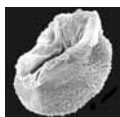# Cryptospores and miospores, their distribution patterns in the Lower Old Red Sandstone of the Anglo-Welsh Basin, and the habitat of their parent plants

JOHN B. RICHARDSON

Palynomorphs are abundant in some fine-grained rocks of the Lower Old Red Sandstone (Lower O.R.S.) of the Anglo-Welsh Basin. In this study the distribution and relative abundance of sporomorphs (cryptospores and miospores) have been examined from samples collected from the uppermost Raglan Marl and St. Maughan's formations from Ammons Hill and Ross on Wye [Ross–Tewkesbury Spur Motorway (M. 50) Herefordshire in the south and from uppermost Red Downton Formation (Ledbury Formation) and Ditton Formation from the Clee Hills (Shropshire) in the north (a distance of over 100 km)]. The stratigraphical interval examined equates largely to the lower and middle parts of the Lochkovian Stage except in the Clee Hills where the uppermost part of the stage may be present. The Lower O.R.S. sequence in the Anglo-Welsh Basin shows progressive offlap with the migration of medial and proximal facies (fluvial environments) to overlie the distal facies (marine-influenced environments) in the south. Dispersed palynomorphs have been examined from sections from the distal margins of the floodplain in the south [Ammons Hill and Ross–Tewkesbury Spur Motorway (M. 50) Herefordshire Sections] to more proximal areas of the floodplain in the north (Clee Hills). The relative abundance of major groups of cryptospores and miospores varies stratigraphically in the M. 50 and Clee Hill Sections reflecting the southern migration of facies belts and, although influenced by water transport, sporomorph distribution data may be used with caution to interpret potential habitats of their parent plants. In some cases cryptospores were dominant in sporomorph assemblages from distal sediments, deposited in a marine-influenced coastal plain, and their parent plants may therefore have been halophytic. In contrast, in the more proximal (upstream) sediments, except for those from the higher parts of the Brown Clee Hill sequence, cryptospores with granulate to apiculate sculpture and miospores, especially those with apiculate sculpture, are dominant. • Key words: Lower Old Red Sandstone, cryptospores, miospores, palynofacies, plant habitats.

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The pioneering work of John Allen on the Lower O.R.S. sediments of the Anglo-Welsh Basin led to a more detailed analysis than had been previously attempted. He made comparisons with Recent sediments and interpreted the facies to have formed in marginal marine to fluvial environments (Allen & Tarlo 1963, Allen 1974) and later with other co-workers *(e.g.,* Allen & Williams 1979, 1981) extended the work on these sediments especially to other parts of the basin (Fig. 1).

Muller (1959) demonstrated that the spores and pollen in Recent sediments of the Orinoco Delta were dispersed mainly by water. However, in the Late Silurian and earliest Devonian, many miospores and some cryptospores were smaller than 25 μm (the upper size indicating adaptation to wind dispersal in modern bryophytes (Mogensen 1981) so the applicability of Muller's work to early land floras and their spores remains limited particularly as the Přídolí and Lochkovian flora was so different from that of the Orinoco Delta today. Further environments of deposition similar to modern dryland river systems (Allen 1986, Marriott & Wright 2004) imply that both wind and water may have been important for dispersal with ephemeral lakes and streams acting as traps for both dust and sporomorphs.

Fossil plant remains

In situ spores (both cryptospores and trilete spores) have been isolated from the sporangia of tiny fragmentary plant axes (see *inter alia* Edwards & Richardson 2000 and references therein). These Lilliputian plant axes are often re-

markably similar but their variable terminal sporangia, and the variety of spores they contain, indicate increasing plant diversity possibly related to adaptation to a wider range of environments. (N.B. The spore zonation, zones and subzones, quoted below is based on Richardson *et al.* 1984, Richardson & McGregor 1986, Richardson *et al.* 2001, and is summarized in Edwards & Richardson 2004 (Fig. 2).

Whilst in the lower Downton Formation (*tripapillatus-spicula* (TS) Zone) and in the lower and middle parts of the Ditton Formation (lower and middle Subzones of the *micrornatus–newportensis* (MN) Zone) these plants had terminal sporangia, in higher parts of the Ditton Formation, in the Clee Hills, plants with both lateral (*Zosterophyllum* Penhallow, 1892) and terminal sporangia (*Salopella* Edwards & Richardson, 1974) occur together. In South Wales miospores are larger in the Senni Formation (the upper *breconensis-zavallatus* (BZ) Zone) and trilete spores are increasingly more diverse compared with cryptospores. The important macrofloras described from the Brecon Beacons by Edwards (1968, 1969, 1970, 1981) occur higher in the Senni Bed Formation where spore assemblages indicate that the beds belong to the *polygonalis – emsiensis* (PE) Zone assemblages (Siegenian/Pragian). The spores from the PE Zone in South Wales have the greatest diversity of miospores with apiculate and biform or murornate sculpture observed in the Anglo-Welsh Basin and show increasing numbers of zonate species. In these higher spore assemblages many miospore species are characteristically larger than Lochkovian (Gedinnian) spores (Richardson 1967).

