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The microfossil record of early land plants

Charles H. Wellman[1] **and Jane Gray**[2]†

[1]*Centre for Palynology, University of Sheffield, Dainton Building, Brook Hill, Sheffield S3 7HF, UK*
[2]*Department of Biology, University of Oregon, Eugene, OR 97403-1210, USA*

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

he earliest fossil evidence for embryophytes consists ntirely of dispersed microfossils. These oldest generally ccepted microfossils are from the Llanvirn (Mid-Ordovician), but it is not until the Wenlock (Late ilurian), some 40 Myr later, that the oldest unequivocal and plant megafossils occur. The early land plant microossil record consists of dispersed spores and phytodebris fragments of cuticles and tubes). Such remains are reserved in large numbers in a variety of environments continental and marine) because: (i) they were comosed of recalcitrant material and readily fossilized; ii) they were produced in vast numbers; and (iii) they ad the potential for long-distance dispersal by wind and water due to their small size. Consequently they have an xcellent fossil record with good spatial and temporal epresentation. However, the dispersed microfossils are ifficult to interpret because they represent discrete parts f whole organisms and phytodebris is fragmentary. Nonetheless, comparisons with purportedly homologous tructures in extant plants, and to a certain extent ounger fossil plants, provide compelling evidence that hey derive from land plants. As the earliest evidence for and plants, they are utilized in interpretation of the ature and affinities of the plants from which they derive. urthermore, their excellent fossil record documents the arly evolution and diversification of land plants, and rovides 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 1996*a* 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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Deceased 9 January 2000.

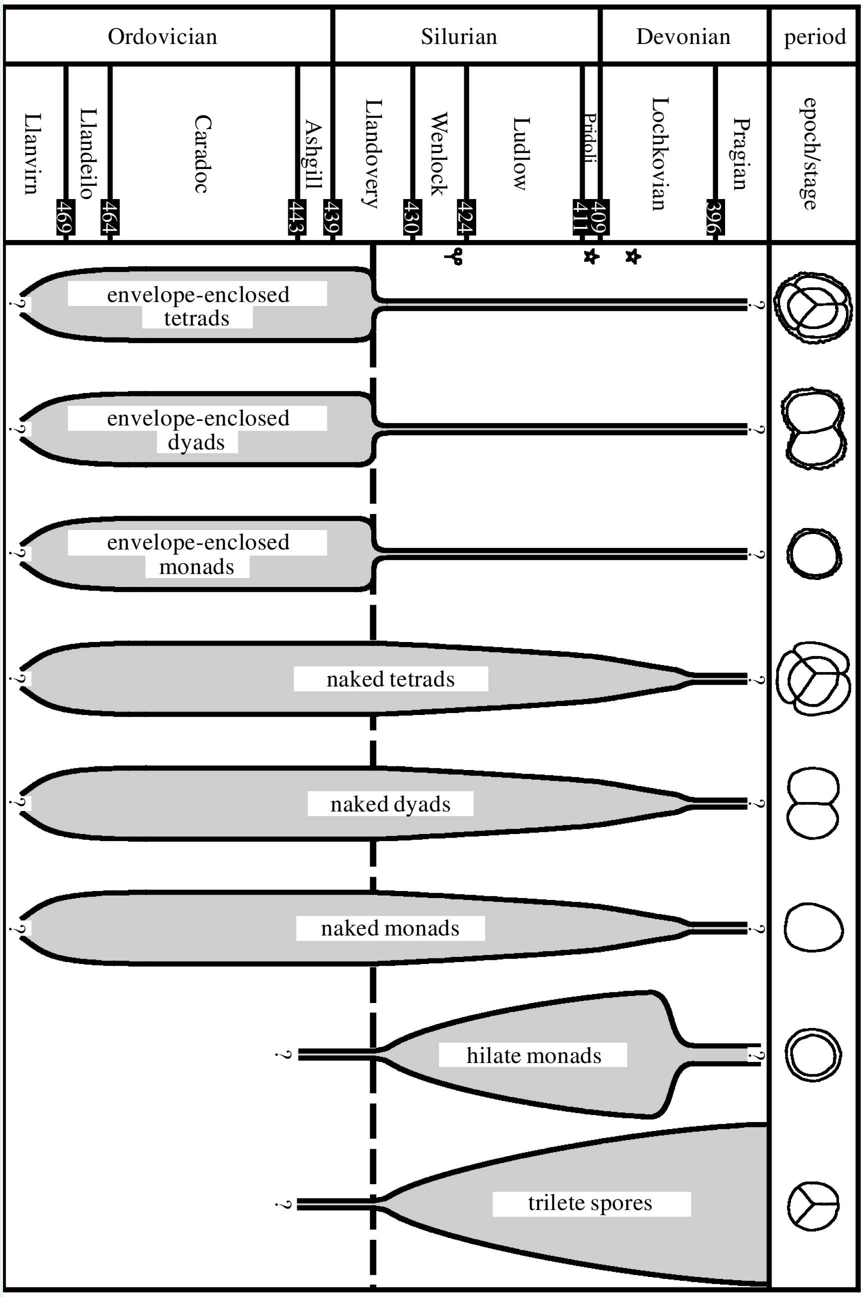
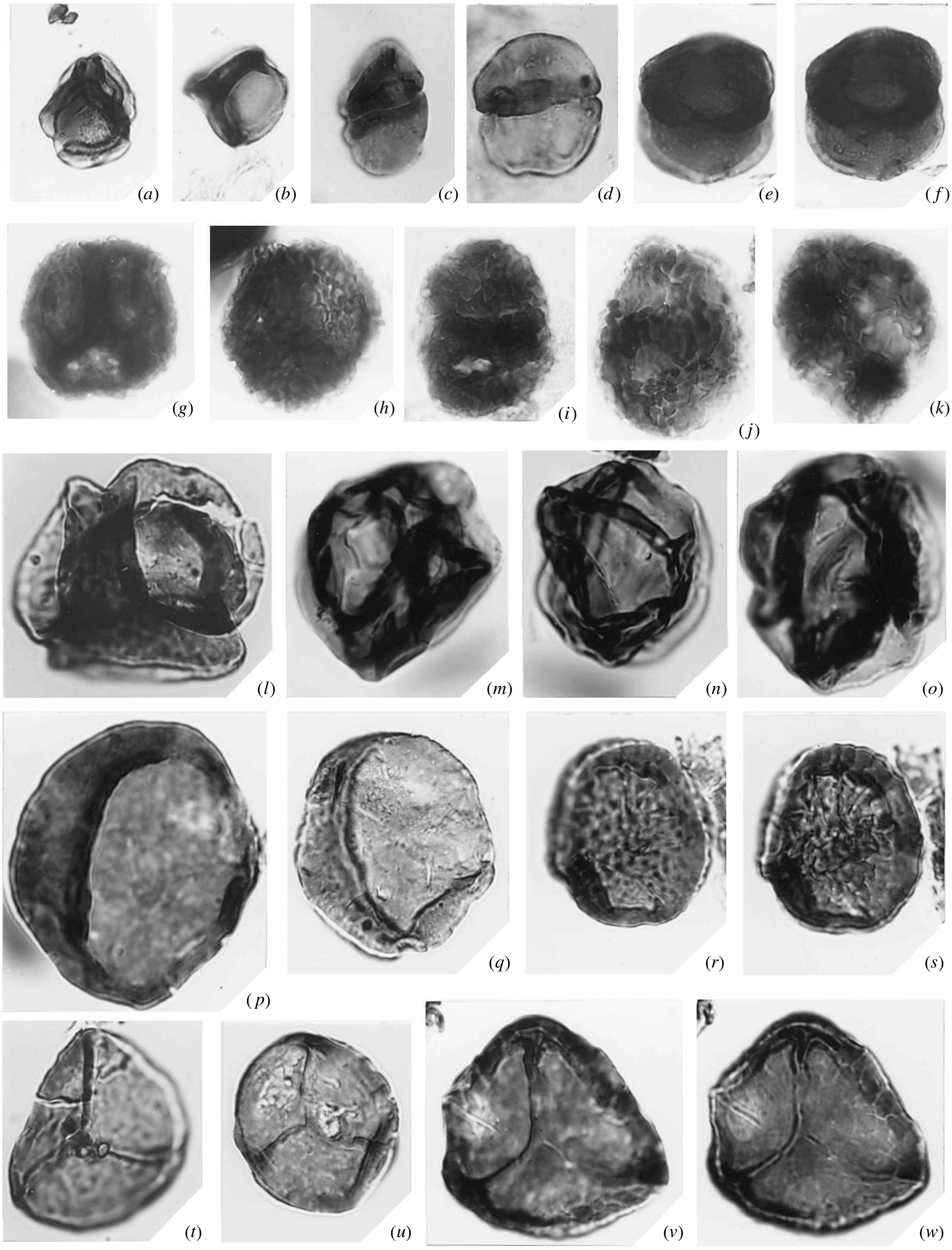


