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Ecological changes in Pennsylvanian (Asturian and early Cantabrian) coal floras inferred from lycophyte microspore abundances

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ABSTRACT**.** — The distribution and relative amounts of six genera of lycophyte microspores, *Lycospora*, *Densosporites*, *Crassispora*, *Cirratriradites*, *Endosporites* and *Cadiospora*, are compared in the Pennsylvanian coals from the Dobrudzha and Forest of Dean coalfields, clastic sediments from the Glace Bay borehole in the Cape Breton Coalfield, and the southern crop of the South Wales coalfield. Inverse relationships are shown between *Lycospora* and *Densosporites* and between *Lycospora* and *Crassispora* in samples from all of the coalfields. The changes in microspore assemblages suggest there were at least five different communities of lycophyte plants growing in the Pennsylvanian swamps. Changes in microspore assemblages at the Asturian/Cantabrian boundary mirror the previously described macrofloral changes at this time.

Keywords: Pennsylvanian, lycophytes, microspores, ecological changes.

1. Introduction

Interpretations of the palaeoecology of Carboniferous vegetation rely on the identification of species of plant fossils, the composition of local populations, the geographical distribution of the plant fossils and their relationship to the lithology in which they are preserved. This has been used to great effect in interpreting Carboniferous vegetation based upon adpressions (e.g. Cleal et al., 2002, 2009, 2012). (Fig. 1).

The distribution of the lycophyte species in fifteen Euramerican coalfields during the Asturian (Fig. 2) was summarized by Thomas (2007, p. 461). This was done by analysing the datasets from the coalfields using unweighted pair group cluster analyses of Jaccard's Coefficients. These were calculated as a measure of the similarity of the various pairs of the floras and giving no weight to species that are absent from the areas being compared. Then these were subjected to unweighted pair clustering, which is generally recommended for analysing binary data (Sokal and Sneath, 1973). The analysis gave the major grouping to include the Variscan coalfields of Cape Breton, southern Britain (including coalfields in South Wales, the Forest of Dean and Bristol and Somerset), Donetz and Dobrudzha. The two western areas with marine influence during Asturian time (Illinois and Iberia) are separated when only vegetative species are used. The analyses also clearly showed that there was a major difference between the species in the lowland coalfields of the Variscan foreland and those in the three intramontane basin coalfields of Zwickau, Bohemia and Upper Silesia.

On a broad front, a synthesis of the Middle Pennsylvanian sedimentological and palaeontological record of terrestrial habitats across the Variscan foreland and adjacent intramontane basins (Cleal et al., 2009, p. 182) suggests a contraction and progressive westward shift of the coal swamps. This was correlated with pulses of tectonic activity that resulted from the northwards migration of the Variscan Front causing disruption to the landscapes and their drainage patterns. The better drained and therefore drier conditions in the coal swamps made them less suitable for the growth of the dominant arborescent and sub-arborescent lycophytes. The lycophyte dominated swamps were, therefore, progressively replaced by vegetation that was dominated by marattialean ferns (DiMichele and Phillips, 1996; DiMichele et al., 1985). Tree fern numbers had in fact started to increase during the Desmoinesian (Phillips and Peppers, 1984), although these were different species to those dominating the Late Pennsylvanian peat swamps. Willard et al. (2007) showed the flora of the Calhoun coal bed (McLeansboro Group, Missourian Series of the Pennsylvanian) of the Illinois Basin to be dominated by tree ferns with subsidiary numbers of pteridosperms and sigillarians. An analysis of coal balls and spores showed there to be a persistent plant population that shifted over the landscape. Then, in the late Pennsylvanian Duquesne coal bed (Ohio), assemblages of tree ferns are again most common, but other assemblages are dominated by pteridosperms, sigillarians (in the lower parts of the coal bed) or *Chaloneria* (Pryor, 1993, 1996). This was suggested to be due to physical changes in the coal swamp during peat accumulation. *Chaloneria* was also one of the few lycophytes that survived the Westphalian/Stephanian boundary extinction in North America (Pigg and Rothwell, 1983).

Tree fern growth of extant species is variable. Many species have an early growth spurt to produce many fronds before slowing down when a certain size is reached. Some, e.g. *Cyathea medullaris* (G. Foster) Swartz may grow as much as 40-

50 cm a year, but later slow to a few centimetres per year. *Cyathea*'s trunks are however only 15-20 cm in diameter. The thicker tree ferns, such as *Dicksonia fibrosa* Colensa have stems up to 2 m in diameter and grow much slower, a few cm/year, than the narrower species of *Cyathea* and can reach a height of 6 m after possibly 100-200 years (Large and Braggins, 2004). The Carboniferous tree ferns were structurally similar to the extant *Dicksonia* species and their slower growth and larger canopies resulted in less evapo-transpiration, which would have caused localised reductions in rainfall. This would have further affected the ability of the lycophytes to survive within the vegetation. By Asturian times the process had accelerated and the swamps in Variscan Euramerica were being progressively replaced by predominantly conifer and cordaite vegetation that favoured much drier substrates. The last development of lycophyte-dominated coal swamps in Variscan Euramerica was of early Cantabrian age. The lycophyte-dominated swamps persisted for longer in the Illinois Basin with the last remnants disappearing probably by middle-late Cantabrian times, as the cycle of contracting wetlands and regional reductions in rainfall generated its own momentum (Peppers and Brady, 1996).

