Wellman, C. H.; Gray, J. (2000). *The microfossil record of early land plants. Philosophical Transactions of the Royal Society B: Biological Sciences, 355(1398), 717–732.* doi:10.1098/rstb.2000.0612

ome of the larger land masses were widely separated. ventually, towards the end of the Lochkovian, hilate ionad 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 vel of organization and possibly some early tracheo-hytes and/or their putative ancestors included in the yniophytoids. 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 utter. 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, ading 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 at 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

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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

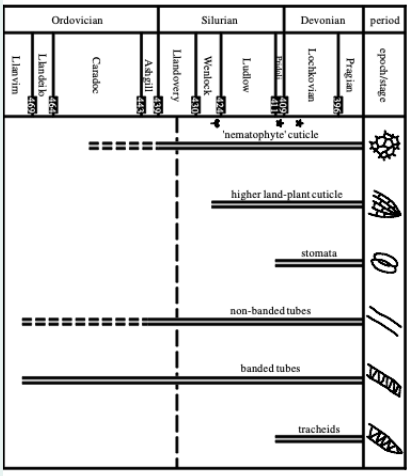

Figure 4. Stratigraphical range chart for early land plant phytodebris. Time-scale from Harland *et al.* (1989). Regarding annotation adjacent to the stratigraphic column: the small '*Cooksonia*' indicates the age of the earliest unequivocal land plant megafossils, the asterisks indicate the age of important 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 complex associations (figures 4 and 5). The affinities of any forms are controversial as they lack a convincing odern counterpart, although recent advances have gone long way towards clarifying their biological relation-ips. 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 uticles, 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 om the early Llanvirn of Bohemia (Vavrdova 1984) and nooth 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

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