Figure 1. Stratigraphical range chart for early land plant spore morphotypes. Time-scale from Harland *et al.* (1989). Regarding annotation adjacent to the stratigraphic column: the small '*Cooksonia*' indicates the age of the earliest unequivocal land plant megafossils, the asterisks indicate the age 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.

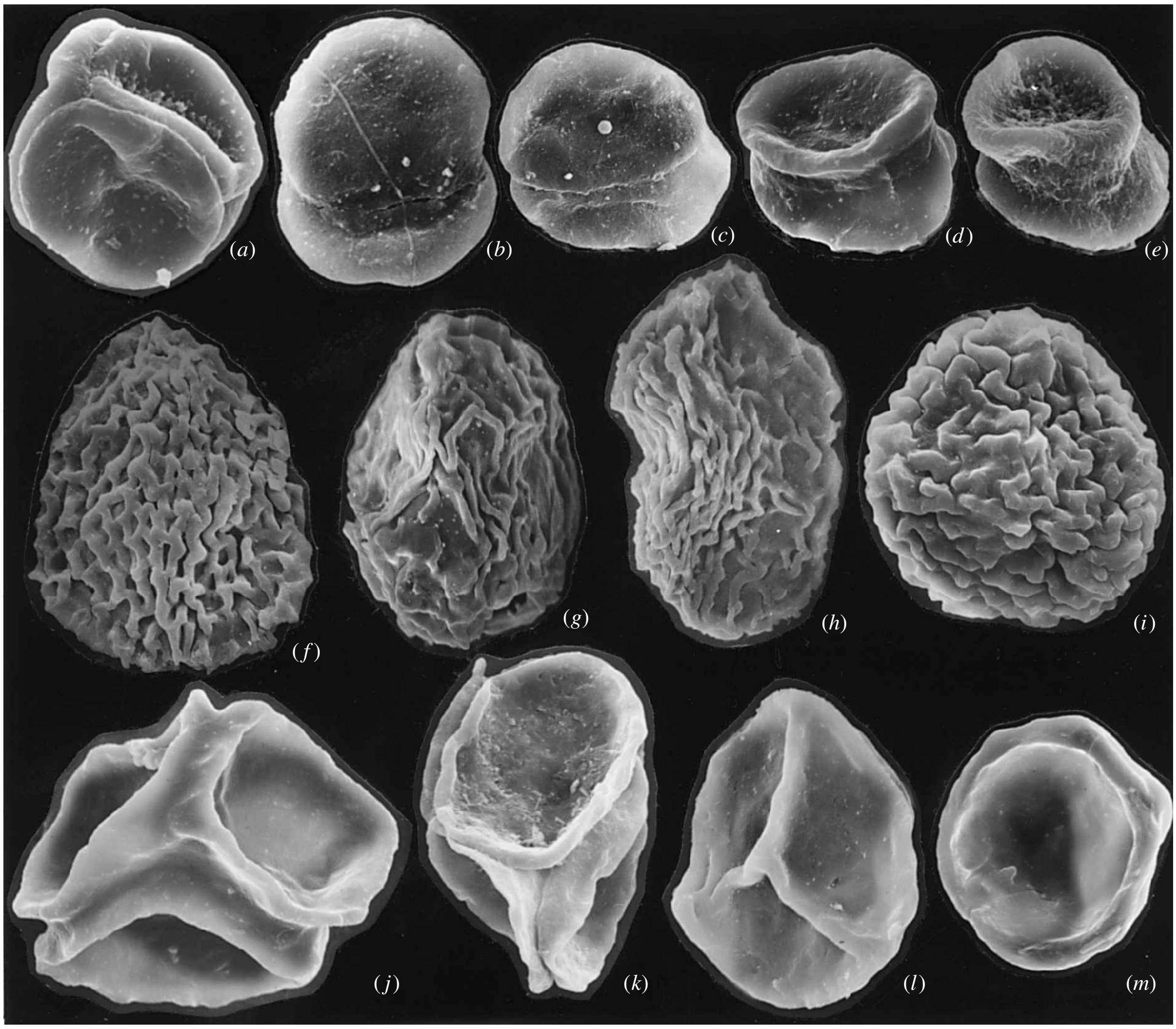
here is a superficial line of attachment between the pores and cohesion probably results from localized xospore links or bridges rather than large-scale fusion. 'hey are termed fused if there is no discernible line of ttachment and cohesion probably results from fusion ver most or all of the contact area. Cohesion may also esult from enclosure within a tight-fitting envelope. The omposition of cryptospores (wall and envelope) is nknown, but their preservation in ancient deposits uggests they constitute sporopollenin or a sporopollenin-ype macromolecule. Since there seems little question that hese structures are spores, the term cryptospore has no axonomic usefulness, but we retain the term here for escriptive convenience.

Reports of Ordovician–Early Silurian dispersed spores re relatively few, but are stratigraphically and geogra-hically widespread, and indicate that cryptospore ssemblages are remarkably constant in composition (both temporally and spatially) throughout this interval (Gray 1985, 1988, 1991; Richardson 1996*a*; 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, 1996*a*; 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



igure 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 ate Wenlock, Late Silurian) (Wellman 1993*b*). (*a*,*b*) Naked, unfused, permanent tetrad (× 1500); (*c*,*d*) naked, unfused, ermanent dyad (× 1500); (*e*, *f*) naked, fused, permanent dyad (× 1500); (*g*, *h*) envelope-enclosed permanent tetrad (× 1500); , *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); ,*u*) laevigate trilete spore (× 1000); (*v*,*w*) ornamented trilete spore (× 1000).



igure 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 f 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 permaent ?dyad (× 1500); (*i*) envelope-enclosed permanent ?monad (× 1500); (*j*) naked, fused, permanent tetrad (× 1210); (*k*) loose etrad (× 1070); (*l*) laevigate trilete spore (× 1380); (*m*) laevigate hilate monad (× 1230).

ormed in dyads that dissociated prior to dispersal figures 2 and 3). Similarly, trilete spores comprise single pores with a distinct trilete scar and three contact areas n their proximal surface, and clearly formed in tetrads hat dissociated prior to dispersal (figures 2 and 3). Dissoiation of the products of (presumably) meiosis suggests a najor change in plant reproductive strategy (see Gray 985; Wellman *et al.* 1998*a*; Edwards *et al.* 1999).

Both trilete spore and hilate monad abundance and iversity increased throughout the Late Silurian. It was reviously considered that their first appearance in bundance, and associated changes in dispersed spore ssemblages, was near-contemporaneous on a global cale. However, recent reports from Ashgill (Upper Ordovician)–Lower Llandovery (Early Silurian) deposits rom Turkey and Saudi Arabia support an early appearnce of both hilate monads and trilete spores in this egion of northeast Gondwana (Steemans *et al.* 1996, 000; Wellman *et al.* 2000*a*). However, the hilate monads nd 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 ominated by a bewildering variety of trilete spores (e.g. ichardson & McGregor 1986). Cryptospores persist in pore assemblages at least until the end of the Lochkovian Early Devonian). Their upper stratigraphic range is oorly documented, but they are seldom reported from ost-Lochkovian strata.

