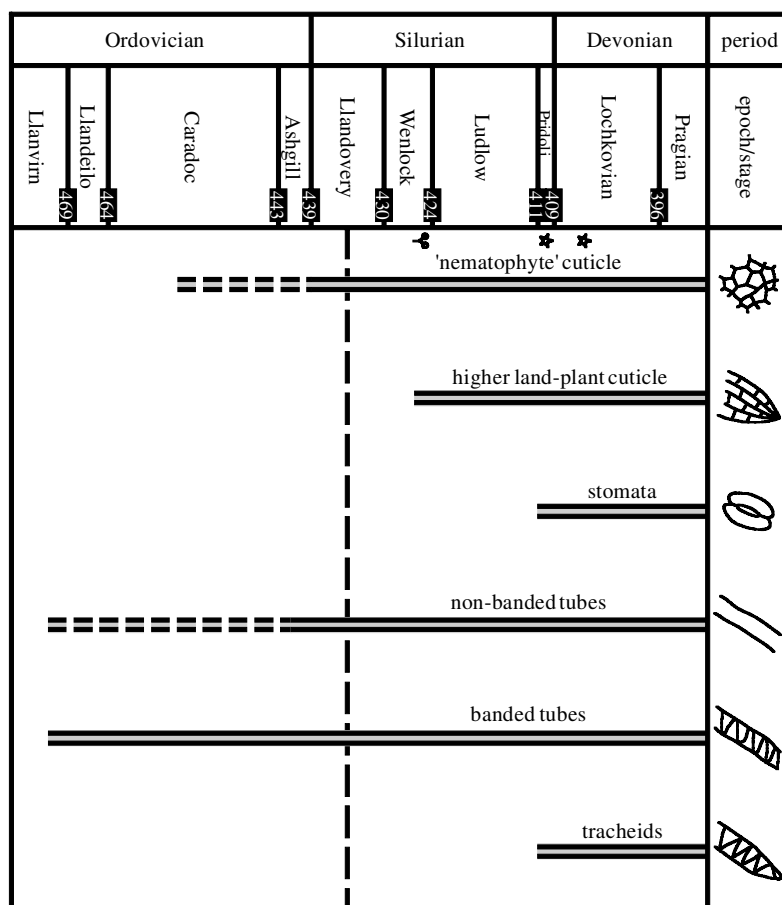
Figure 4. Stratigraphical range chart for early land plant phytodebris. Time-scale from Harland *et al*. (1989). Regarding annotation adjacent to the stratigraphic column: the small '*Cooksonia*' indicates the age of the earliest unequivocal land plant megafossils, the asterisks indicate the age of important plant mesofossil assemblages (i.e. Ludford Lane-Pridoli; North Brown Clee Hill-Lochkovian). The dashed time-line indicates the position of the major change in the nature of dispersed spore assemblages in the Llandovery.

primarily of fragments of cuticle, tubular structures (aseptate) and filaments (septate), which occur isolated or in complex associations (figures 4 and 5). The affinities of many forms are controversial as they lack a convincing modern counterpart, although recent advances have gone a long way towards clarifying their biological relationships. They undoubtedly derive from non-marine organisms because they occur in continental deposits, and have a similar distribution to ?equivalent (analogous or homologous) fragments derived from extant land plants (cuticles, conducting tissues) and fungi (filaments).

(a) *The fossil record*

The earliest fragments of cuticle are reported from the Caradoc (Late Ordovician) (Gray *et al*. 1982), and they are relatively abundant in the Llandovery (Early Silurian). By the Wenlock (Late Silurian), ornamented cuticles, and forms clearly derived from tracheophytes, are present. The fossil record of Ordovician–Early Devonian dispersed cuticles has recently been reviewed by Gray (1985), Gensel *et al*. (1991), Edwards & Wellman (1996) and Edwards *et al*. (1996*b*).