A comparison of the Bulgarian (Dobrudzha), southern British, and Nova Scotian (Cape Breton, Canada) macrofloras shows that those from Britain and the Sydney coal field are generally more similar to each other than to the Dobrudzha macrofloras (Cleal et al., 2009), which may be explained by the somewhat higher elevation of the latter area during the late Westphalian. However, the lycophytes appear to show a different arrangement, with the Dobrudzha and British macrofloras being more similar (Thomas, 2007, p. 461; Thomas in Cleal et al., 2009, p. 228). At this time, the only explanation for this discrepancy appears to be the number of indigenous species of *Lepidodendron* in Nova Scotia.

Attempting to do the same kind of analysis with dispersed spores is rather different. Such spores can be prepared both from coal seams, where they can be related to the coal petrology, and from sediments associated with the coals. Dispersed spores are classified according to the system suggested by Potonié and Kremp (1954, 1955) improved by Dettmann (1963) and Smith and Butterworth (1967). Since then a great number of microspore species have been described and differences of opinion have arisen over the acceptable limits of variation used in delimitating both genera and species. Some authors have accepted little variation while others have taken a broad approach and often synonymised previously described taxa. The commonest genera of lycophyte spores are shown in Fig. 3.

Published accounts of *in situ* spores recovered from fructifications and the knowledge of the affinities of these fructifications (e.g. Thomas, 1970; Thomas et al., 2009; Drábková et al., 2004; Bek and Opluštil, 2006; Bek et al., 2008; Bek et al., 2009 a,b; Opluštil and Bek, 2009; Bek, 2012, 2013; Thomas and Bek, 2014) permit us to make palaeoecological interpretations from the microspore assemblages. The fructifications known to have spores comparable to the dispersed spore genera together with the parent plants of these fructifications are given in Table 1. With our expanding knowledge of this interrelationship between dispersed spores and the parent plants that produced them, our understanding of Carboniferous palaeoecology is increasing all the time. However, the use of older information on dispersed microspores now has certain problems, especially when some of the published identifications are only at generic level.

The types of *Lepidodendron* with terminal-phase branching have been referred by DiMichele and Bateman (1992) on the basis of coal ball studies to *Synchysidendron* while those with fertile deciduous branches on their main trunk have been referred to *Diaphorodendron* by DiMichele (1985). While we are using spores to recognise genera and cannot make any inferences of their internal anatomy we are using *Lepidodendron* in its original broad sense. Thomas (1970) distinguished between those *Lycospora* from *Flemingites* and those from *Lepidostrobus*, but since then Bek (2012) has divided *Lycospora* into six groups and reduced the number of species that he recognised. He then transferred those *Lycospora* referable to *Flemingites* to a new genus *Microspinosporites* (Bek, 2013).

A recent re-investigation of *Omphalophloios* by Bek et al. (2015) has shown that its spores are referred to the genera *Densosporites* and *Cristatisporites* whereas Smith (1962), on the available evidence at that time (Chaloner, 1954, 1958), thought *Densosporites* spores came from the herbaceous *Selaginella*.

A further problem is encountered in using relative abundances of spores to interpret changes in vegetation, because the spore output varies considerably between individual plants. The largest arborescent lycophytes such as *Lepidodendron* and *Lepidophloios* had crowns of branches with a great many cones, either terminally or born on lateral branches inside the crown (see for example Opluštil, 2010). *Ulodendron* was another arborescent lycophyte, although probably smaller then *Lepidodendron* and *Lepidophloios*, with permanently attached leaves (Thomas 1067, 1968). *Paralycopodites* is probably the anatomically preserved equivalent of *Ulodendron*. Both *Lepidophloios* and *Ulodendron* have many fewer species than *Lepidodendron* and are much less commonly found in compression floras (Thomas, 2007; Thomas and Tenchov, 2004). These larger lycophytes produced vast numbers of microspores while individuals of the smaller species of *Sigillaria* and *Omphalophloios*, based upon the number of sporangia, would probably have produced comparatively fewer microspores. The larger lycophyte grew in the wet peat-producing swamps with *Lepidohloios* preferring the wettest areas and *Ulodendron* preferring environments with some sediment input, being usually associated with coal seam seat-earth and clastic partings (DiMichele and Phillips (1988). According to DiMichele and Phillips (1994), sigillarian trees are more often found in clastic deposits rather than in peat and the common occurrence of their trunks in channel lags and organic shales suggests that they grew on channel margins or on wet floodplains fringing channels. They comment that tracking the abundance of *Sigillaria* on their *Crassispora* microspores appears to underestimate the number of parent plants. What is not clear is the output of spores from assemblages of plants. The arborescent species were large but individually took up more space, while *Sigillaria* and *Omphalophloios* probably formed denser stands. It is undoubtedly the case that the microspores from the tallest lycophytes would have been carried further by wind currents.

Notwithstanding the problems over recent taxonomic changes and the difficulties over assessing spore output, this study assesses some of the more recent published accounts of dispersed lycophyte spores to see if relationships between the genera can be widely established to show some constancy of associations of plants. The idea initially came from the work undertaken by Dimitrova as part of the NATO Science Programme (Project EST-CLS 976716) "Climatic and Vegetational Changes in the Late Carboniferous tropical belt" (in Cleal et al., 2002; Dimitrova et al., 2005, 2010, 2011) and contributions to IGCP 469 "Late Variscan terrestrial biotas and palaeoenvironments" (Dimitrova et al., 2010, 2011). Samples from across the Varisan foreland came from coal seams in the Dobrudzha and the Forest of Dean coalfields and from clastic sediments associated with the coal seams in the Sydney and South Wales coalfields (Fig. 4).