The usefulness of dispersed spore taxa to plant studies is increased when their sporomorphs are found in their sporangia. However, although there has been a remarkable increase in the knowledge of uppermost Silurian and Lower Devonian *in situ* spore taxa over the last 30 years, the parent plants of many sporomorph taxa remain unknown. This may be due to preservation related to the degradation of plant remains during transport especially as some plants may have lived in sites, *e.g.*, upland areas, beyond the depositional basin. In spite of difficulties caused by transport from the habitats of their parent plants, and possibly from suffering a series of reworking events, some of which may have been more or less penecontemporaneous, cryptospores and miospores show distribution patterns that may afford clues to the original distribution patterns of their parent plants. Patterns of abundance and distribution of major sporomorph groups, both lateral and stratigraphical, are described below from Shropshire in the north to Hereford in the south.

Work on pollen and spore distribution in modern tropical sediments (*e.g.*, Muller 1959) has attracted much interest in the last half century but generalisations applicable to the upper Lower Palaeozoic and the Upper Palaeozoic are difficult to make. One major difference is that during the interval of time covered by the present work (upper Přídolí

to Lochkovian and Lower Pragian) the flora initially consisted of Lilliputian–sized plants with preserved axes only a few millimetres long; but these plants were later accompanied and replaced by bushy-sized plants about a metre high (see Edwards & Richardson 2004, Table 2).

Plants that had monopodial, or dichotomously branching, naked axes, often bearing terminal sporangia, are known in the Anglo-Welsh area from the Gorstian and Ludfordian (Ludlow). Elsewhere erect naked axes have been described from lower Silurian rocks of Maine, U.S.A. (Schopf *et al.* 1966), and rhyniophytoids (possible Rhynopsida) with dichotomously-branched axes and terminal sporangia (including one with similar sporangial shape to *C. hemisphaerica* Lang, 1937) from the Upper Wenlock of Ireland (Edwards & Feehan 1980). The Upper Wenlock witnessed the appearance of cryptospores with verrucate sculpture and of miospores with equatorial crassitudes and exines with verrucate-muronrate sculpture similar to those found *in situ* in the upper Silurian (Ludlow and Downton Series) where laevigate [*Ambitisporites* (Hoffmeister) Richardson & Lister, 1969], and verrucate-crassitate spores (*Synorisporites* Richardson & Lister, 1969), and spores with a microgranulate sculpture, are also found in *Cooksonia* Lang, 1937. Retusoid spores from *Pertonella dactylethra* Fanning, Edwards & Richardson, 1991 (originally compared with *Retusotriletes coronadus* Rodriguez, 1983 (*pars*) and later described as *Apiculiretusispora arcidecus* Richardson, Rodriguez & Sutherland, 2001) have variable apiculate sculpture usually confined to the curvaturae.

From the evidence available, most of these plants had trilete spores, and in their respective type areas, unambiguously trilete laevigate spores are known in sediments no older than the late Llandovery (Burgess 1987, 1991) and sculptured trilete miospores from the late Wenlock (Burgess & Richardson 1991, 1995). Prior to this time permanent tetrads, pseudodyads, and hilate monads derived from loose dyads are known (Gray 1985, Richardson 1985). However, loose dyads are not common in spore floras until the upper Přídolí and lower Lochkovian where in some areas they are dominant. In the upper Lochkovian and lower Pragian (Siegenian) the rhyniophytoids with no known tracheids and the Rhynopsida (*Cooksoniales*) which had tracheids, were accompanied by larger plants (Zosterophylls) (Edwards & Richardson 1974, Edwards 2003) with lateral sporangia. Associated with these axes were plants of unknown affinity known from "sheets" and, often complex, tubes. However, no known plants reached tree-like proportions until the Middle Devonian (Gilboa "Forest", Goldring 1924) and the absence of large erect plants in the late Silurian and Early Devonian (Lochkovian) must have had a great influence on spore dispersal patterns.