The earliest tubular structures are ornamented forms from the early Llanvirn of Bohemia (Vavrdova 1984) and smooth forms from the Ashgill of southern Britain (Burgess & Edwards 1991). A proliferation of different types of tubular structure (including types with external ornament and others with internal annular or spiral thickenings) occurs in the Wenlock (Late Silurian), and similarly diverse forms exist until at least the Early Devonian. In addition to variation in their internal and external ornament, tubular structures vary in presence/ absence of branching and nature of terminal structures (if present). They commonly occur in complex associations.

The earliest reported filaments are from the Llandovery (Early Silurian) and they have been reported sporadically throughout the Silurian and Lower Devonian. The filaments are usually branched, sometimes with flask-shaped protuberances, and the septa may, or may not, be perforate (figure 5*c*). The occurrence of Ordovician/Early Devonian tubular structures and filaments is reviewed by Gray (1985), Burgess & Edwards (1991), Gensel *et al*. (1991), Wellman (1995) and Edwards & Wellman (1996).

(b) *Affinities*

The affinities of dispersed phytodebris are conjectural and aroused much controversy in the past. Early suggestions that they derived from land plants and/or fungi were based largely on inferences following comparisons with similar structures in extant forms (summarized in Gray 1985). However, caution was advised (e.g. Banks 1975), and it was even suggested that some forms may derive from marine organisms, although such an origin has now been rejected following their recovery from continental deposits. More recently the early land plant megafossil/mesofossil record has turned up a number of
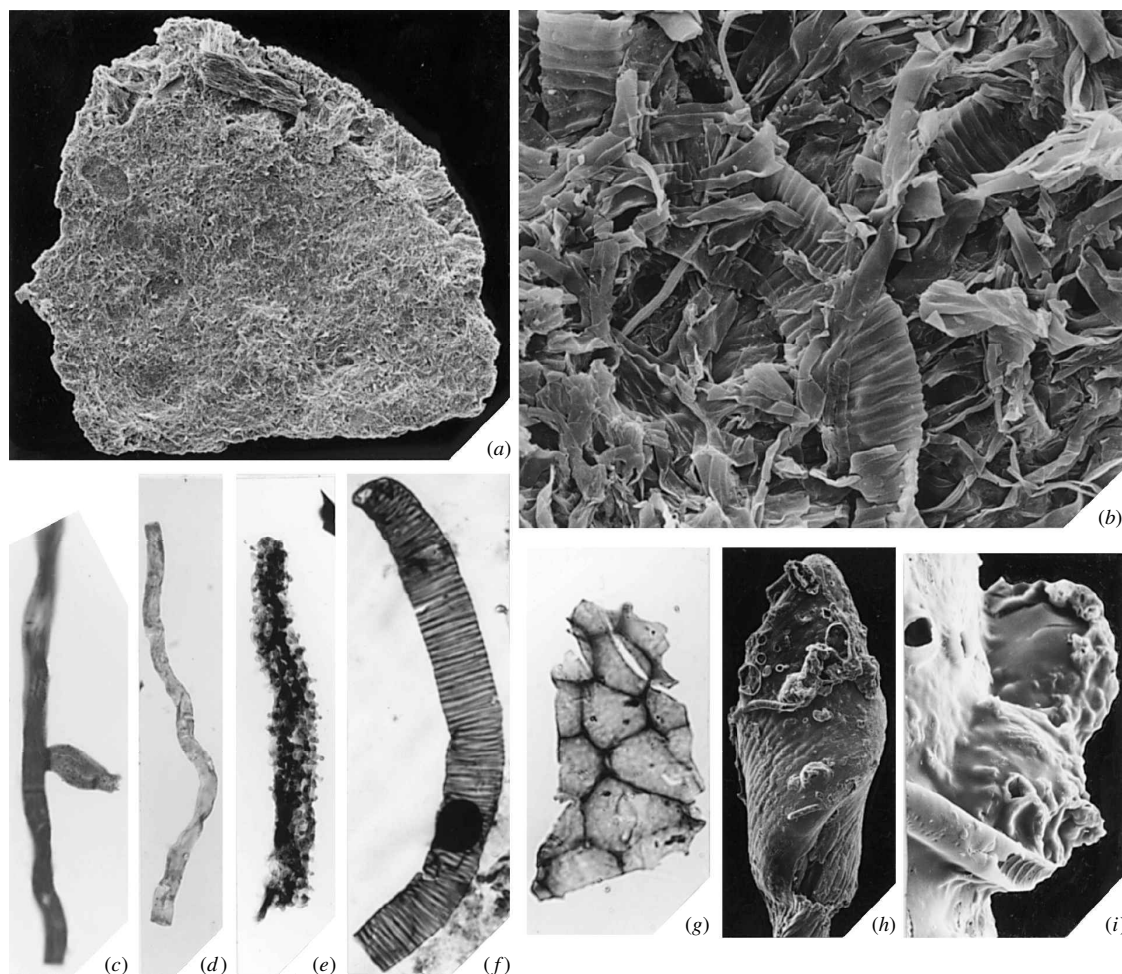
Figure 5. LM and SEM images of nematophytes and dispersed phytodebris. (*a,b,h,i*) courtesy of Professor Dianne Edwards, from the Ditton Group of North Brown Clee Hill, Shropshire, England (Lochkovian, Early Devonian) (Edwards 1996); (*c,f*) from the Lower Old Red Sandstone of Lorne, Scotland (earliest Lochkovian, Early Devonian) (Wellman 1995); (*d,e,g*) from the Silurian of the Arabian peninsula. (*a*) Nematophyte (× 65); (*b*) close up of (*a*) revealing tubular organization including banded and laevigate forms (× 1075); (*c*) fungal hypha (× 320), note flask-shaped protuberance and internal septae; (*d*) laevigate tube (× 320); (*e*) tube with external ornament (× 320); (*f*) banded tube (× 250); (*g*) dispersed cuticle (× 870); (*h*) *Tortilicaulis* sporangium with banded tubes attached via an amorphous film which in places forms pustules (× 1000) (see Edwards *et al.* 1996*b*); (*i*) Close up of (*h*) illustrating an internally thickened tube attached via the amorphous film with pustules (× 550).

