REASSESSMENT OF DYADS CONTAINED IN A LATE SILURIAN RHYNIOPHYTOID SPORANGIUM

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ABSTRACT. A sporangial cluster of dyads of Přídolí age, first described by Lang in 1937, was investigated using Confocal Laser Scanning Microscopy (CLSM) supplemented by additional transmitted white light microscopy. CLSM images were most useful in determining the topology of an internal membrane found in well-preserved spore pairs. Detailed morphological characterization failed to resolve unambiguously either the ploidy or the botanical affiliation of these spores, but comparison with other fossils indicates a rhyniophytoid affinity for this sporangium, and that the included spores are most probably meiospores.

THE recognition that spores from early plants were often released in the form of permanent tetrads and dyads (Gray and Boucot 1971; Pratt *et al.* 1978; Strother and Traverse 1979) forms the basis of the cryptospore concept as originally proposed by Richardson *et al.* (1984). The abundance of obligate tetrads in the Silurian fossil record has led to speculation that early land plants were most probably at a bryophytic grade of evolution (Gray 1985; Richardson 1985) but, unlike obligate tetrads which are commonly the dispersed unit in extant hepatics, dyads are simply not normally found in any modern cryptogams. This has hampered efforts to determine their phylogenetic affinities, although the relation of the dyad form to sporogenesis has been discussed previously (Fanning *et al.* 1991; Strother 1991; Hemsley 1994*b*).

Obligate dyads and monads derived from dyads are relatively common in palynological macerations from Ordovician and Silurian near-shore marine deposits, these having been transported with sediments from their original terrestrial location. Their record begins in the Llanvirn. In the Wenlock, dyads may dominate the cryptospore fraction of an assemblage. For example, in the type Wenlock area, dyads and halves of dyad pairs constitute over 80 per cent. of the cryptospore taxa present (based on presence/absence data in Burgess and Richardson 1991). The last occurrence of dyads is in the Early Devonian (Lochkovian) reported by Wellman (1993). The basic dyad form is *Dyadospora* Strother and Traverse, which is, simply defined, a smooth-walled, obligate dyad. Sculptured forms appear in the Homerian (upper Wenlock) where several genera have been proposed to account for observed morphological variability (Burgess and Richardson 1991; Strother 1991). Bipolar spore-like palynomorphs, originally described as diacrodioid acritarchs (Strother and Traverse 1979), are now referred to the genus *Pseudodyadospora* Johnson. Both Johnson (1985) and Richardson (1988) have discussed the problems associated with these forms without well-formed inner (proximal) walls.

In situ dyads have been isolated from *Sallopella*-like sporangia of Přídolí (late Silurian) age from Perton Lane, Herefordshire by Fanning *et al.* (1991). They described loosely attached, laevigate dyads with diameters ranging from 39–68 μm, which are morphologically similar to, but generally larger than *Dyadospora murusattenuata* Strother and Traverse. Dyads were isolated from three elongate sporangia with rounded ends averaging 4·8 mm long and 0·8 mm wide. The occurrence of dyads in sporangia of rhyniophytoid aspect adds weight to the possibility that such spores were derived from embryophytes, and are not of algal or nematophyte origin (Strother 1991). Fanning *et al.* (1991) and Hemsley (1994*b*) discussed the possible development origins for regularly occurring, meiotically produced dyads; Strother (1991) reviewed the evidence for irregular meiotic production of dyads.

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Researchers studying dispersed dyads (Strother and Traverse 1979; Strother 1991) and those studying the *in situ* spores from sporangial masses (Fanning *et al.* 1991) have consistently mentioned a unique sporangial mass composed entirely of dyads, originally described by Lang (1937, p. 274). The elongate spore-mass from Tin Mill Race (Přídolí) is about 4·5 mm long, and 'slightly less than 1 mm' in width with a rounded tip (Text-fig. 1A), corresponding closely in gross dimensions to those of spore masses described by Fanning *et al.* (1991). Lang described the enclosed spores as bi-cellular, noted the inclusion of dark bodies within each cell, and surmised that the paired cells might possibly represent 'an early division on the direction of germination'. He mentioned that the internal bodies gave 'an absurd suggestion of nuclei with chromosomes', but he clearly did not support such an interpretation.