For the Late Silurian–Early Devonian interval there is onsiderable variation in the calibre of reporting for the ispersed spore record, with different time intervals xhibiting substantial differences in the number and uality of reports, and the extent of their palaeogeograhical coverage. This creates problems when attempting to dentify palaeophytogeographical variations, which are urther enhanced by difficulties associated with recogizing the effects of small-scale variation dependent on ocal environmental control (e.g. substrate, altitude, etc.), ubtle facies effects and non-contemporaneity due to incorect correlation of strata. Nonetheless, certain patterns are eginning to emerge, and are summarized below. Recent etailed reviews are provided by Richardson (1996*a*), teemans (1999) and Edwards & Wellman (2000).

For the Late Silurian there is acceptable reporting of pore assemblages from the palaeocontinents Laurentia, valonia and Baltica, which were closely associated and onstituted part of a large cluster of land that straddled he Equator, and from northern Gondwana, which lay urther to the south and was separated by a relatively arge ocean. Reporting from elsewhere is sparse. equences of spore assemblages from Laurentia, Avalonia nd Baltica are notably similar in composition, suggesting hat this land mass contained a flora representing a single alaeophytogeographical realm, and subtle differences robably reflect small-scale variation related to localized ariations in environmental conditions. However, seuences of spore assemblages from northern Gondwana e.g. Spain, north Africa and Brazil; J. Gray, unpublished ata), although sharing many elements in common with hose from Laurentia, Avalonia and Baltica, also exhibit arked differences, suggesting they belong to a different alaeophytogeographical realm (Richardson & Ioannides 973; Rodriguez 1983; Tekbali & Wood 1991).

By earliest Devonian times, Laurentia, Avalonia and altica were all essentially part of the same large ontinent (the 'Old Red Sandstone continent'), which was ow not far removed from Gondwana, the distance etween them having diminished through the Late ilurian. The vast majority of spore assemblages known rom the Lochkovian (Early Devonian) is from the 'Old ed Sandstone continent' and northern Gondwana, with ew reported assemblages from elsewhere. One might xpect differences between the sequences of spore assemlages from these two regions to become less apparent as he two palaeophytogeographical realms moved closer ogether and permitted interaction between their biota, nd preliminary research seems to indicate that this was he case. However, comparisons between Lochkovian pore assemblages are difficult because localized variation ppears to have become more prevalent by this time, ampering the identification of larger-scale variation. he small-scale variation probably reflects a combination f effects, including variation due to localized differences n environmental conditions and facies effects, which are ifficult 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 he Ashgill palaeokarst on Manitoulin Island, Ontario Gray 1988), the early Llandovery Tuscarora Formation n the Millerstown section, Pennsylvania (Gray 1988) and he early Llandovery Tuscarora Formation at the Mill Iall locality, Pennsylvania (Johnson 1985), which are the ldest and appear to contains only cryptospores.

(iii) *Comparisons with extant embryophyte spores*

Early higher land plant/embryophyte spores are imilar to the reproductive propagules of extant land lants in terms of size, gross morphology and possession f a thick sporopollenin spore wall (regarded as a ynapomorphy for embryophytes). Sporopollenin walls nay have multiple functions (Graham & Gray 2000), one ieing to protect propagules during transport following ubaerial release (e.g. Blackmore & Barnes 1987). Thus he possession of such walls in early higher land plant pores provides excellent evidence that they were unctionally similar to their modern counterparts. 'urthermore, the small size of early land plant spores is vithin the range of subaerially dispersed spores produced y extant free-sporing plants. Based largely on analogy vith the reproductive propagules of extant embryophytes, Gray (1985, 1991 and references therein) has argued ersuasively that the obligate spore tetrad of the fossil ecord is an ancestral character in embryophytes and that uch tetrads derive from land plants at a bryophyte, most kely hepatic, grade of organization. She notes that mong extant free-sporing embryophytes only hepatics egularly produce permanent tetrads as mature spores, ome of which are contained within an envelope similar o those enclosing certain fossil spore tetrads, but that a etrad regularly occurs in the spore ontogeny of embryohytes. The affinities of hilate monads and dyads are nore equivocal, primarily because such morphologies do ıot have an obvious modern counterpart (Wellman *et al.* 998*a*) either in mature spores or in spore ontogeny. Dyads rarely occur in extant (non-angiosperm) embryohytes, and only through meiotic abnormalities (Fanning *t al.* 1991; Gray 1993; Richardson 1996*b*; Wellman *et al.* 998*a*,*b*). The abundance of dyads in early land plant pore assemblages indicates that they were commonly roduced and are therefore probably not the products of neiotic abnormalities. Their occurrence is most comfortbly explained by invoking successive meiosis, with eparation occurring following the first meiotic division nd sporopollenin deposition on the products of the econd division. It has been noted that monads, dyads nd tetrads often have identical envelopes, and some uthors have suggested that they are closely related, erhaps even deriving from a single species (Johnson 985; Richardson 1988, 1992; Strother 1991; Hemsley 994). However, fixing affinity on the basis of a single haracter is problematic. Trilete spores dissociated from uvenile tetrads have a clear counterpart among extant mbryophytes, where their production is widespread mong free-sporing tracheophytes and also occurs poradically among bryophytes (e.g. Gray 1985).

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

Studies of *in situ* spores supply the only direct link etween the dispersed spore and plant megafossil ecords, 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 re absent from liverworts, but present in hornworts, nosses and vascular plants (although losses are not ncommon in these groups, and are generally considered o be related to ecological factors and functional requirenents) (see review in Kenrick & Crane 1997).