The authorities and reference for the named species of megafossils and microspores are given in section 4.

2. Spore assemblages

2.1. *Sydney Basin, Cape Breton, Canada*

The Sydney Basin is a 450 km long fault-bounded depression within the Canadian Maritimes Basin that extends between Cape Breton, Nova Scotia, and Newfoundland. The Carboniferous succession is about 1.2 km thick, including marine and terrestrial Mississippian and Pennsylvanian deposits and a coal-bearing sequence that is essentially non-marine (Gibling et al., 2004). There is also an overlying red-bed sequence (Pictou Group) that is probably of Cantabrian (Early Kasimovian) age, although it is only known from boreholes (Zodrow in Cleal et al., 2009, p. 186).

The Sydney Coalfield on Cape Breton Island, Nova Scotia, Canada has a well-exposed succession of Asturian terrestrial, coal-bearing strata, with continuous outcrop accessible along the east coast of the island (Fig. 5). Moreover, the rank of coalification here is very low, in the range of 0.6–0.7% vitrinite reflectance, and the palynofloras are excellently preserved. Previous palynological studies on the Sydney Coalfield emphasized biostratigraphy (reviewed by Hacquebard, 1997), but Hacquebard et al. (1965) also included an integrated study of palynology and coal petrography of the 1.6 m thick Harbour Seam (Lower Sydney Mines Formation) in the Sydney Coalfield to determine the detailed ecological structure of the peat-substrate vegetation that formed the seam. Hacquebard et al. (1965) demonstrated that there were three major types of vegetation. The lower third (clarite) had roughly equal numbers of *Lycospora* and *Punctatisporites* suggesting a mixed growth of arborescent lycophytes and herbaceous ferns. The central part (mainly clarite with duroclarite and clarodurite) was dominated by *Lycospora* suggesting a forested bog of *Lepidodendron*/*Lepidophloios*. The upper third (two thirds clarite, one third duroclarite and some duroclarite) was dominated by *Punctatisporites* with a significantly reduced number of *Lycospora*, which was interpreted as reed moor dominated by herbaceous ferns.

Information on the macroflora has been given by Bell (1938), Zodrow and McCandish (1980), Calder (1998), Calder et al. (1996), Zodrow et al. (2001). The lycophytes are summarised by Thomas and Tenchov (2004, p.107), Thomas (2007, p. 458) and Thomas (in Cleal et al., 2009, p. 223). The only lycophyte fructification known from Cape Breton is *Flemingites russelianus* (Binney) Brack-Hanes and Thomas with *Lycospora* microspores of the *Microspinosporites* group.

The most complete account of the Sydney Coalfield palynology is in unpublished reports by Dolby (1988, 1989), who thought the oldest part of the sequence to be probably no older than Duckmantian in age and the highest productive sample to be no younger than “Stephanian D”. The base of the Sydney Mines Formation lies within the Asturian with the base of the Cantabrian placed above the Hub Seam.

Dimitrova summarised the biostratigraphical significance of fossil spores and pollen from the upper part of the Sydney Coalfield sequence (Sydney Mines Formation – Asturian) (Dimitrova in Cleal et al., 2002; Dimitrova et al., 2010, p. 392). This work was based partly on a re-assessment of Dolby’s palynological preparations and partly on preparations from hand-specimens collected by Erwin Zodrow from the Sydney Mines Formation.

The lycophyte counts show that *Lycospora*, from *Lepidodendron* and/or *Lepidophloios*, was the dominant genus in all the coal samples except at Point Aconi. *Crassispora* (from *Sigillaria*) is the only other genus to rise above 1% and then at only one horizon. *Lycospora* and *Densosporites* have a negative correlation (Table 2).

Lycospora pusilla, L. pellucida, and *L. granulata* (from *Lepidodendron* and *Lepidophloios*) are rare in Bras d'Or Section samples and *Endosporites zonalis* is more abundant than *Endosporites globiformis* (from *Chaloneria*) in sample 13 (239 m). In the Glace Bay H-1A Borehole at 3550 feet (Sample R- 413-013 COR), *Endosporites* is abundant, but *Lycospora pusilla* and *L. pellucida* are rare suggesting that the flora at that time was dominated by the relatively small *Chaloneria*, This agrees with the suggestion that *Chaloneria* occurs in a variety of communities, but usually not with *Lycospora*-producing arborescent lycophytes (DiMichele, 1979; Helfrich and Hower, 1989). The arborescent lepidodendroids were probably restricted to a few of the possibly wetter areas. At 3480 feet (Sample R-413-012 COR), *Lycospora pusilla, L. punctata*, *Endosporites globiformis* and *E. zonalis* are abundant but *Cadiospora* (from *Sigillaria brardii*) is absent. At 3410 feet (Sample R-413-011 COR and 3170 feet (Sample R-413-009 COR) *Lycospora* (*Lepidodendron*/*Lepidophloios*) is abundant. At the latter depth *Endosporites zonalis, E. globiformis, Cadiospora magna, Cadiospora* sp., *Cirratriradites annulatus* and *C. saturni* are present, showing a change from a wet forest of the arborescent lycophytes to a more mixed community including *Omphalophloios, Sigillaria* and *Selaginella*. This assemblage consisted of subarborescent, arborescent and herbaceous lycophytes, but the question remains about where the *Selaginella* species were growing. Pšenička and Opluštil (2013) described some different types of *Selaginella* from the Radnice Basin, in western Bohemia. The occurrence of one in association with arborescent lycopophyte branches and the lianas *Sphenophyllum*-species, *Corynepteris angustissima* or *Oligocarpia lindsaeoides* preserved in volcanic ash, above the roof of Lower Radnice Coal, suggest that these plants grew in the crowns of arborescent plants. There were others that they concluded were scramblers around the bases of the larger lycophytes.