In the Anglo-Welsh Basin calcrete horizons (concretionary and conglomeratic) in the Lower O.R.S. rhythmic sequences do not become widespread until the Dittonian.
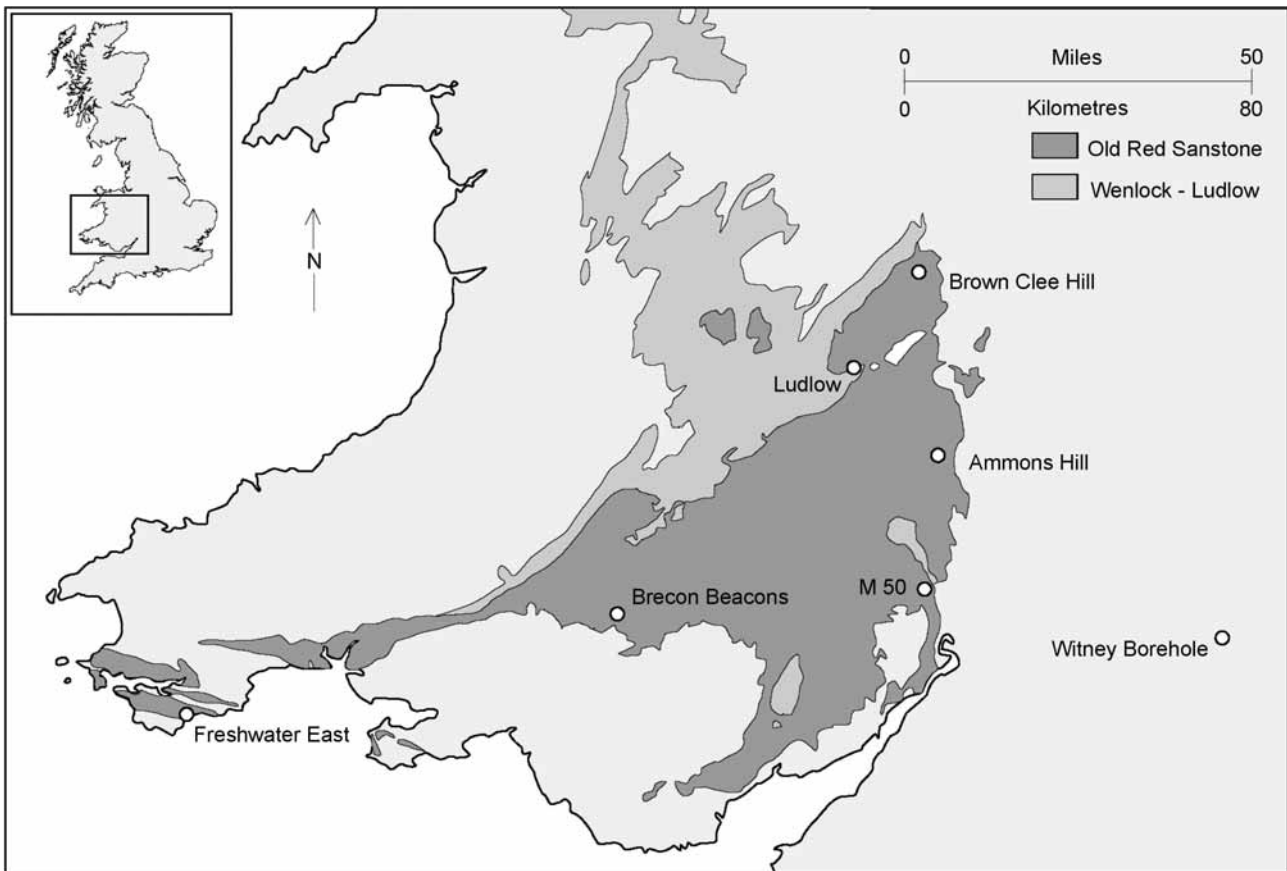
Figure 1. Map of the Anglo-Welsh Basin showing the main localities mentioned in the text.

The base of the Ditton Formation was traditionally placed at a prominent concretionary calcrete horizon known as the "*Psammosteus*" Limestones Member (Ball & Dineley 1961, Allen & Tarlo 1963) and usually placed at the base of the Ditton Formation. The "*Psammosteus*" Limestones were regarded originally as possibly diachronous but, where known, the lower subzone of the MN Zone always occurs in strata above this Formation. The horizon of the "*Psammosteus*" Limestones is so widespread, and the calcretes often so massive, that it is possible that this horizon represents a major arid interval between the Downton and Ditton formations and as a "climatic event" may have been more or less synchronous.

Edwards & Richardson (2004) hypothesised that "interfluvial areas, where calcretes are interpreted as relicts of vertisols and a seasonally dry climate, provided refugia in the Lower Devonian for the cryptospore-bearing plants which dominated Ordovician and Lower Silurian land vegetation, while vascular plants colonized areas in the immediate vicinity of rivers". This implies that these plants had durable sporomorphs, and possibly short life cycles, capable of responding to ephemeral moist conditions. The Ordovician and Lower Silurian sporomorph assemblages lacked the marked dominance and variety of cryptospore

dyads and monads observed in the lowermost Lochkovian. The reasons for this possible evolutionary change to abundant dyads is unclear; especially as this dominance has only been found so far in spore assemblages from the Lower O.R.S. in the Anglo-Welsh Basin peripheral to the O.R.S. Continent. In contrast, spore assemblages belonging to the same spore subzones from the Lower O.R.S. in the Midland Valley of Scotland, a basin in the interior of the O.R.S. Continent, lack the variety and numerical abundance of cryptospores observed in the Anglo-Welsh Basin sediments (Edwards & Richardson 2004).

Materials and method

Samples have been examined from upper Přídolí (?) and Lochkovian sequences in the Clee Hills, Shropshire (Richardson & Lister 1969, Richardson, unpublished work), Ross–Tewkesbury Spur Motorway (M. 50), Herefordshire (Allen & Dineley 1976, Richardson *et al.* 2000, 2001) and Ammons Hill, Herefordshire (Barclay *et al.* 1994). General maps of the basin are given in Richardson & Lister 1969 and Richardson & Edwards 2004. Localities studied in this work are shown on Fig. 1.