Consideration of dispersed spore assemblages from udford Lane and North Brown Clee Hill allows us to auge the extent to which the *in situ* record reflects the ispersed record. Permanent tetrads and dyads (including nvelope-enclosed forms) were relatively minor compoents of dispersed spore assemblages dominated by hilate onads and trilete spores. Studies of *in situ* spores reflect his situation in that specimens with tetrads and dyads are xtremely rare but those containing hilate monads and ilete spores are abundant. However, not all trilete spore orphotypes have been discovered *in situ*. *In situ* patinate pores and *in situ Emphanisporites*-type spores are extremely ncommon (Edwards & Richardson 2000), although oth spore types are abundant in dispersed spore assemlages, and even coprolites, from the mesofossil-bearing orizons. These findings may be a consequence of: i) preservational artefact (the missing spore types may erive from plants with low preservation potential); ii) palaeogeographical effects (the missing spore types ay derive from plants from outside of the depositional asin—an unlikely scenario as the spores are preserved in oprolites at this locality); (iii) facies effects (the missing pore types may derive from larger plants not represented mong the assemblages of small, highly sorted mesossils).

(v) *Spore wall ultrastructure*

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

To date, studies of wall ultrastructure in early land lant spores are in their infancy, and two principal lines of quiry have been explored. Some of the earlier cryptopores have been studied based on analysis of isolated ispersed spores from the Late Ordovician (Ashgill)–arly Silurian (Llandovery) of Ohio, USA (Taylor 995*a*,*b*, 1996, 1997). Later cryptospores and trilete spores ave been studied based on analysis of *in situ* spores exceponally preserved in mesofossils from the latest Silurian Ludford Lane) and earliest Devonian (North Brown lee Hill) localities in the Welsh Borderland (Rogerson *et* *l.* 1993; Edwards *et al.* 1995*b*, 1996*a*, 1999; Wellman 1999; ellman *et al.* 1998*a*,*b*). Studies on Late Silurian–Early evonian dispersed spores remains an unexploited, but otentially extremely useful, data source. Nonetheless, any early land plant spore morphotypes have now been ltrastructurally 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* *l.* 1999). For example, Edwards *et al.* (1999) and Habgood 2000) have recently suggested, based on evidence derived rom ultrastructural studies of fossil material, that cryptopore envelopes may have been tapetally derived, a ossibility previously discussed by Gray (1991).

(vi) *Conclusions*

Studies on early land plant spores are providing an nportant source of information in attempts to undertand the affinities and phylogenetic relationships of early igher land plants. This is particularly true for the arliest land plants, which left no megafossil record, as we re dependent on the dispersed microfossil record as our nly source of information. Analysis of these earliest land lant spores suggests that the producers were bryophyteke if not bryophytes (Gray 1985, 1991). It is anticipated hat our understanding of early land plant spores will ontinue to improve as further localities are discovered, nd more work is undertaken on these and pre-existing ocalities, particularly if these searches should turn up ody fossils of the spore producers. Additionally, it is robable that some of the identified gaps in knowledge vill be filled following further research on *in situ* spores nd spore wall ultrastructure, which may shed further ght on the evolutionary relationships of early land lants. Researchers are also utilizing different methods of hylogenetic analysis on the primary data set. For xample, Kenrick & Crane (1997) have recently underaken a detailed cladistic analysis of early land plants, vhich incorporates some of the data derived from studies f early land plant spores. At this juncture it is interesting o note that certain recent cladistic analyses (based on norphological and/or molecular data) indicate that the oryophytes' are paraphyletic with respect to the tracheohytes, but the three major lineages of 'bryophytes' (livervorts, hornworts and mosses) are all monophyletic, and ccupy basal positions within the embryophytes, with one f these lineages (probably the mosses) sister group to the racheophytes (see Mishler *et al.* 1994; Kenrick & Crane 1997) and references therein). Thus it might be anticipated s previously suggested (Gray 1985, 1991 and other refernces) that the earliest land plants were bryophyte-like ?cryptospore-producers), with tracheophytes (?trilete pore-producers) appearing somewhat later. However, it nust be borne in mind that early land plant classification nd phylogenetic interpretation are in a state of flux, and he biological integrity and evolutionary relationships of nany higher taxa are uncertain (e.g. Kenrick & Crane 997). Furthermore, many early fossil plants, such as the hyniophytoids, are of unknown affinity, and it is possible hat 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 he quantity and quality of reports and their palaeogeoraphical coverage for different stratigraphical levels. Two eneralizations can be made: (i) as one moves up column he dispersed spore record becomes better known; ii) there is an overrepresentation of reports from eastern orth America (Laurentia), western Europe (Laurentia, valonia 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 ilate monads are more controversial. Some appear to erive from rhyniophytoids (a group erected for plants of ncertain affinities); some may represent tracheophytes, hile others may represent non-vascular plants, perhaps ncluding 'primitive' groups ancestral to the vascular lants. Other cryptospore morphotypes remained as ersistent, although not abundant, elements of dispersed pore assemblages, attesting to the continuation of certain ryptospore-producing plants, although there was clearly serious reduction in the importance of the forms produ-ing envelope-enclosed spores. As more evidence becomes vailable, the possibility that trilete spores first appeared n northern Gondwana seems more likely, fuelling specu-ation that this may have been a 'centre of origin' for racheophytes.