At 2650 feet (Sample R-413-005 COR) *Lycospora* is abundant and at 2437 ft *Lycospora* reaches 40% of the total count. At 2020-2030 feet (Sample R-365-006 COR), *Lycospora* and *Cirratriradites anulatus* (from *Selaginella*) are among the dominant taxa. At 1710-1720 ft (Sample R-365-004 COR), *Lycospora* and *Endosporites globiformis* are abundant. According to Dolby, the section is Westphalian D to Stephanian in age, with the series boundary placed at 2650 feet (808 m). Samples 4 and 5 (989441-1, 989442), taken from the McAulay Seam, as with the Shoemaker Seam flora, are dominated by trilete spores including *Lycospora* spp., *Densosporites* spp., *Endosporites globiformis*, *Endosporites* sp., *Cirratriradites saturni* and *Crassispora* spp. showing a mixture of *Lepidodendron*/*Lepidophloios*, *Sporangiostrobus* (= *Omphalophloios*), *Chaloneria* and *Sigillaria brardii*. The presence of *Chaloneria* at this level is mirrored in mid-continental USA where their spores became more important in a number of thin coals near the base of the Stephanian showing that the genus moved from being patchy in the late Westphalian to being much more extensive in the Stephanian (Phillips and Peppers, 1984). The mixed assemblage does not appear to agree with the suggestion of DiMichele and Phillips (1994) that *Sporangiostrobus* (= *Omphalophloios*) plants were most successful when competition was low whether by disturbance or nutrient limitation.

2.2. *South Wales, UK*

This is the largest and stratigraphically most complete remnant of coal-bearing strata of the Variscan foreland. It has a current areal extent of c. 2,300 km^2, although the basin was originally much wider before it was subjected to up to 60% tectonic shortening (Gayer and Jones, 1989). It is historically the most extensively-worked coalfield in southern Britain and consequently the most studied.

The lower part of the Lower Coal Measures Formation consists mainly of fine-grained lithologies with thin and impersistent coals interpreted as deposits in a lower delta plain or coastal plain environment (Hartley, 1993). The upper part of the Lower Coal Measures and the Upper Coal Measures formations have thicker coal seams with clastics derived mostly from northerly and easterly sources. The coals and less frequent marine incursions are indicative of an upper delta plain environment in this part of the succession (Opluštil, Cleal and Kędzio in Cleal et al., 2009).

The overlying barren Pennant Sandstone Formation is diachronous across the basin and reaches its maximum thickness of 1,700 m, in the central part of the basin (Kelling, 1974). The youngest unit in the central part of the coalfield, the Grovesend Formation, is marked by a change from sandstone to mudstone-dominated succession with thin, only locally mineable, coals and subordinate sandstones in its upper part indicating a predominantly floodplain deposition in a meandering and/or anastomosing fluvial system. The occasional presence of red-beds may indicate periods of reduced subsidence resulting in a lowering of the water table (Opluštil, Cleal and Kędzior in Cleal et al., 2009, p. 192).

The macroflora of the South Wales Coalfield has been studied by many people including Kidston (1894), Davies (1921, 1929), Dix (1933, 1934), Moore and Cox (1943), Moore (1945, 1948), Cleal (1978, 1984), Zodrow and Cleal (1985), Cleal et al. (2009), Evans et al. (2000, 2001, 2003) and Thomas and Cleal (2001). The lycophyte macroflora of the South Wales Coalfield has not been studied in detail, although some information is given in Thomas and Tenchov (2004, p.107), Thomas (2007, p. 458) and Thomas (in Cleal et al., 2009, p. 223). The only lycophyte fructification known from the Asturian of South Wales is *Flemingites russelianus* with *Lycospora* microspores of the group now referred to *Microspinosporites*.

The microspores in the upper part of the Pennant of South Wales were investigated by using clastic sediment samples originating from above the Daren Ddu and Llantwit No. 3 seams at the top of the Asturian and the Llantwit No. 2, and Llantwit No. 1 seams in the Cantabrian (Fig. 6). The samples were taken from specimens in the David Davies Collection (see Thomas (1986) for further information on Davies and his collection) in the National Museum of Wales, Cardiff (Dimitrova et al., 2005).

The lycophyte spore genera *Lycospora*, *Densosporites*, *Crassispora*, *Cirratriradites*, *Endosporites* and *Cadiospora* are amongst the spores recovered from the samples and their relative occurrences are shown in Table 3. The lycophytes made up over one-third of the total palynoflora above the Daren Ddu and No. 1 Llantwit seams peaking in abundance at the base of the Cantabrian where they made up nearly 60% of the total palynoflora recovered from above the No. 2 Llantwit Seam. Of these 58% were *Lycospora* which then declined to 30% above the No. 3 Llantwit seam. *Densosporites* shows an inverse proportion of the percentages of *Lycospora* in its counts being 27% above the Daren Ddu and 10% above the Llantwit No 1 seams where there are correspondingly low *Lycospora* counts. Where *Lycospora* is dominant above the Llantwit No 2 seam there are no *Densosporites*. Of the other lycophyte genera present in these palynofloras, *Cirratriradites* (C. *kosankie*, *C. plicata*), from

Selaginella, and *Endosporites* (*E. formosus, E. globiformis*), from *Chaloneria*, show some positive correlation with *Densosporites*. The counts of the only species of *Crassispora* (*C. magna*), from *Sigillaria*, are not correlated with those of any other genus.