For each sample 250 sporomorphs (cryptospores and miospores) were counted and the identified taxa were placed into major groups based on their structure and sculpture. Initial counts were undertaken and graphs made to determine the point at which the taxa curve flattened out, in other words the point at which however many further spores were counted no new taxa were discovered; this level was reached when 200 to 250 sporomorphs had been counted.

Preparations with a MPA prefix are in the collections of the British Geological Survey at Keyworth, all the remaining sporomorphs are in the collections of the Department of Palaeontology, Natural History Museum, London.

Description of sporomorph profiles

Clues to the habitats of early land plants may be gleaned from three sources. Firstly, the distribution patterns of cryptospores and miospores in relation to broad sedimentary environments, secondly, the nature and distribution of their parent plants and thirdly, and perhaps most tenuously, how the sculptural patterns of the sporomorphs changed through time.

Distribution patterns of sporomorphs in the Anglo-Welsh Basin Lower O.R.S. [Ross–Tewkesbury Spur Motorway (M. 50) and Brown Clee Hill sections] show similar patterns in sporomorph assemblages and the same pattern is repeated in the stratigraphical sequences in both areas where the facies changes from proximal to distal facies in an offlapping succession. In contrast at Ammons Hill where marine influenced sediments (proximal facies) occur throughout the section the pattern of sporomorph groups shows a more or less constant pattern (Richardson 2002, 2006).

Lower Old Red Sandstone sections at Ammons Hill and Ross–Tewkesbury Spur Motorway (M. 50), Herefordshire

Sporomorph assemblages in the Lower O.R.S. section at the disused railway cutting at Ammons Hill are of Old Red Sandstone facies but contain brackish water faunas and small numbers of acritarchs (marine phytoplankton). The section is faulted and part of the section has sporomorph assemblages similar to the upper part of the Raglan Marl Formation (*Aneurospora* Zone), whereas the zonal index species *Streelispora newportensis* (Chaloner & Streel) Richardson & Lister, 1969 indicative of the Lower MN Subzone, appears above shell bed AH 20/21, and higher in samples AH 9 and AH 5 which are from green mudstone/siltstone intervals (Barclay *et al.* 1994, fig. 3). Below, in sample MP25239 at *ca* 32 m above the base of the section, the species *Leonispora argovegae* Cramer & Diez,

1975 occurs and this may be in a downfaulted part of the section because this species is an indicator of the Lower MN Subzone in both the Ross–Tewkesbury Spur Motorway (M. 50) Section and in the Cantabrian Mountains in Spain (Geras and La Vid Sections). In the Ross–Tewkesbury Spur Motorway (M. 50) section the *Aneurospora* Zone (containing non-papillate *Aneurospora*) appears in the upper part of the Raglan Marl Formation above the *Apiculiretusispora* sp. E Zone (Richardson MS). Thus, if these relatively poor, lower assemblages are not impoverished then they are earlier than MN assemblages but are, nevertheless, probably of early or earliest Devonian age because of comparisons with Spain and Podolia (Richardson *et al.* 2000).

Palynofacies

Ammons Hill Section (Fig. 2A)

AH numbers refer to shale intervals sampled (see the section illustrated in Barclay *et al.* 1994, fig. 3). MPA numbers refer to samples studied.

Faulting complicates the Ammons Hill succession and the stratigraphy is approximate. Except for one sample (MPA 25198) from an outcrop of the Raglan Marl Formation, separated from the main outcrop by the Brockhampton Fault, the section is probably all in the St. Maughan's Formation. The section is the only one studied that shows evidence for brackish water faunas above the level of the "*Psammosteus*" Limestones (*i.e.* in the overlying St. Maughan's Formation). The faunas include bivalves (modiolopsids), leperditid ostracods (both thought to inhabit brackish water environments) and vertebrate remains. Acritarchs (marine phytoplankton) occur in small numbers in this section (0.4 to 1.2%) and are probably *in situ*. Acritarchs (marine phytoplankton) occur in small numbers in this section (0.4 to 1.2%) and, because of the environments indicated by the associated fauna, are probably not reworked.