interesting fossils relevant to the debate. Other avenues of research, such as geochemical analysis, have also been explored. In the following account important contributions to our understanding of the affinities of phytodebris are summarized.

(i) *Inferences based on similar structures in extant organisms*

It has long been recognized that the dispersed cuticles are morphologically similar to the cuticles of extant land plants. However, it is not until the Wenlock (Late Silurian) that cuticles can be unequivocally assigned to tracheophytes. These show marked alignment of epidermal cells, often with stomata, that clearly derive from axes, and forms with well-defined outlines, occasionally with attached spores, that derive from their sporangia. However, the earlier forms, which persist until at least the Early Devonian, are more enigmatic. They lack stomata and have cellular patterns unlike those in extant land plants. However, cuticle appears to be an adaptation for protection in subaerially exposed plants, and its presence therefore suggests that at least part of the parent plant was subaerially exposed at least some of the time.

The dispersed tubular structures have less convincing analogues among structures present in extant land plants. It has long been noted that forms with internal annular/spiral thickenings resemble the tracheids of extant tracheophytes (figure 5*f*). They are often referred to descriptively as tracheid-like tubes in the older literature (Gray & Boucot 1977, 1979). However, these tubes clearly differ from tracheids in terms of structure. Nonetheless, it has frequently been suggested that some of the different forms of tubular structures may have functioned as conducting cells, even if they are not strictly homologous with the tracheids of tracheophytes. Gray & Boucot (1977, pp. 164–168, 1979, p. 62) have thoroughly reviewed the

question of the possible relationship of these tracheid-like tubes to other organisms and concluded as we do here that most could be attributed to nematophytes.

Some of the dispersed filaments bear a striking resemblance to the hyphae of extant fungi, and it has been suggested that they provide evidence for terrestrial fungi of ascomycete affinity (Sherwood-Pike & Gray 1985). Additional, more compelling, evidence is in the form of associated spores, including multiseptate spores, that are difficult to interpret as anything but ascomycetaceous ascospores or the conidial stage of an ascomycete (Sherwood-Pike & Gray 1985).