In the shales above the Daren Ddu, the dominant species of *Lycospora* are *L. punctata*, *L.* cf. *brevijuga* and *L. pellucida* which are all of the type that are referable to *Lepidostrobus* from *Lepidophloios,* although it should be noted that the holotypes of these three species were Bolsovian (Bek. 2012). The *Densosporites* species are *D. spherotriangulus* and *D. granulosus,* belongimg to *Omphalophloios*. In the No. 2 Llantwit samples the dominant species of *Lycospora* are *L. pusilla* and *L. granulata* together with some other unidentified *Lycospora* spp. Both these *Lycospora* species are without broad equatorial flanges (cingulum) and have ornamented distal surfaces (i.e. *Microspinosporites*) in contrast to those recovered from the Daren Ddu which have broad equatorial flanges and smooth distal surfaces. This change in *Lycospora* species must have been a direct result of decreasing numbers of microsporangiate *Lycospora*-producing cones of the genus *Lepidostrobus* (thought to belong to *Lepidophloios*) and an increase of those from the bisporangiate cones of the genus *Flemingites* (belonging to *Lepidodendron*) (Thomas, 1970; Thomas and Dytko, 1980; Brack-Hanes and Thomas, 1983; Bek, 2012). There are no *Densosporites* recorded from this seam although *Cirratriradites annuliformis* and *Endosporites* sp are present in low numbers. This assemblage suggests a slightly drier environment with a forest of *Lepidodendron* and an understory of *Sellaginella* and *Chaloneria*. This appears to confirm the idea of DiMichele and Phillips (1984) who, in their study of coal ball floras, suggest that *Lepidophloios* commonly dominates the lowest diversity assemblages, which is consistent with a flooded peat surface.

The assemblage above the Llantwit No. 1 Seam shows a dramatic decline in the lycophytes with the dominant genus being *Lycospora*. Dimitrova et al. (2005, p. 816) have shown this decline to be inversely correlated with the abundance of ‘extra-basinal plants’. The changing palynology, culminating in a marked ‘spike’ in the abundance of the lycophytes near the Westphalian-Stephanian boundary, indicates an expansion of swamp conditions resulting from an increase of wetness through much of the succession. However, after the Llantwit No. 1 Seam, the marked drop in the proportion of lycophyte spores suggests there to have been a marked contraction of the lycophyte-dominated wetland habitats and peat formation must have stopped after the No.1 Llantwit seam was laid down because there are no subsequent coals in this uppermost part of the coalfield sequence. This loss of peat-forming communities was probably due to a decrease in water from increased drainage resulting from major topographical and landscape changes following on from the early Stephanian Variscan tectonic activity (Cleal and Thomas, 2005, p. 21).

2.3. The Forest of Dean, UK

This small 100 km^2 coalfield is an erosional and tectonic remnant of the northern margin of the foreland basin belt in southern Britain. The Pennsylvanian strata that lie unconformably on mainly Mississippian and Devonian sediments did not start until late Asturian times and lasted until the early Cantabrian (Opluštil, Cleal and Kędzior in Cleal et al., 2009, p. 194).

The macroflora has been described by Wagner and Spinner (1972) who placed the Westphalian-Stephanian boundary in the upper part of the Household Coal

Member. Information on the lycophyte macroflora has been summarized by Thomas and Tenchov (2004 p. 106), Thomas (2007, p. 458) and Thomas (in Cleal et al., 2009, p. 223). Spinner (1965) has described the lycophyte megaspores.

New data on the microspore floras in the Forest of Dean coals comes from examining slides in the Spinner Collection (University of Sheffield) that were prepared from coal samples at various levels in the Pennant and Supra-Pennant Formations – Asturian and Cantabrian (Dimitrova in Cleal et al., 2002). Here, the Household Coal Member spans the Asturian/Cantabrian boundary, with the top two seams correlating to the top two Llantwit seams of the South Wales Coalfield – both being Cantabrian in age (Fig. 7). Lycophyte spores recovered from these coals are shown in Table 4. Although the analysis was not as detailed as that for South Wales, it did show that *Lycospora* is a dominant species in the Yorkley, Coleford High Delf, and Whittington seams and very common in the Brazilly Seam (45%) and No Coal Seam in the Household Coals Member (all in the upper Asturian) and also in the Woorgreen Coals (Dilke Hospital) in the Woorgreen Member (Cantabrian). *Densosporites* is only found in the Yorkley seam where at 63% it overshadows the lowest *Lycospora* count of 3% suggesting a dramatic change in the vegetation from arborescent lycophyte forest to a more open *Omphalophloios* community. This may have been induced by a decrease in surface water reducing the ability of the larger lycophytes to colonise the area, thereby opening up the area for *Omphalophloios* to take over.

2.4. Dobrudzha, Bulgaria

The Dobrudzha Basin, 500 km^2 in size, was one of a series of depressions along the large faults around the Donetz Basin with this particular basin being bounded by the Shabla and Seltse faults. Deposition occurred in meandering, high sinuosity or braided rivers that often drained into a lake in the central part of the basin surrounded by floodplain swamps and lakes. The strata of the Makedonka, Velkova, and Krupen Formation (upper Duckmantian to lower Asturian) are mainly grey in colour indicating high water tables, but in the Gurkovo Formation (spanning the upper part of the Asturian and the lower part of the Cantabrian) red-beds appear that indicate the onset of lower water tables and more arid conditions (Fig. 8). There is some evidence of volcanic activity in the surrounding area, with major basin-wide tonsteins occurring in the Gurkovo Formation (Tenchov, 2005, 2007; Tenchov and Kędzior in Cleal et al., 2009, p. 200).