Following the turnover in the nature of dispersed pore assemblages noted above, trilete spores and hilate onads had a major diversification, which probably eflects a diversification in the early tracheophytes (and ossibly also their putative 'ancestors' that may occur mong the rhyniophytoids). At about this time (late Venlock–early Ludlow) we find the first evidence for gnificant palaeophytogeographical differentiation (see .5), which is not surprising as this was a time when ome of the larger land masses were widely separated. ventually, towards the end of the Lochkovian, hilate onad abundance diminishes, leaving a flora dominated y trilete spore-producing plants, with cryptospore-roducing plants being a minor component. It may be gnificant that this pattern—a reduction in palaeophy-ographical differentiation—has been documented in reas that indicate a reduction in continental separation, ut that paradoxically show increased provincialism in arine invertebrates and vertebrates (A. J. Boucot, ersonal communication). The post-Lochkovian (Early evonian) paucity of cryptospores attests to large-scale xtinction among some of the 'lineages' at bryophyte evel of organization and possibly some early tracheo-hytes and/or their putative ancestors included in the hyniophytoids. It relates as well to tetrad dissociation ithin at least one 'lineage' of tetrad producers (see iscussion in Gray 1985, 1991).

(iii) *Measures of diversity*

There is often a reluctance to use dispersed spore diver-ty as a proxy for land plants' diversity because of oncerns that the former may not necessarily reflect the atter. It is frequently noted, based on observations of oth extant and fossil plants, that: (i) the same taxon ay produce a variety of different spore morphologies, eading to an overestimate in diversity; (ii) similar spores re produced by different plant groups, resulting in an nderestimate of diversity.

There is no *in situ* record for the earliest cryptospore roducers, and hence it is difficult to test whether or not ispersed spore diversity reflects true diversity. Moreover, everal potential pitfalls have been noted. First, it is clear hat many taxa are morphologically simple, and it is ighly likely that such similar forms could have been roduced by a number of plant types (i.e. homoplasy bounds), but it would be difficult or impossible to distin-uish between their dispersed spores. Second, it has been oted 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.* (1998*b*) 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

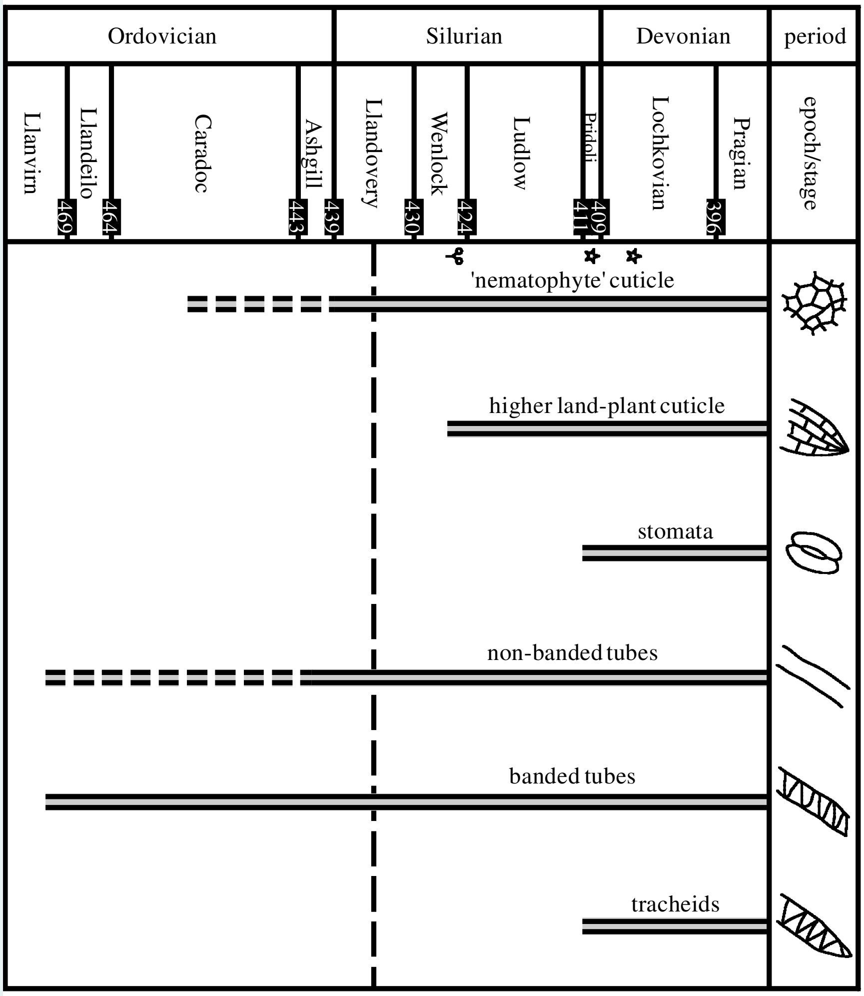


Figure 4. Stratigraphical range chart for early land plant phytodebris. Time-scale from Harland *et al.* (1989). Regarding annotation adjacent to the stratigraphic column: the small '*Cooksonia*' indicates the age of the earliest unequivocal land plant megafossils, the asterisks indicate the age of important 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.