Recently, Kroken *et al.* (1996) suggested that some of the dispersed cuticles and tubular structures may represent the fragmentary remains of fossil bryophytes. Their hypothesis is based on observations on the fragments that survive after extant bryophytes are treated with high-temperature acid hydrolysis (i.e. recalcitrant fragments that one would expect to survive in the fossil record). The fragments bear superficial resemblance to certain early land plant phytodebris, although there are a number of differences relating to the size and symmetry of the fossils. This novel avenue of research is exciting and may in the future prove extremely rewarding. One should bear in mind that this research is in its infancy and to date only a few extant bryophyte taxa have been examined.

(ii) *The plant megafossil/mesofossil record*

The early land plant megafossil record consists of unequivocal tracheophytes (rhyniophytes, zosterophylls, lycopsids, etc.), rhyniophytoids of uncertain status, in addition to the enigmatic nematophytes. It has been demonstrated that higher land plants are the source of some of the dispersed cuticles since at least the Wenlock (Late Silurian), a not unsurprising finding considering the abundance of fragmented land plant cuticle that is incorporated into present-day sediments. However, it is to the enigmatic nematophytes that many have turned in their search for the source of many of the other dispersed remains.

Nematophytes are a group of putative land plants of uncertain affinity, with somatic organization based on a complex association of tubes (often including tubes with internal annular or spiral thickenings), and believed by Lang to possess a cuticular covering (Lang 1937; see also Gray 1984). They are known principally through rather uninformative coalified compressions (e.g. Lang 1937; Strother 1988). However, uncompressed fragments are abundant in the recently discovered exceptionally preserved mesofossil assemblages from the Welsh Borderland, and these specimens are providing valuable new information on the morphology and anatomy of these organisms (figure 5*a,b*). It is clear that many of the dispersed tubular structures (particularly laevigate and internally thickened forms) are similar to those in nematophytes, particularly as some of the dispersed forms regularly occur in associations similar to those observed in the megafossils/mesofossils. However, the covering of nematophytes is difficult to examine in the megafossils/mesofossils, and there is some doubt as to whether it is the source of dispersed fragments of cuticle. Nonetheless, recent chemical analyses demonstrate that the dispersed 'nematophyte' cuticle does not have the same chemical composition as that from axial higher land plants, adding weight to the suggestion that they are fundamentally different, and raising queries concerning their affinities and function (Edwards *et al.* 1996*b*).

It has been suggested that some of the nematophytes (*Prototaxites*) were terrestrial fungi (e.g. Hueber 1996). Recent evidence supporting this hypothesis is the discovery of internally thickened tubes seemingly growing on (Edwards *et al.* 1996*b*, 1998) and within the tissues (Edwards & Richardson 2000) of higher land plants (figure 5*h,i*). It is possible that these tubes were either attacking the plant while alive (pathogens) or dead (decomposers).

Another interesting possibility is that some of the nematophytes represent lichens. The reported 'lichenized cyanobacteria' in the Rhynie Chert (Early Devonian) (Taylor *et al.* 1995, 1997) suggests great antiquity for these organisms. However, Poinar *et al.* (2000) state that there is no indication that the Devonian association, which involves a zygomycete and a cyanobacterium, is a stable one of the type demanded in the physiological interaction of a lichen symbiosis. Indeed Taylor *et al.* (1997, p. 1003) note that the fossil 'lacks the structural organization of the modern lichen thallus'. Moreover, the resemblance of the 'mycobiont' to Zygomycota is additional cause for scepticism since the mycobionts of extant lichens are usually ascomycetes or rarely basidio-mycetes. No extant true lichen involves a zygomycete (Poinar *et al.* 2000).

Fungal or lichen affinities for nematophytes must remain in the realm of speculation, although either possibility might help explain the anomalous chemical composition of 'cuticle' attributed to this taxon.

(iii) *Conclusions*

It is clear that the affinities of many forms of dispersed phytodebris remain conjectural. While many of the younger dispersed cuticles derive from higher land plants, a nematophyte origin seems most plausible for some of the remainder. The majority of tubular structures probably also derives from nematophytes, and some dispersed filaments doubtless derive from terrestrial fungi. However, the affinities of the nematophytes remain highly controversial, although some see evidence for fungal or lichen affinities (Hueber 1996; Edwards *et al.* 1996*b*, 1998; Edwards & Richardson 2000).