Tenchov (1987) has given the best overview of the macroflora including details of the lycophytes. Further information on the lycophyte macroflora has been given by Thomas and Tenchov (2004), Thomas (2007, p. 458), Thomas (in Cleal et al., 2009, p. 223) and Tenchov and Thomas (2015).

Detailed spore counts were made by Dimitrova from coals recovered from boreholes though the Asturian Krupen and Gurkova Formations (Dimitrova, 2004, Dimitrova and Cleal, 2007). The lycophyte spore genera *Lycospora*, *Densosporites, Crassispora, Cirratriradites, Endosporites* and *Cadiospora* were amongst those recovered from the samples and their relative occurrences are shown in in the Gurkova Formation (Table 5). There is an inverse correlation between *Lycospora* and *Densosporites* in many of the samples from the boreholes. This is especially noticeable in the Gurkovo Formation borehole (Table 6) where *Densosporites* is only present at one depth when its high percentage (26% of all spores present in the sample) contrasts with the only recorded complete absence of *Lycospora*. In the Krupen Formation borehole (Table 7)where the *Lycospora* counts are high the *Densosporites* counts are low and vice versa. Interestingly, the *Crassispora* counts are also inversely proportional to the *Densosporites* counts, although the *Lycospora* and *Crassispora* counts themselves are not correlated in any way. *Cirratriradites* counts are not correlated in any way to those of any of the other genera.

3. Results

3.1. Inverse relationship between Lycospora and Densosporites.

The microspore analyses from all the coalfields show certain similarities in the associations with *Lycospora* and *Densosporites* being inversely proportional (Fig. 9) . This is especially noticeable in the Dobrudzha coalfield where it is repeatedly shown in many of the samples in the Krupen Formation, suggesting alternating conditions and assemblages of plants from the arborescent lycophytes producing the *Lycospora* microspores to the smaller lycophytes that yielded the *Densosporites* microspores.

In South Wales there is a similar relationship especially in the highest seams in the sequence. The No. 3 Llantwit is the uppermost seam in the Asturian where *Lycospora* make up 30% of the total spores. Then, in the two Cantabrian seams the lower No 2 Llantwit is dominated by *Lycospora* with no *Densosporites*, while the upper No 1 Llantwit has only 27% *Lycospora* but 10% *Densosporites*.

In the Forest of Dean coalfield there is a similar relationship with *Lycospora* being dominant in all the coals except in the Yorkley seam, which is dominated by *Densosporites* with no *Lycospora.*

In contrast, all the seams in the upper part of the Sydney coalfield sequence are dominated by *Lycospora*, showing the arborescent lycophytes *Lepidodendron* and *Lepidophloios* to be the major plants in the flora while *Sigillaria* is the only other plant represented by 1% *Crassispora* at only one horizon. In the Glace Bay H-1A borehole the situation is very different with most of the samples showing a converse relationship between *Lycospora* and *Endosporites* but not with *Densosporites*. At one horizon (3170 ft), *Endosporites* is associated with both *Cadiospora* and *Cirratriradites* suggesting an unusual plant assemblage of *Chaloneria*, *Sigillaria* and *Selaginella*.

3.2. *Stratigraphy*.

Previous analyses of the late Carboniferous microfossil floras have provided a number of stratigraphical and ecological information. Peppers and Brady (1996) showed that *Lycospora granulata* (from *Flemingites*, the cone of *Lepidodendron*) is one of the most abundant spores at the top of the Desmoinesian Stage throughout much of the central and western interior coalfields of the USA. In Kansas, for example, the lycophyte spores *Lycospora granulata*, *Crassispora kosankei* (from *Sigillariostrobus*) and *Granulatisporites medius* (from small ferns) make up more than three-quarters of the spore assemblage just below the Desmoinesian and Missourian (Stephanian) boundary. However, *Lycospora*, *Densosporites*, *Cirratriradites* and *Granulatisporites* are absent above the boundary, where *Endosporites* and *Crassispora* show increases in abundance. This suggests a change from an assemblage dominated by *Lepidodendron*, *Lepidophloios* and *Selaginella* to one dominated by more compact lycophytes such as *Chaloneria* and *Sigillaria*.

Similar evidence was given by Bek (in Cleal et al., 2012, p. 221) who showed that, in Western Europe and north-eastern Canada, spores of lycopsids generally declined from the Westphalian to the Stephanian, especially *Lycospora* and *Cappasporites* that were produced by the arborescent plants of the *Lepidodendron*- and *Lepidophloio*s-type. These plants, which preferred wetter environments, became less common with only some of them surviving into the Stephanian. Exceptions among the arborescent lycopsids were the sigillarians that produced spores of the *Crassispora* and *Cadiospora*-types. Bek gave the range of *Cadiospora* as starting within the Bolsovian but being most typically found in stratigraphically younger strata of Asturian and Cantabrian age, which corresponds with records of its parent plants that survived the extinction of most arborescent lycopsids at the Moscovian-Kasimovian boundary. Representatives of sub-arborescent lycopsids (*Omphalophloios*, *Polysporia/Chaloneria* and *Spencerites*) that produced *Densosporites* and spores of the *Endosporites* and *Spencerisporites*-types also survived the extinction of the arborescent lycopsid forms with their remains being found in Stephanian as well as Westphalian strata. However, based on the palynological record some species of *Polysporia/Chaloneria* grew in Westphalian times while others grew in Stephanian times.