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

(a) *The fossil record*

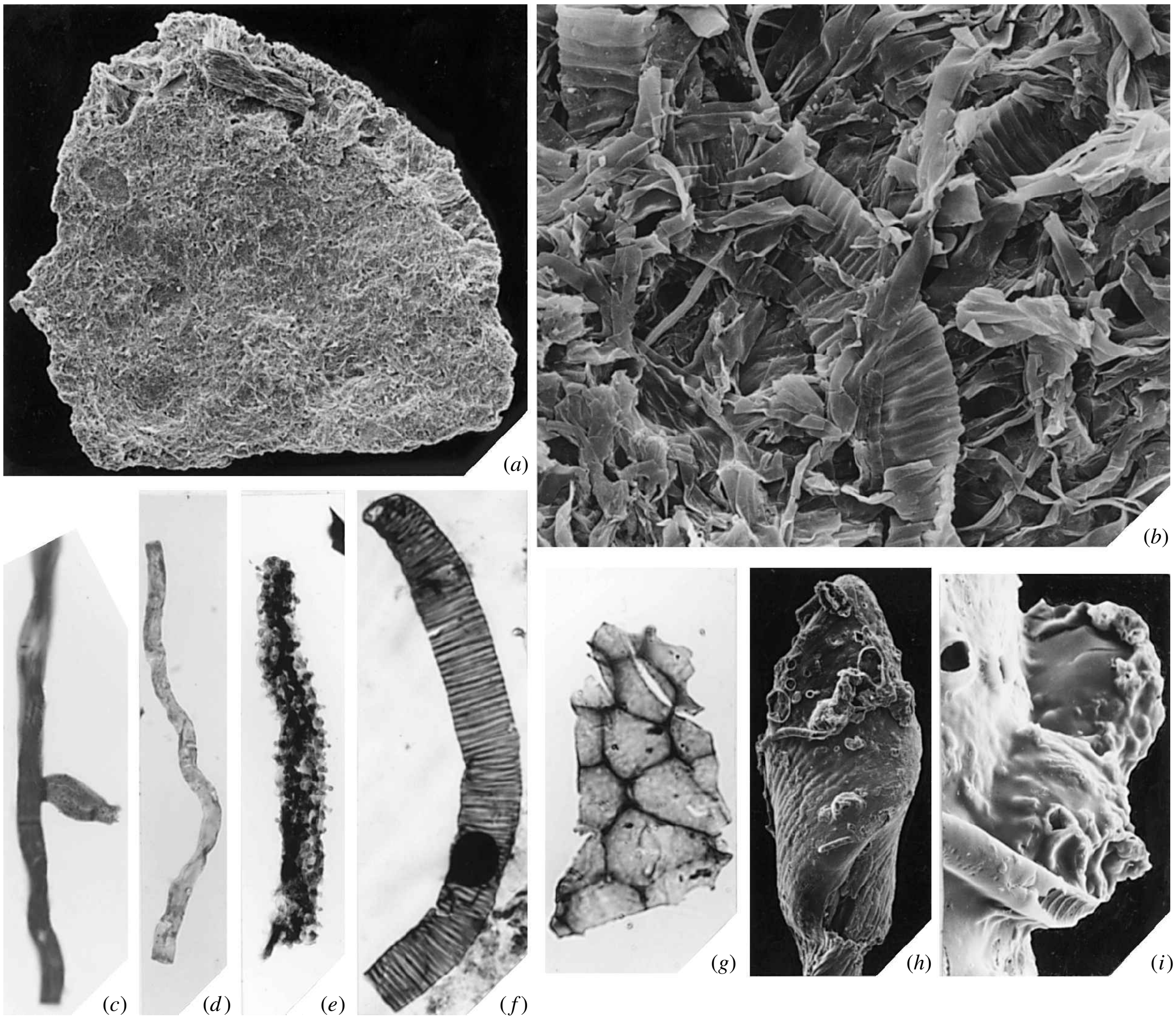
The earliest fragments of cuticle are reported from the aradoc (Late Ordovician) (Gray *et al.* 1982), and they re relatively abundant in the Llandovery (Early ilurian). By the Wenlock (Late Silurian), ornamented uticles, and forms clearly derived from tracheophytes, re present. The fossil record of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

The earliest tubular structures are ornamented forms rom the early Llanvirn of Bohemia (Vavrdova 1984) and mooth forms from the Ashgill of southern Britain Burgess & Edwards 1991). A proliferation of different ypes of tubular structure (including types with external rnament 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



igure 5. LM and SEM images of nematophytes and dispersed phytodebris. (*a*,*b*,*h*,*i*) courtesy of Professor Dianne Edwards, from e Ditton Group of North Brown Clee Hill, Shropshire, England (Lochkovian, Early Devonian) (Edwards 1996); (*c*, *f*) from the ower Old Red Sandstone of Lorne, Scotland (earliest Lochkovian, Early Devonian) (Wellman 1995); (*d*,*e*,*g*) from the Silurian f the Arabian peninsula. (*a*) Nematophyte (×65); (*b*) close up of (*a*) revealing tubular organization including banded and evigate 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* porangium with banded tubes attached via an amorphous film which in places forms pustules (×1000) (see Edwards *et al.* 996*b*); (*i*) Close up of (*h*) illustrating an internally thickened tube attached via the amorphous film with pustules (×550).

nteresting fossils relevant to the debate. Other avenues of esearch, such as geochemical analysis, have also been xplored. In the following account important contributions to our understanding of the affinities of phytodebris re summarized.

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

It has long been recognized that the dispersed cuticles re morphologically similar to the cuticles of extant land lants. However, it is not until the Wenlock (Late ilurian) that cuticles can be unequivocally assigned to racheophytes. These show marked alignment of pidermal cells, often with stomata, that clearly derive rom axes, and forms with well-defined outlines, occasionlly with attached spores, that derive from their porangia. However, the earlier forms, which persist until t least the Early Devonian, are more enigmatic. They ack 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 uestion of the possible relationship of these tracheid-like ubes to other organisms and concluded as we do here hat most could be attributed to nematophytes.