(c) *Observations on the dispersed phytodebris fossil record*

It is clear from the early land plant microfossil and megafossil record that nematophytes were an important element of early terrestrial ecosystems (cf. Gray & Boucot 1977, 1979; Gray 1984), both in terms of abundance and diversity. They include a variety of forms including thalloid (e.g. *Nematothallus*) and axial (e.g. *Prototaxites*). It also seems likely that they included by far the largest organisms in early terrestrial ecosystems (specimens of *Prototaxites* over 1m wide have been reported). Recent work on latest Silurian–earliest Devonian exceptionally preserved mesofossil assemblages from the Welsh Borderland is providing further details of nematophyte structure and revealing a diverse array of new forms. However, reproductive structures remain unknown, and the

affinities and mode of life of these bizarre tissues/organisms remain obscure.

4. CONCLUSIONS

Reconstruction and interpretation of the early terrestrial vegetation is hampered by the inadequacies of the early land plant fossil record, which is incomplete and biased. This is particularly the case for the earliest land plants, as there is no megafossil record, and we rely on dispersed microfossils, which provide more limited evidence as to the nature and affinities of the producers. However, finds of new fossils continue to provide evidence that increases our understanding of early land plants and terrestrial ecosystems. An example is the wealth of new information, derived from the reports of Ordovician–Lower Silurian microfossil assemblages from Saudi Arabia, that is forcing us to reconsider previous interpretations regarding the evolution and palaeophytogeography of early land plants. Similarly, a wealth of new data is coming to light based on work on the latest Silurian–earliest Devonian exceptionally preserved mesofossil assemblages from the Welsh Borderland. Work on the mesofossils is demonstrating the vast diversity of early land plants, while examination of dispersed spore assemblages from the same localities indicates that many of the spore-producers have not yet been identified and true diversity is in fact even larger. It is imperative that we continue to locate new material (microfossil, mesofossil and megafossil) and fill in the gaps in the temporal/spatial record of early land plants. For example, there are as yet no reports of Upper Silurian–Lower Devonian dispersed spore assemblages from Australasia, a continent famed for the anomalous early occurrence of relatively large lycopsids (Garratt 1978).

In addition to new material, new techniques and novel lines of enquiry are also being explored. There are a number of notable examples. Chemical analysis of fossil material, such as that on dispersed cuticles performed by Edwards *et al.* (1996b), is producing exciting results, although identification and interpretation of diagenetic effects is currently proving frustrating. Comparisons between dispersed phytodebris and fragments of extant bryophytes that are likely to survive in the fossil record (e.g. Kroken *et al.* 1996) may eventually prove fruitful. Studies of wall ultrastructure in early land plant spores are still in their infancy, but are already providing a wealth of new information (e.g. Taylor 1997; Wellman *et al.* 1998).

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Discussion

P. Kenrick (*Department of Palaeontology, The Natural History Museum, London*). Modern phylogenetic research clearly shows that land plants are a monophyletic group. This implies a single point of origin. Based on the fossil record of dispersed spores, can we pinpoint the origin of land plants to a specific Ordovician landmass?

Is it possible to say anything about how the colonization of the various Ordovician landmasses (Laurentia, Baltica, Gondwana) proceeded following the origin of land plants?

C. Wellman and J. Gray. As noted in our paper, the earliest known dispersed spores interpreted as derived from embryophytes are from the Llanvirn (Mid-Ordovician) of Bohemia and Saudi Arabia. By the Caradoc similar spores are known from Libya and southern Britain and similar Ashgill assemblages have been reported from South Africa, Libya, Turkey, Bohemia, Germany, southern Britain, eastern North America and China. Some of these Late Ordovician assemblages are preserved in continental deposits that theoretically should provide better control on their provenance.

While it is tempting to attach evolutionary significance to the early occurrences in Bohemia and Saudi Arabia, the Ordovician database, outlined above, is too limited for us to speculate on the location of a 'single point of origin' for higher land plants/embryophytes, if indeed a 'first appearance' of dispersed spores can be assumed under any circumstances to correspond to 'a single point of origin'. The best premise with fossils, especially poorly known, small fossils with a wide dispersal potential, is to assume that 'first appearance' may have little to do with 'point of origin'.