In South Wales, the Forest of Dean and in the Glace Bay borehole in Cape Breton the situation is different because here *Lycospora* continues into the Stephanian. Indeed, samples from the Cantabrian Llantwit seams have yielded all six genera, although in very small percentages above the uppermost Llantwit No. 1 seam. Such a continuation above the Westpahlian reflects the situation in Saar-Lorraine (Alpern, 1963; Alpern and Libeuf, 1966; Alpern et al., 1967) and in the limnic basins of central France and the Donetz basin (Liabeuf and Alpern, 1969, 1970; Liabeuf et al., 1969) where *Lycospora* continues in to the Stephanian, although in much reduced numbers. Again *Lepidodendron* and *Lepidophloios* must have been dying out leaving other genera such as *Sigillaria* and *Selaginella* to survive further into the Stephanian.

3.3. *Palaeoecology*

An inverse relationship between the dispersed microspore genera *Lycospora* and *Densosporites* and between *Lycospora* and *Crassispora* was reported by Smith (1957, 1962, 1964, 1968) and Smith and Butterworth (1967) and shown to correlate with changes in coal lithology that were themselves interpreted as the result of interplay between water table depth and the climatic conditions of humidity, rainfall and temperature. Smith (1964) showed four basic spore assemblages associated with different coal petrographic types in his studies of the West Yorkshire Langsettian to lower Bolsovian coals. With much more recent information of *in situ* spores recovered from fructifications (Bek, 2012; Bek and Opluštil, 1998, 2004; Bek et al., 2001; Bek and Šimůnek, 2005; Brack-Hanes and Thomas, 1983; Opluštil et al., 2009; Pigg and Rothwell, 1983; Thomas 1970, 1978, 2005; Thomas and Bek, 2014; Thomas and Dytko, 1980) we can now interpret Smith's spore phases much better. Smith's *Lycospora* Phase was dominated by *Lycospora brevijuga* and *L. pusilla* (i.e. from *Lepidostrobus* Brongniart the cone of *Lepidophloios* Sternberg) together with some *Endosporites globuliformis* (from *Chaloneria* and/or *Polysporia*); his Transition Phase, amongst others, by *Densosporites duriti*, and *D. loricatus* (from *Selaginella* and *Omphalophloios*) and *Lycospora granulata* (from *Flemingites* Carruthers, the cone of *Lepidodendron* Sternberg) together with some *Endosporites zonalis* (from *Chaloneria*); his *Densospora* Phase by *Densosporites sphaerotriangulatis* Kosanke (probably *Omphalophloios*); and his Incursion Phase by *Crassispora kosankei* (Potonié and Kremp) Bharadwaj (from *Sigillariostrobus*, the cone of *Sigillaria* Brongniart).

Habib and Groth (1967) also demonstrated an inverse correlation between *Lycospora* and *Densosporites* in their study of the Lower Kittanning coal and the overlying Lower Kittanning shale (Lower Allegheny Group) in western Pennsylvania. They interpreted the change from a *Lycospora* dominated assemblage to a *Densosporites* dominated one as a result of marine incursion forcing the *Lycospora*-producing plants to migrate towards the more freshwater back-swamp areas, being replaced by the more saline-tolerant *Densosporites*-producing plants. As suggested elsewhere (Thomas, 1978, p. 354), this could also be the result of the brackish water infiltrating the water-logged peat and affecting the deeper rooted arborescent lycophytes such as *Lepidodendron* and *Lepidophloios* that produced *Lycospora* microspores in their cones, permitting the shallower-rooted *Densosporites*-producing plants to occupy the peat surface. The *Lycospora* species identified by Habib and Groth in their three sections are in fact *L. trigonoreticulata* (from *Flemingites*, the cone of *Lepidodendron*) and *L. pseudoannulata* with a broad equatorial flange (from *Lepidostrobus*, the cone of *Lepidophloios*).

As the studies of the coal sample analyses from Dobrudzha and the Forest of Dean were primarily stratigraphical, no account was taken of the coal macerals to undertake work similar to Smith (1964), and the analyses from Cape Breton and South Wales were from clastic sediments. Nevertheless, the varying percentages of the lycophyte spores recovered must reflect the different types of macerals that were studied for their spores. Apart from taking this as an explanation of the inverse relationships of *Lycopora* with both *Densosporites* and *Crassispora* and the fact that either both *Lycopsora pusilla* and *L. brevijuga* or *L. granulata* are present in greater numbers, we cannot take the comparison with the Smith's analysis of the Yorkshire coals any further at this time. However, it is worth stressing that this inverse relationship seems to hold good for clastic deposits as well as for coals.