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

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

(ii) *The plant megafossil/mesofossil record*

The early land plant megafossil record consists of nequivocal tracheophytes (rhyniophytes, zosterophylls, ycopsids, etc.), rhyniophytoids of uncertain status, in ddition to the enigmatic nematophytes. It has been emonstrated that higher land plants are the source of ome of the dispersed cuticles since at least the Wenlock Late Silurian), a not unsurprising finding considering he abundance of fragmented land plant cuticle that is ncorporated into present-day sediments. However, it is to he enigmatic nematophytes that many have turned in heir search for the source of many of the other dispersed emains.

Nematophytes are a group of putative land plants of ncertain affinity, with somatic organization based on a omplex association of tubes (often including tubes with nternal annular or spiral thickenings), and believed by ang to possess a cuticular covering (Lang 1937; see also Gray 1984). They are known principally through rather ninformative coalified compressions (e.g. Lang 1937; trother 1988). However, uncompressed fragments are bundant in the recently discovered exceptionally reserved mesofossil assemblages from the Welsh Borderand, and these specimens are providing valuable new nformation on the morphology and anatomy of these rganisms (figure 5*a*,*b*). It is clear that many of the ispersed tubular structures (particularly laevigate and nternally thickened forms) are similar to those in nemaophytes, particularly as some of the dispersed forms egularly occur in associations similar to those observed n the megafossils/mesofossils. However, the covering of ematophytes is difficult to examine in the megafossils/ esofossils, and there is some doubt as to whether it is the ource of dispersed fragments of cuticle. Nonetheless, ecent 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 basidiomycetes. 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 ffinities and mode of life of these bizarre tissues/ rganisms remain obscure.

4. CONCLUSIONS

Reconstruction and interpretation of the early terres- rial vegetation is hampered by the inadequacies of the arly land plant fossil record, which is incomplete and iased. This is particularly the case for the earliest land lants, as there is no megafossil record, and we rely on ispersed microfossils, which provide more limited vidence as to the nature and affinities of the producers. Iowever, finds of new fossils continue to provide evidence hat increases our understanding of early land plants and errestrial ecosystems. An example is the wealth of new nformation, derived from the reports of Ordovician– ower Silurian microfossil assemblages from Saudi rabia, that is forcing us to reconsider previous inter- retations regarding the evolution and palaeophyto- eography of early land plants. Similarly, a wealth of new ata is coming to light based on work on the latest ilurian–earliest Devonian exceptionally preserved meso- ossil assemblages from the Welsh Borderland. Work on he mesofossils is demonstrating the vast diversity of early and plants, while examination of dispersed spore assem- lages from the same localities indicates that many of the pore-producers have not yet been identified and true iversity is in fact even larger. It is imperative that we ontinue to locate new material (microfossil, mesofossil nd megafossil) and fill in the gaps in the temporal/ patial record of early land plants. For example, there are s yet no reports of Upper Silurian–Lower Devonian ispersed spore assemblages from Australasia, a continent amed for the anomalous early occurrence of relatively arge lycopsids (Garratt 1978).

In addition to new material, new techniques and novel ines of enquiry are also being explored. There are a umber of notable examples. Chemical analysis of fossil naterial, such as that on dispersed cuticles performed by dwards *et al.* (1996*b*), is producing exciting results, lthough identification and interpretation of diagenetic ffects is currently proving frustrating. Comparisons etween dispersed phytodebris and fragments of extant ryophytes that are likely to survive in the fossil record .g. Kroken *et al.* 1996) may eventually prove fruitful. tudies of wall ultrastructure in early land plant spores re still in their infancy, but are already providing a vealth of new information (e.g. Taylor 1997; Wellman *et l.* 1998).

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Discussion

. Kenrick (*Department of Palaeontology, The Natural History useum, London*). Modern phylogenetic research clearly hows 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' pores, i.e. they were not transported into an environnent suitable for germination. Very rarely do dispersed arly land plant spores exhibit evidence of germination, lthough certain trilete spores occasionally exhibit gaping utures that may indicate that the gametophyte emerged hrough this suture, and very occasionally germinating pores are exquisitely preserved in exceptionally reserved floras, for example in the Rhynie Chert (Lyon 957; Bhutta 1973; Remy & Hass 1996).

Gray (1985) suggested that 'for spore-producing land lants the obligate spore tetrad appears to be the primiive reproductive unit; the single spore split from the etrad at maturity, derivative' and that 'distal dehiscence s primitive . . . proximal dehiscence derivative'. She thorughly reviewed the literature on extant tetrad-producing ryophytes and germination in their spore tetrads and we efer you to that source for details, some summarized ere. In obligate tetrads produced by living liverworts ermination is via the distal (i.e. free) surface (Duthie & Garside 1936; Proskauer 1954; Schuster 1981). Interestngly, in a number of extant bryophyte spores that are ispersed as monads (i.e. following dissociation of the etrad) dehiscence is also via the distal surface (Proskauer 961). This is even the case for some species that produce rilete spores, for example spores of most species of *Riccia* Duthie & Garside 1936), the endemic Indian *Stephensonlla* (Mehra & Kachroo 1952) and other taxa.

With regard to this debate, there are a number of ther pertinent observations. Permanent dyads and etrads are often preserved with the distal wall ollapsed, suggesting that the distal wall was thin. ections of such spores confirm that this is often the ase (Wellman *et al.* 1998; Edwards *et al.* 1999). Perhaps he distal wall of these spores was thin in order to facilate dehiscence. Interestingly, Taylor (1997) sectioned ispersed permanent dyads from latest Ordovician–arliest Silurian deposits of Ohio, and noted simple reaks/regions of thinning that occurred on the distal urface 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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