Given its potential importance, we have re-examined this specimen. The advent of the confocal laser scanning microscope (CLSM), with its potential to obtain high resolution within a thin focal plane, offered the additional prospect of a non-destructive technique that could reveal new information about these mysterious dyads. We present here results of our investigation utilizing this instrument together with supporting observations by conventional light microscopy (LM), and offer some thoughts on their likely derivation.

MATERIALS AND METHODS

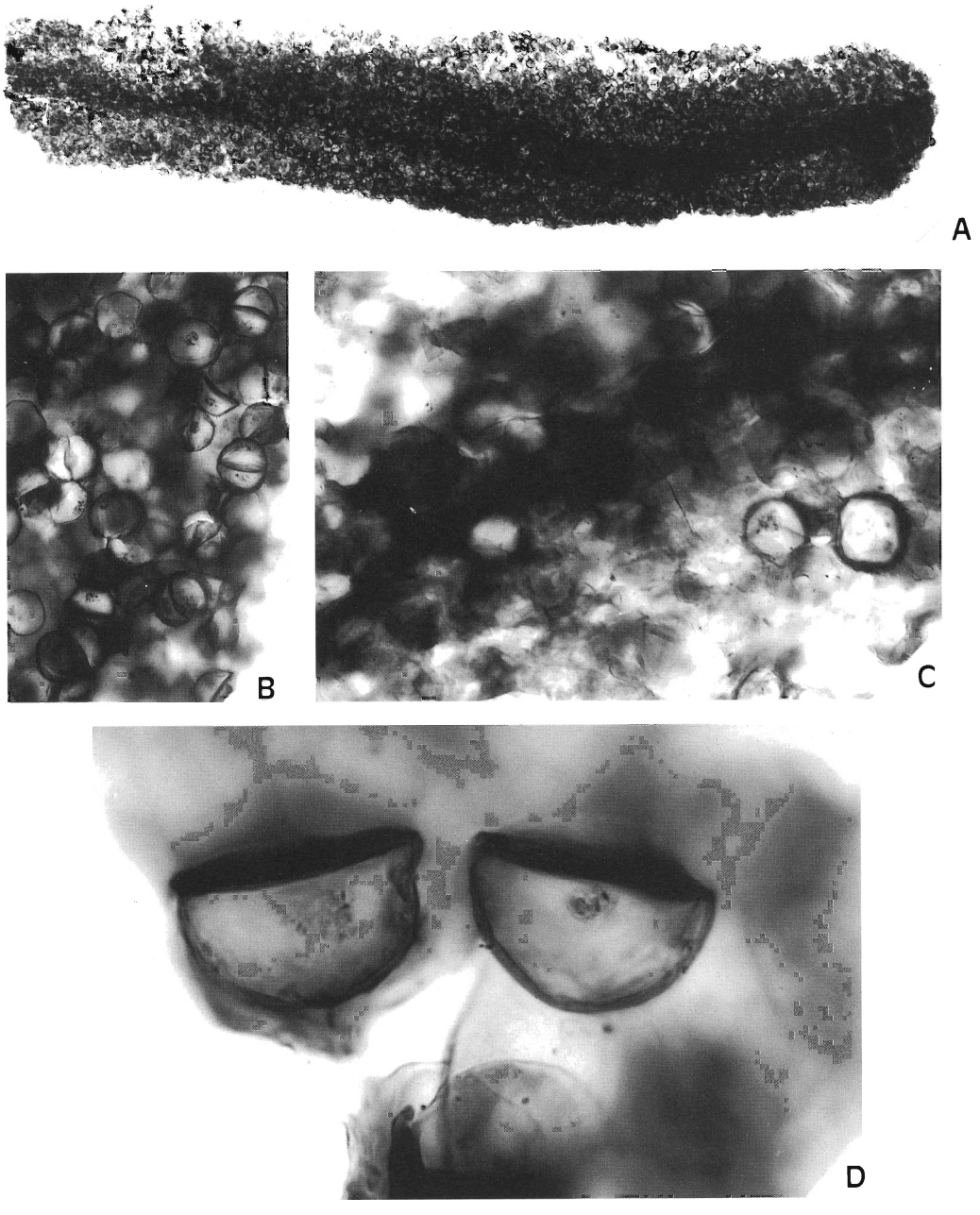
The sporangium, housed in The Natural History Museum, London (V.54654, Lang's original number 764), was 'recovered' by Lang when he used the transfer technique on a specimen, unrelated to the present study, from Tin Mill Race, Shropshire. This technique applied to such material would have involved the use of hydrofluoric acid and presumably the sporangium was recovered from the debris which fell into the HF from the developing transfer. The sporangium was mounted, by Lang, in Canada Balsalm on a glass slide with cover-slip.