The section is faulted but sample MP25198 (6 m) possibly belongs to the *Aneurospora* Zone; and therefore, maybe from the Raglan Marl Formation, samples MP 25239 (9 m) to MP 25242 (19 m) (AH 37 and AH 34) contain *Leonispora argovegae*, *Aneurospora* spp. and *Ibereospora* sp. and probably belong to the St. Maughan's Formation (Lower MN Subzone), whereas higher assemblages definitely belonging to the Lower MN Subzone, samples MP 25246 (AH 21, AH 9 and AH 5 *ca* between 59–70 m) occur at the top of the section. However, the sporomorphs are poorly preserved and the assemblages around 32 m and 42 m could belong either to the *Aneurospora* Zone or they may be impoverished lower MN assemblages. Therefore, it is possible that all the samples
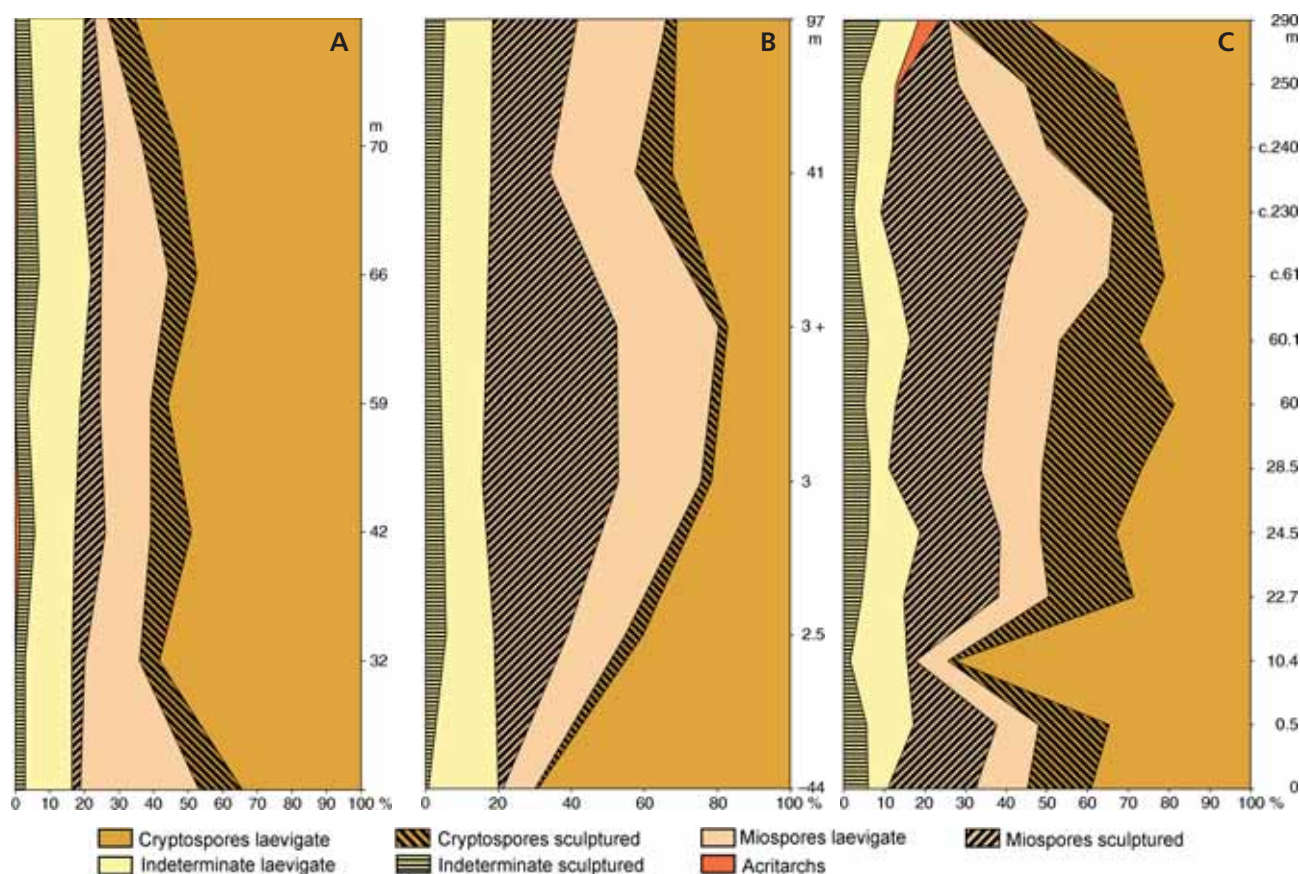
Figure 2. Sporomorph profiles from three sections in the Anglo-Welsh Basin. • A – Ammons Hill, Herefordshire. • B – Ross–Tewkesbury Spur Motorway (M 50), Herefordshire. • C – Clee Hills, Shropshire. • Please note that the acritarchs in the Ammons Hill Section are more or less contemporaneous whereas those at the top of the Clee Hill sequence are reworked. The stratigraphical levels given in metres at the base of the diagrams (y axis) indicate approximate levels above and (–) below the Psammosteus Limestones.

illustrated from Ammons Hill (Fig. 2A) are from the Raglan Marl Formation.

The Ammons Hill succession is the only section studied to show a consistently high percentage of laevigate cryptospores. Apart from the lowest sample counted (6 m), where laevigate cryptospores are around 34%, the percentage ranges from 48 to 66%. As this is in an area of distal alluvial deposition, and, as the faunas show, near areas of marine influence, it is tempting to propose that plants bearing laevigate cryptospores were the dominant vegetation in marginal marine areas. Laevigate miospores are also most abundant in the lowest sample (6 m).

Ross–Tewkesbury Spur Motorway (M. 50) Section (Fig. 2B)

Allen & Dineley (1976) described the stratigraphy, logged the section and determined the vertebrate fossils. Palynomorphs have been recovered from the upper 44 m of the Raglan Marl Formation (*Aneurospora* Zone) and 97 m

of the St. Maughan's Formation (Lower, Middle and possibly lower Upper MN Subzones). Laevigate cryptospores constitute nearly 70% of the lowest sample (in the upper part of the Raglan Marl Formation) and rapidly decrease to just over 17% in the lower part of the St. Maughan's Formation. In contrast sculptured miospores represent just over 1% of the Raglan Marl Formation sample but within the same interval of the lower St. Maughan's Formation (3 m) the proportion increases to over 37%. The lower part of the St. Maughan's Formation contains massive sandstones (possibly meandering channel deposits) with thin shale/silt intercalations containing well preserved sporomorphs which were probably derived from more upstream alluvial environments then rapidly dumped.