Anything approaching representative palaeogeographic reporting of dispersed embryophyte spores is first achieved in the Ashgill. By this time, however, more or less identical dispersed spore assemblages are widespread. Again, because of the limited database, it is presently impossible to comment on how the colonization of the various Ordovician land masses proceeded following the origin of land plants. We suspect that colonization would have been rapid due to the considerable dispersal potential of these spores related to their small size, thick protective wall and their capability to reproduce from a single dispersal propagule (see discussion in Gray 1985).

W. G. Chaloner (*Department of Geology, Royal Holloway University of London, Surrey, UK*). Do any specimens of the Ordovician 'obligate tetrads' that you have shown us give any indication of where they germinated? Did the process of germination force the members of the tetrad apart (i.e. did they germinate through the proximal face) or do any of the tetrads show signs of an aperture on the exposed (distal) faces of the spores?

As a further but closely related question, do you know how the tetrads of the Marchantialean liverworts (with which Gray has compared these obligate tetrads) germinate? Does the site of germination in the fossil tetrads (if any evidence for this exists) give support for a liverwort affinity?

C. Wellman and J. Gray. As far as we are aware none of the dispersed obligate tetrads from the Ordovician–Lower Devonian provide any indication of where they germinated. This, however, is not surprising. Most, if not all, of these dispersed spores probably represent 'failed'

spores, i.e. they were not transported into an environment suitable for germination. Very rarely do dispersed early land plant spores exhibit evidence of germination, although certain trilete spores occasionally exhibit gaping sutures that may indicate that the gametophyte emerged through this suture, and very occasionally germinating spores are exquisitely preserved in exceptionally preserved floras, for example in the Rhynie Chert (Lyon 1957; Bhutta 1973; Remy & Hass 1996).

Gray (1985) suggested that 'for spore-producing land plants the obligate spore tetrad appears to be the primitive reproductive unit; the single spore split from the tetrad at maturity, derivative' and that 'distal dehiscence is primitive . . . proximal dehiscence derivative'. She thoroughly reviewed the literature on extant tetrad-producing bryophytes and germination in their spore tetrads and we refer you to that source for details, some summarized here. In obligate tetrads produced by living liverworts germination is via the distal (i.e. free) surface (Duthie & Garside 1936; Proskauer 1954; Schuster 1981). Interestingly, in a number of extant bryophyte spores that are dispersed as monads (i.e. following dissociation of the tetrad) dehiscence is also via the distal surface (Proskauer 1961). This is even the case for some species that produce trilete spores, for example spores of most species of *Riccia* (Duthie & Garside 1936), the endemic Indian *Stephensoniella* (Mehra & Kachroo 1952) and other taxa.

With regard to this debate, there are a number of other pertinent observations. Permanent dyads and tetrads are often preserved with the distal wall collapsed, suggesting that the distal wall was thin. Sections of such spores confirm that this is often the case (Wellman *et al*. 1998; Edwards *et al*. 1999). Perhaps the distal wall of these spores was thin in order to facilitate dehiscence. Interestingly, Taylor (1997) sectioned dispersed permanent dyads from latest Ordovician–earliest Silurian deposits of Ohio, and noted simple breaks/regions of thinning that occurred on the distal surface of the spores comprising the dyads. He

suggested that they might represent 'primitive sutures', although we consider this interpretation dubious and suspect that these structures may be artefactual. Where we do have evidence for germinating spores in the fossil record (i.e. the Rhynie Chert) the situation is not always as simple as one might expect. Remy & Hass (1996) note that the plant *Aglaophyton major* produced trilete spores that in certain horizons are fairly frequently preserved in the process of germinating. The spores are usually oriented with the proximal surface facing up, and the gametophyte emerging through the trilete mark, such that the spore wall splits into three regular valves. Occasionally, however, the spores are oriented with the distal surface facing up, and the walls in these spores often show irregular ruptures or are ruptured into irregular parts.

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