A Leitz Ortholux II microscope was used for light microscopy (LM) in the present study, utilizing Bright Field and Differential Interference microscopy. Confocal laser microscopy was undertaken using a Leica CLSM based on an Aristoplan microscope with two fluorescence channels and an Argon/Krypton laser (three lines of 488, 568 and 647 nm) made available to us by Leica UK Ltd. Details of the methodology and colour imaging are outlined by Shute and Hemsley (1995).

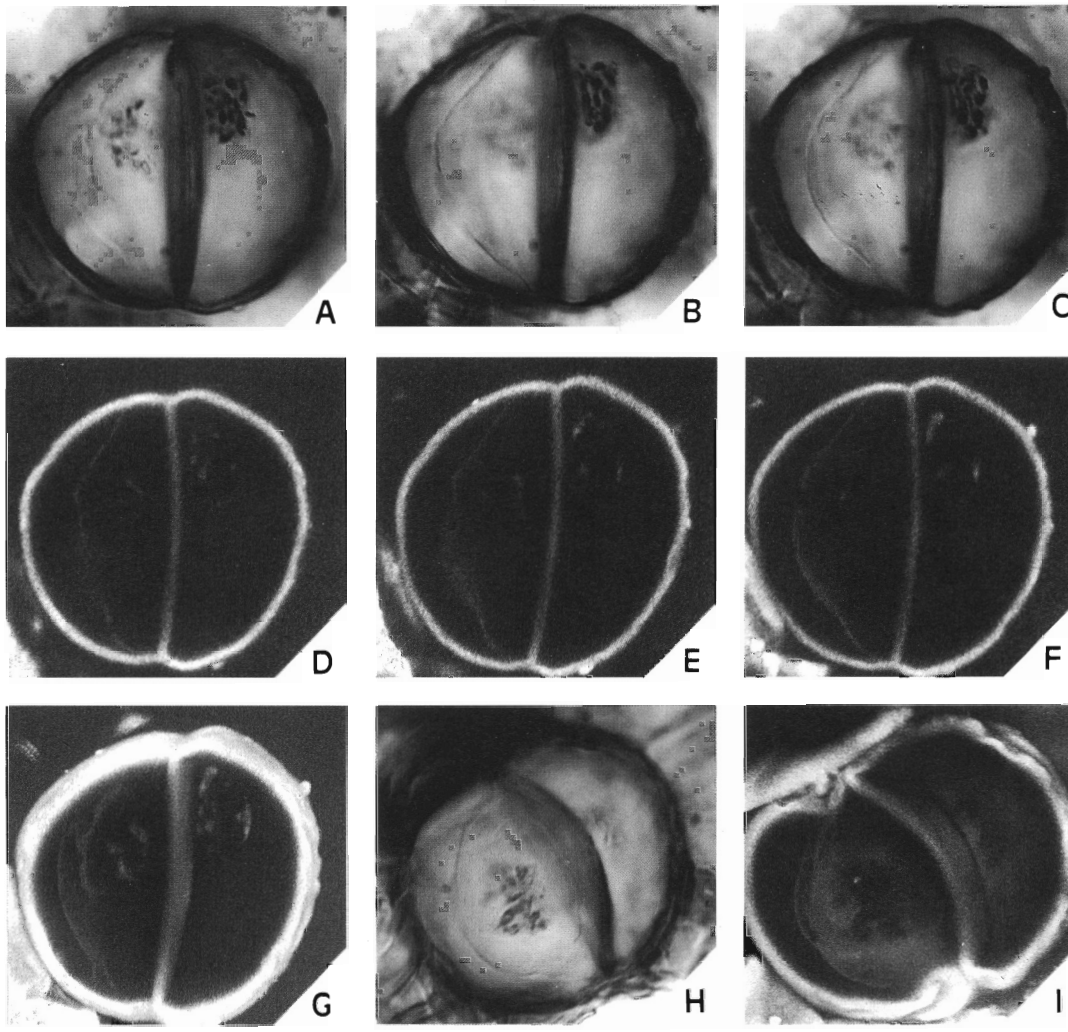
DESCRIPTION

The sporangium has somewhat parallel sides with a rounded tip as clearly illustrated in Text-figure 1A. Careful LM examination reveals a diaphanous outer layer, characterized by a pattern of cracks (e.g. Text-fig. 1B) and, in a portion of the basal section of the spore mass, an interior, faintly striated tissue (Text-fig. 1C). The position of the two layers described above can be confirmed by focusing sequentially through the specimen, which retains some depth in an axis normal to the plane of compression. These layers can be interpreted as supporting the interpretation of the spore mass as the remains of a mature sporangium, with the outer layer representing the remains of a cuticular layer and the inner, striated tissue representing either immature sporangial tissue or the remains of a columella. There is little support for the possibility that the 'striae' represent vascular tissue; the preservation is simply too faint to show structural detail. It is possible, however, that the interior striated tissue represents structural tissue. The spore mass contains roughly 2000 spore dyads.

The originally cylindrical specimen is compressed to 75 μm, a thickness which may be due in part to the mode of preservation, apparent in the spores themselves; they appear to be three-dimensionally preserved, rather than being crushed completely flat. One explanation for this preservation is that the sporangium was petrified with a mineral infilling, possibly silica, prior to complete compaction from burial and subsequent diagenesis. The use of HF by Lang would have removed any possible original silica preservation and no silica or other mineral was detected in the sporangium under cross nicols; however, the similarity of cellular-level preservation with that seen in late Proterozoic cyanobacterial mats (Strother *et al.* 1983) and Palaeozoic silicified peats (Knoll 1985) is remarkable. Variations in appearance of spores within the spore-mass may be due to



TEXT-FIG. 1. A, Lang's specimen 764, the entire sporangial contents; × 30. B, part of the sporangium illustrating dyads within the spore mass; × 150. C, a central part of the spore mass showing the striations discussed in the text; × 200. D, one of the relatively rare, separated dyads showing their basic shape. Both halves contain dark bodies adjacent to the contact face; × 800. All LM with bright field illumination.