Brown Clee Hill (Fig. 2C)

This is a composite section based on the examination of samples from stream sections around Brown Clee Hill

through the upper Red Downton Formation and the Ditton Formation. Few sporomorphs have been recovered from the upper part of Red Downton Formation and none of these assemblages is good enough for detailed palynological analysis. The Ditton Formation is approximately 440 m thick and through a thickness of *ca* 300 m above the "*Psammosteus*" Limestone the sporomorphs have been counted. The uppermost spores encountered were from higher beds, from near the top of the Ditton Formation (*ca* 440 m) but either the assemblages were too poorly preserved, or their stratigraphical position too uncertain, and these have been therefore excluded from the counts.

The sections in this area are the only ones to cover all three subzones (lower, middle and upper) of the *micrornatus–newportensis* (MN Zone) and possibly include further zones, a possible *Emphanisporites micrornatus* var. *sinuosus–gedinniensis* Zone (see Breuer *et al.* 2005) and specimens similar to *E. zavallatus* appearing near the top of the sequence. The latter species forming a link with assemblages from the lower Senni Formation of South Wales (Richardson *et al.* 1982) where the *breconensis–zavallatus* (BZ) Zone occurs in the basal Senni Formation lying above upper MN Subzone assemblages from the upper part of the Red Marl Formation (Richardson *et al.* 1982). However, in the upper parts of the Ditton Formation the relationship is not clearly seen.

The succession of sporomorph counts based on sporomorph assemblages from the Clee Hill sections shows a double peak in laevigate cryptospores. A sharp peak at 10.4 m above the base of the Ditton Formation is the most marked at over 70%. This correlates with a similar peak in the Lower MN Subzone levels of distal floodplain deposits *i.e.* those nearest to the sea. Above this level, in Brown Clee Hill, the proportion of laevigate cryptospores is fairly constant at between 20–30%. At the top of the sequence, in the most proximal parts of the sequence that still yield sporomorphs, laevigate cryptospores are again abundant but, in contrast to the lower peak, they include a large proportion of alete monad cryptospores whereas those in the lower peak contain far more dyads and the hilate monads derived from them. It is at this level that the reworked acritarchs are most prominent and it is possible that some of the alete cryptospores are also reworked.

In the Brown Clee Hill Sections acritarchs have only been found at the top of a coarsening upwards sequence and are reworked, a trend that is continued as increasing proportions of acritarchs are reworked into the Senni Formation (Siegenian/Pragian) of South Wales where acritarchs of varied age and provenance are abundant (Hassan 1982). Assemblages with abundant reworked acritarchs were also described from the Lower O.R.S. of probable Emsian age from the Witney borehole (Richardson & Rasul 1978, 1979).

Synthesis of sporomorph data

Distal margins of the alluvial plain (Fig. 2A–C)

Laevigate cryptospores occur abundantly in the upper Raglan Marl Formation and lower St. Maughan's Formation in the M. 50 Motorway Section (17–70%) and Ammons Hill samples (35–66%). In the upper Raglan Marl Formation (M. 50 section) 45% of the 70% is formed by cryptospore dyads and monads of the genus *Laevolancis*. Laevigate cryptospores also show a distinct peak in the Lower Ditton Formation at around 10m above the Psammosteus Limestone in the Brown Clee Hill samples (over 70%) where again dyads and hilate monads make up over 50%. These sediments were deposited on a distal alluvial plain and were in part marine influenced (Ball & Dineley 1961, Allen & Tarlo 1963, Barclay *et al.* 1994). The high proportion of laevigate cryptospores decreases rapidly higher in the successions in the M. 50 and Brown Clee Hill sequences which may preclude the possibility that these abundant cryptospores were derived from plants living predominantly in more proximal alluvial environments. In contrast in the Ammons Hill samples, in which there are indications of marine influence throughout the section, the abundance of laevigate cryptospores is between 50 and 60% except for the lowermost sample. Acritarchs occur in many of the samples from Ammons Hill, and although not common, tend to be most abundant in samples immediately prior to and after samples where smooth cryptospores are between 50–60% of the total assemblage. It thus appears that the abundance of these cryptospores is not entirely due to sorting during transport but may be related partly to the habitat of their parent plants and indeed these plants may have been halophytic. Thus hilate monad cryptospores separated from dyads that are frequently common at these levels may have been produced by plants living close to the sea. An alternative hypothesis would be that wind or water currents concentrated unsculptured cryptospore monads in nearshore alluvial environments; but the latter process would tend to concentrate sporomorphs of different sizes rather than separating distinct groups *e.g.*, laevigate monads and dyads.