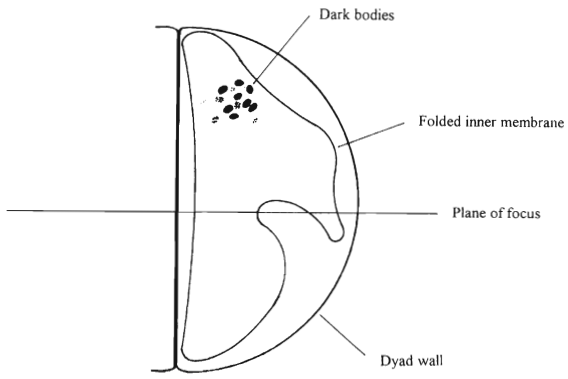
TEXT-FIG. 2. A–C, different focus sequence of the same dyad; ×800. D–F, 0·5 μm optical sections of the dyad illustrated in A–C; ×800. G, composite image of 20, 0·5 μm sections in the central region of the same dyad; ×800. H, a different dyad from the spore mass; ×800. I, the dyad illustrated in H, but as a composite of 20, 0·5 μm sections through the pair, superimposed on a transmitted light image; ×900. A–C, and H, LM interference microscopy. D–G and I, CLSM.

taphonomic effects, caused by differing degrees of petrification, which in turn permits the retention of morphological and topological detail. Alternatively, it is possible that the fine-grained nature of the surrounding clastic grains permits support of a three-dimensional structure of small fragments.

The preservational mode (whatever its geological origin) which is expressed in the specimen, enables us to describe spore pairs in terms of their gross morphology and the topological relations of the various components which make up the dyads. In general aspect, the spores consist of two nearly hemispherical pairs which are joined together in a common, fused wall, forming a proximal face (Text-fig. 1B). The external dimensions of fully, three-dimensionally preserved dyads is about 50 × 45 μm. Towards the periphery of the spore cluster, the partition wall is not always clearly seen.

This may be a preservational effect, or, if spores without well demarcated proximal walls represent immature forms, this might indicate centrifugal development within the original sporangium (Hemsley 1994*b*). The distal, outer wall of the dyads is 1–2 μm thick. Based primarily on their hemispherical shape, the dispersed equivalent to these spores would probably correspond to *Dyadospora murusdensa* Strother and Traverse.

Better preserved spores show an inner wall (membrane) in addition to the more rigid, outer coat (Text-figs 1D, 2A–C). CLSM proved helpful in determining the position, number and extent of internal membranes within these spores. Using the LM, a single membrane, apparently attached at the circumference of the contact face (Text-fig. 2B), can occasionally be detected crossing the centre of the spore. With the CLSM, it was possible to confirm the existence of this inner membrane (Text-fig. 2D–F). Initially it appeared that multiple, concentric membranes were present within the spore wall, but subsequent examination revealed only one membrane per cell. This single membrane may be distorted such that multiple crossings of the same membrane may occur in a single optical plane (Text-figs 2D, G, 3). The internal membrane (less than 1 μm in thickness) appears to be a detached,



TEXT-FIG. 3. Many of the dyads in Langs' sporangium contain a detached inner membrane, somewhat thinner than the main dyad wall. Where dark inner bodies are present, the membrane is drawn toward these structures. The convolutions of the inner membrane can give rise to the appearance of multiple internal membranes in thin optical section.

bag-like inner wall layer (Text-fig. 2G–I). It is often adherent to the contact face of the spore and generally well separated from the distal surface. Where a cluster of dark bodies (see below) occurs, the membrane is pulled inward at a point adjacent to the cluster (see Text-fig. 3). The CLSM did not resolve any ultrastructural detail of the outer spore wall (exine?) or the inner detached membrane, although both showed considerable autofluorescence. A diffuse autofluorescence within the shrunken membrane is clearly illustrated by the CLSM in Text-figure 2I. The common wall of the dyad displays a lesser degree of autofluorescence than the outer wall (Text-fig. 2D–G, I).

One of the most noticeable features of many of the better preserved individual spores are clusters of small, dark, condensed and somewhat ovoid to reniform bodies (granules). The granule clusters are always topologically enclosed within the interior membranes described above and they often lie near the contact face. The aggregate clusters of dark bodies are usually about 10 μm or so in diameter but this varies considerably with preservation. The individual bodies are 1×2 μm or less in size and are generally reniform to peanut-shaped to somewhat irregular in outline. Occasionally, the bodies appear to be paired although it is clear that this is not always the case, and it could be only a question of coincidence. CLSM did not clarify any detail of the granules, nor of their arrangement within the spore. This may have been due, in part, to their lack of autofluorescence (a feature which at least suggests a different composition from the thick outer wall and membranes).

DISCUSSION AND INTERPRETATIONS

Clearly Lang's 'spore-mass' represents the fossil remains of a sporangium. The elongate shape with rounded ends is suggestive of rhyniophytoid affinity and, when the similarity of their contents of cryptospore dyads is taken into account, this specimen seems very similar to the *Sallopella*-like

sporangia described by Fanning *et al.* (1988) from Perton Lane. The additional observation of possible external cuticle and some sort of internal striated tissue in the position of a central basal stalk or columella, strengthens this interpretation.

The spores themselves provide an opportunity for some interesting observations, particularly with respect to the topology of their wall components and cell contents in relation to the sporogenesis of dyads. The granular bodies seen in numerous cells are perhaps analogues of the condensed entire cells seen in silicified cyanobacteria from late Proterozoic deposits (e.g. Schopf 1968; Strother *et al.* 1983) and in modern silicification experiments performed on various algal and cyanobacterial cells (Knoll and Barghoorn 1975; Francis *et al.* 1978). Strother *et al.* (1983) were able to demonstrate that, in *Oscillatoriopsis variabilis*, multiple condensed granular bodies, similar to those preserved here, represented the probable degradational remains of entire cell contents. In these cyanobacterial cells, it is not possible that the granules represent condensed chromosomes, but it is clear that multiple granules occur per original cell. This is also the case here, where perhaps 18 to 24 granules are found per individual spore cell. Thus, we consider it possible that the condensed granules are a mineralization product of the degradational remnants of the entire cell contents of the former spore, cytoplasm plus nucleoplasm.

Topologically, the inner membrane, as preserved in these specimens, lies between the outermost rigid spore wall and the condensed granules. We considered three possible sources for this membrane: plasmalemma, primary (cellulosic) wall, or an inner layer of the exine which was exterior to the primary cell wall. The preservation of a true plasmalemma (the bilipid cell membrane) would certainly be remarkable. The somewhat partially invaginated, clearly shrunken nature of the inner membrane does appear to demonstrate possible response of the semipermiable plasmalemma during plasmolysis. This certainly could be the case if silicification was proceeded by the infusion of molecular silicic acid from a hypertonic solution of interstitial water, the basis of the model proposed by Leo and Barghoorn (1976). Since the mucopolysaccharides of cyanobacterial sheaths are often quite well preserved in chert, the silicification of a bilipid membrane should also be possible, although it has yet to be demonstrated experimentally. Butterfield *et al.* (1994) have recently argued, quite convincingly, that a wide variety of organic polymers found in plant and algal tissues could have been preserved under favourable taphonomic conditions. It is perhaps more likely that these inner membranes represent the shrunken cellulosic primary walls or a separating endexinal layer, which also could have responded to osmotic changes that occurred during early diagenesis. However, differences in the degree of autofluorescence between the membrane and the outer wall suggest a difference in composition. This in turn would suggest that the inner membrane is *not* composed of sporopollenin which is presumably the chief component of the outer, more robust wall.

The diffuse autofluorescence seen within the shrunken membrane (Text-fig. 2I) indicates a richer organic content preserved in this region. During plasmolysis, in response to Le Chatlier's principle, water diffuses through the semipermiable plasmalemma, effectively concentrating the original cytoplasm into a shrunken cell volume. This observation supports the possibility that the fossilized membrane marks the position of the original plasmalemma because, during plasmolysis, cytoplasm rich in high molecular weight polymers would have remained behind, effectively trapped by the plasmalemma. Presumably, the degraded remains of these organic polymers are now causing the observed autofluorescence.