Medial alluvial plain

Ascending the sequence in the M. 50 and Clee Hill Sections through the upper Lower MN, Middle and Upper MN Subzones the Lower Old Red Sandstone the sediments offlap as the fall line migrates southwards. According to some models this was an area of high-sinuosity, low-slope, meandering streams (Allen 1974) with broad, flat interfluves where standing bodies of water would be ephemeral depending on the frequency of rains (Marriot & Wright

2004). Sculptured cryptospores initially increase and their parent plants may have lived in interfluve areas, where the water table was variable, and may have taken advantage of rapid growth and dispersal at times of infrequent rainfall.

Proximal alluvial plain

The sections studied in the upper part of the Ditton Formation in the Brown Clee Hills are the only ones interpreted as formed on a proximal alluvial plain. In this part of the Ditton Formation (Lochkovian) the sporomorph assemblages show several distinctive features not seen in the other sections studied. Firstly, there is a peak of alete cryptospores. This peak differs from the Lower Ditton Formation peak because a large number of the cryptospores are alete and not hilate forms (*i.e.* separated from dyads). Secondly, laevigate and sculptured miospores decline rapidly at the top of the sequence and thirdly, sculptured cryptospores retain, more or less, a constant proportion throughout the section and are important even in the highest sample. In the upper part of the sequence, that is beds from the Middle MN Subzone and upwards there is an increase in variety of laevigate and sculptured variants of species of the genus *Emphanisporites* and morphs of *E. micrornatus* Richardson & Lister, 1969 with spines appear that are more common in the overlying Pragian. In contrast to many miospore species very few (except distally granulate forms *E.* cf. *micrornatus* and *E. micrornatus*) have been found *in situ* and plant remains with these spores are rare. It is therefore possible that plants producing the spores of *Emphanisporites* inhabited more upland areas and the sporangial remains had been transported from outside the main depositional basin (Edwards & Richardson 2000). Reworked acritarchs only occur in the upper part of the sequence and indicate uplift of the hinterland and migration of the alluvium southwards.

Early Devonian dispersed sporomorphs: palynology and vegetation

The successions in the three areas (Ammons Hill, M. 50, and Brown Clee Hill) show parts of three palynological phases but it is only in Brown Clee Hill that the most complete succession is seen. Firstly near the base of the sequence there is a high percentage of hilate cryptospores. This is present in both the upper part of the Raglan Marl and lower part of the St. Maughan's (Lower Ditton) formations and coincides with marginal marine (distal) environments. Overall the percentage of cryptospores is much greater in the External Facies of the Lower Old Red Sandstone (floodplain environments around the margins of the Old Red Sandstone Continent) than in the Internal Facies represented by depositional basins within the Continent such as the Midland Valley of Scotland (Edwards & Richardson 2004). A possible explanation may be that at least some of the parent plants of these cryptospores were halophytic. In the Anglo-Welsh successions the miospores are more important and laevigate cryptospores are less abundant in the more proximal facies (higher in the stratigraphical sequence). Edwards & Richardson (2004) hypothesised that "interfluvial areas, where calcretes are interpreted as relicts of vertisols and a seasonally dry climate, provided refugia in the Lower Devonian for the cryptospore-producing plants which dominated Ordovician and Lower Silurian land vegetation, while vascular plants colonized areas in the immediate vicinity of rivers".

Early land plants and sporomorphs

What is known of the parent plants of Upper Silurian and Lower Devonian sporomorphs has increased dramatically through the work of Edwards and jointly supervised students (for references see Edwards & Richardson 2004). What previously were dismissed as plant "scraps" have yielded data showing that possibly two types of plants were present. Both may show erect, dichotomously-branched axes. In one plant group there is no evidence for vascular tissue (rhyniophytoids) and in the other the axes have variably developed vascular traces. Differences between rhyniophytoids and rhyniophytes (Rhynopsida) may be a result of incomplete knowledge caused by preservation effects or may reflect differences in the early evolution of vascular plants. In addition there are sporangial masses, which reveal little, or nothing, about the nature of their parent plants. Some of the latter include masses of dyads (Lang 1937) and others are from uniaxial sporangia also containing cryptospores (Fanning *et al.* 1991) as well as spore masses (Wellman *et al.* 1998). The true nature of the rhyniophytoids is an enigma and comparison with bryophytes is probably misleading based on lack of preservation of plant tissues (*e.g.*, vascular tissue). It is probably safer to refer to the cryptospores as belonging to a group of unknown land plants that were probably non-vascular (Richardson 1992). Some modern liverworts produce permanent tetrads (*e.g.*, *Sphaerocarpos* Linnaeus, 1753 and *Riccia* Boehmer, 1760) but no modern liverworts producing dyads and hilate monads, so abundant in the Lower O.R.S. of the Welsh Borders, are known. In fact permanent sporomorph dyads, loose dyads, and hilate monads derived from them are unknown in post-Lower Devonian strata with the exception of limited occurrences in the Middle and Upper Devonian (*e.g.*, *Laevolancis divellomedia*; Chibrikova 1959, Balme 1988). Whatever the affinities of the plants that produced the wealth of dyads and hilate monads in the Lochkovian they appear to be extinct today, or, if they per-

sisted, their parent plants have developed different spore types. Several hilate monads have identical sculpture to some trilete spores and therefore their parent plants may at times have produced dyads and, at others, tetrads and then developed into plants producing trilete spores only. In addition there is evidence for possible hybridization (Richardson 1996a) so it is possible that plants with trilete spores gradually replaced dyad producing plants, possibly because development from loose tetrads had advantages not present in those from dyads and monad cryptospores. It is equally possible that the parent plants largely became extinct. Was a factor in this process the progressive invasion of cryptospore-plant habitats by more rapidly evolving Rhynopsida possibly related to increasing rainfall and the increasing permanence of wet habitats?