Multiple wall layers have been detected in fossil spores derived from a number of early plant groups (Gensel and White 1983; Taylor and Taylor 1987; Hemsley 1989*a*; Shute and Edwards 1989; Rogerson *et al.* 1993; Hemsley 1994*a*; Hemsley *et al.* 1994; Taylor 1995). Therefore the occurrence of a distinct inner wall membrane is of no great significance in the determination of the affiliation of these dyads. Detachable membranes have been found within fossil bryophyte spores (e.g. the Rhaetic *Naiadita*; Hemsley 1989*b*) and represent the true exine, the thicker wall layer being interpreted as perine (Harris 1939). Detachable membranes, detected in dyads by Taylor (1995), have also been interpreted as indicating bryophytic affinity. Given the numerous differences between Lang's dyads and the tetrads of known bryophytes, observation of detachable membranes cannot

be considered as suggesting a bryophytic relationship, but may shed light on the nature of the individual layers.

Regardless of the exact nature of the preserved inner membrane, the topological relation between condensed granules, inner membrane and spore wall leaves little doubt that each spore of the dyad pair represents a single cell. This leads to the obvious question, what is the ploidy of each cell of the dyad pair? The simplest explanation is that there is a delay between Meiosis I and II, such that the daughter cells of the first division become fully separated before the onset of Meiosis II. This view was favoured by Fanning *et al.* (1991). It requires only a shift in the timing of a single cell division during sporogenesis. Similar examples of heterochrony abound in the evolutionary record where they are responsible for numerous significant evolutionary changes (Gould 1977).

Lang's comment that one cell of the pair was perhaps the first vegetative cell of the gametophyte seems unlikely because both cells of the dyads look so spore-like and it appears that they both functioned as diaspores. Their occurrence in a sporangial mass appears to support their haploid status whilst the possession of an exine and the similarity to dispersed dyads appears to confirm their functional maturity. The poor autofluorescence of the common wall between dyads may reflect poor sporopollenin impregnation and strengthens our belief that these spores were dispersed as dyads.

Dyads could represent diploid cells with a sporopolleninous coat. This could have occurred either through mitotic division of the spore mother cell or through the abortion of Meiosis I. There is some slight evidence for this possibility based on volumetric comparisons of similar forms of dispersed dyads and tetrads in which dyad pair volume approaches that for the entire tetrads (P. K. Strother, pers. obs.). Obviously, unless both tetrads and dyads are found in the same sporangium, it will be very difficult to demonstrate conclusively ploidy in the dyads using this method.

CONCLUSIONS

It is not likely that the dyad spore pairs represent meiospores in which one of two daughter cells (from either Meiosis I or II) has aborted, as is found in some megaspores of the Carboniferous fern *Stauropteris* (Chaloner 1958; Hemsley 1990) and the seed-megaspores of some Carboniferous lepidodendrids (e.g. *Cystosporites*; Hemsley 1993). Preservation is so good in these spores that we would expect to find some structural evidence for such an aborted cell. The arrangement, described in this paper, of structures within each of the spore walls strongly indicates that there was only one cell per mature spore. Our findings, therefore, support those of Fanning *et al.* (1988).

The structure and morphology of the plants responsible for dyad production are largely unknown apart from their sporangia; however, Lang's sporangium, in conjunction with the Perton Lane material, leads us to suspect rhyniophytoid affinity. The occurrence of an internal membrane is perhaps more probably a reflection of taphonomic differences in preservation between coalified (two dimensional) and petrified (three dimensional) spores. The details of the inner membrane and degrees of autofluorescence observed using the CLSM support the maturity and functionality of these dyads, and confirm that the interplay of meiosis and sporopollenin deposition in the earliest land-adapted plants was either not as rigidly controlled as in subsequent spore-bearing plants or was timed differently (Hemsley 1994*b*). This accords well with the theory that trilete spores originated from a primitive, obligate tetrad condition through progenesis of sporogenesis relative to sporangium maturation (Strother 1991).

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