The dispersed miospore record reveals a trend in sporomorph sculpture through time that, apart from retusoid spores, is the same for each structural miospore type (Richardson 1980, 1988, 1996b; Richardson & Burgess 1999). This trend is present in some cryptospores (see Richardson 1999c) but is most clearly seen in trilete spores. The pattern of distal sculpture from laevigate to verrucate-murornate to apiculate occurs in spores with an equatorial crassitude namely *Ambitisporites* (laevigate), *Synorisporites* (verrucate-murornate), and *Streelispora-Aneurospora* (apiculate) from the upper Llandovery, upper Wenlock and upper Ludlow (upper Ludfordian). In distally patinate-proximally hilate miospores the pattern is repeated. This trend in spore sculpture may indicate that it was due to environmental adaptations possibly ensuring spore germination in favourable conditions. The increase in spinose spores of the genera *Apiculiretusispora, Dibolisporites* and *Emphanisporites* in the Pragian may be another "fashion" in spore sculpture reflecting an evolutionary/environmental control.

One dramatic piece of research (Fanning *et al.* 1988, 1991) showed that the pattern in spore sculpture was not random because apparently identical dichotomously-branched axes of the genus *Cooksonia* from different stratigraphical horizons, produced equatorially-crassitate trilete spores with laevigate and verrucate exines [Lower Downton (Přídolí)] and apiculate exines [Lower Ditton (Lower Lochkovian)] which is perhaps a clear indication of how important the spores were in relation to land plant evolution at that time and is possibly related to the plants spreading into new habitats (Richardson & Burgess 1999).

Conclusions

At the base of the Lower O.R.S. sequence in Shropshire sedimentological evidence indicates a brief marine transgression followed by regression (Downton Castle Formation, Allen 1974). Palynological evidence based on land derived

sporomorphs and marine microfossils indicated parallel events (Richardson & Rasul 1990). After the Temeside Formation there is a gap in palynological data until the upper part of the Red Marl and Ditton formations. The sequence in the Ditton Formation "records the establishment during a marine regression of extensive and persistent alluvial plains" characterized by fining upwards cyclothems (Allen 1974). During this interval there is an abundance of laevigate dyads and hilate monad cryptospores in proximal alluvial sediments.

In medial alluvial sediments sculptured cryptospores are more abundant and there is a greater variety of trilete sculptured spores. The parent plants of the sculptured cryptospores may have inhabited ephemeral environments and been dispersed by wind and water. In the case of the trilete spores their plants may have lived closer to the main river channels meandering across the alluvial plain but the trends in spore sculpture from laevigate to apiculate may indicate a tendency for adaptation to a variety of habitats as well.

Medial and proximal parts of the drainage basin contain increasing numbers of variants, especially distally sculptured variants, of the genus *Emphanisporites* (Edwards & Richardson 2000) but the spores are uncommon and this fact along with the scarcity of mesofossil producers led the authors' to suggest that the parent plants of these distinctive spores grew in the upper reaches of the drainage basin. The Rhynie Chert deposits may also indicate proximal, or near proximal, alluvial plain environments.

Proximal alluvial areas also show a peak of laevigate cryptospores but these are dominated by alete monads and may involve reworking of lower Lochkovian and older sediments. This is marked in the upper two samples where the peak contains a higher proportion of alete monads than the lower peak. The upper two samples show a decrease in the numbers of miospores and, in part at least this may be due also to the numbers of reworked alete cryptospores. Proximal and distal alluvial sediments are similar in both having an abundance of alete cryptospores but the much greater abundance of laevigate hilate monads, dyads and pseudodyads in the more proximal alluvial plain sediments forms the greatest difference in the palynofacies of the two areas.

In the higher parts of the Brown Clee Hills the sediments show evidence for reworking of acritarchs and reflects Allen's analysis of pebble data which shows that detritus came from metamorphic rocks prior to deposition of the Ditton Formation but in higher beds pebbles of Silurian limestone have been found. In the present work reworked acritarchs are present high in the Ditton Formation and also indicate that fossiliferous Lower Palaeozoic rocks were being eroded at the time. If this were the case there is little doubt that older Lower O.R.S. deposits would be reworked also (see also Allen & Williams 1979). The model provided by Allen & Williams (1979, fig. 3) that shows earlier

Lower Old Red Sandstone sediments being eroded near proximal areas of the alluvial plain is closely similar to the one envisaged here.

Acknowledgements

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