Taking all the evidence from these studies of the microspore floras it is possible to suggest a number of ecological scenarios for the lycophytes using the present ecological interpretations of the ecology of the lysophytes (table 7). These are:

1. Dominant *Lycospora* with relatively few *Densosporites*, *Crassispora*, *Cirratriradites* that suggests a closed swamp forest of *Lepidodendron*/*Lepidophloios* with slightly elevated patches of *Omphalophloios*, and *Sigillaria*, with a possible understory of scrambling or epiphytic *Selaginella* (Fig. 10A).
2. *Lycospora* and *Crassispora* of not too different numbers suggests a mixed, possible patchy, swamp forest of *Lepidodendron*/*Lepidophloios* and *Sigillaria* (Fig. 10B).
3. *Lycospora* and *Crassispora* of fairly similar numbers with some *Densosporites* and *Cirratriradites* that suggests a mixed, possibly patchy, swamp forest of *Lepidodendron*/*Lepidophloios* and *Sigillaria* with few slightly elevated patches of *Omphalophloios* and *Selaginella* that may be scrambling or epiphytic (Fig. 10C).
4. Dominant *Densosporites* with varying amounts of *Lycospora* and much fewer *Crassispora* and *Cirratriradites* that suggests an *Omphalophloios* dominated community with some patches of swamp with *Lepidodendron*/*Lepidophloios, Sigillaria* and scrambling *Selaginella* (Fig.10D).
5. Dominant *Cadiospora* with *Crassispora* and *Lycospora* that suggests a community dominated by *Sigillaria brardii* with patches of *Lepidodendron*/*Lepidophloios* and other species of *Sigillaria*. This community is especially obvious in Nova Scotia at the Asturian/Stephanian boundary which is a stratigraphic horizon where *Lepidodendron*

and *Lepidophloios* are known to decline while *Sigillaria brardii* continues throughout the Cantabrian and the Stephanian (Fig. 10E).

4. Discussion

The recent increase in our knowledge about the relationships of dispersed spores to fructifications and in many cases to the parent plants enables dispersed spore assemblages to be interpreted in terms of plant assemblages. The present paper gives an indication of the type of study that can now be made. Reviewing the lycophyte spores in published papers on spore stratigraphy has shown that it is possible to recognise five different and discrete assemblages of spores leading us to interpret these in terms of communities of their parent plants (Fig. 9). This study was restricted to spore assemblages known from Asturian and Cantabrian deposits of the Variscan foreland but there is great opportunity to extend the study stratigraphically throughout the Euramerican Pennsylvanian, taking in the intermontane basins and the American continental coalfields. This would lead to a much greater understanding of where and when certain lycophytes became more widespread and dominant. Such studies could be extended to other groups such as the ferns (e.g. Millay and Taylor, 1974; Millay 1982; Bek and Opluštil, 1998), the sphenophytes (e.g. Good, 1975; Serret and Brousmiche, 1987; Bek and Opluštil, 1998; Bek and Libertin 2010) the Cordaites (e.g. Millay and Taylor, 1974; Trivett and Rothwell, 1985), the conifers (e.g. Florin, 1936), and the Noeggerathiales (Bek, 2017). It should then be possible to collate all the information to discover the interrelationships between the groups to build up a more complete picture of the changing assemblages within the actively growing Pennsylvanian peat.

5 Taxonomic names of taxa mentioned in the text together with authorship, citations and references

5a. Macroplants

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Polysporia Newberry 1873. Ohio Geological Survey Report 1 p. 362, pl. 41, figs 5,6.

Selaginella Palisot de Beauvois 1805 Prodrome des cinquième et sixième familles des l'aethéogamie. Les mousses. Les lycopodes: 112 pp., Paris (Fournier).

Sigillaria Brongniart 1822. Museum National Histoire Naturelle, Paris Mémoire 8.

Sigillaria brardii Brongniart 1828 Prodrome d'une Histoire des Vgtaux Fossiles, Levraux, Paris p. 65.

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5b. Microspores

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Cirratriradites annulatus Kosanke and Brokawand in Kosanke 1950. Illinois Geological Survey Bulletin 74, 35, pl. 7, fig. 4.

Cirratriradites annuliformis Kosanke and Brokow in Kosanke 1950. Illinois Geological Survey Bulletin. Surv. 74, 35, pl. 7, fig. 6.

Cirratriradites saturni (Ibrahim) Schopf, Wilson and Bentall 1944. Illinois Geological Survey Report of Investigations 91, 44.

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Crassispora (Bharadwaj) Sullivan 1964. Palaeonotology 7, 375.

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Densosporites durti Potonié and Kremp 1956. P. 118, figs 383, 384.

Densosporites granulosus Kosanke 1950. Illinois Geological. Survey Bulletin 74, 32, pl. 6, fig. 8.

Densosporites loricatus (Loose) Schopf, Wilson and Bentall 1944. p. 40, pl. 6, fig.5.

Densosporites sphaerotriangulus Kosanke 1950. Illinois Geological. Survey Bulletin 74, 33, pl. 6, fig. 7.

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Endosporites formosus Kosanke 1950. Illinois State Geological Survey Bulletin 74, p. 36, pl. 7, fig. 9.

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Lycospora (Schopf, Wilson and Bentall) Potonié and Kremp 1954 Geologische Jahrbuch 69, p. 156(

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Lycospora trigonoreticulata (Loose) Potonié and Kremp 1955. Palaeontographica B 99, 104, pl.17, figs 351-354.

Punctatisporites (Ibrahim) Potonié and Kremp 1954 Geologische Jahrbuch 69, p. 120.

5.3. Megaspores

Cystosporites Schopf 1938 Illinois Geological Survey Report 50, p.pp 42, 44, pl.1 fig. 11.

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Lagenicula (Bennie and Kidston) Potonié and Kremp 1955. Palaeontographica 18, p.118, fig. 35.

Lagenoisporites Potonié and Kremp 1955. Palaeontographica 88, p. 121, fig, 35,

Triangulatisporites (Potonié and Kremp) Karczewska 1976 Acta Palaeontologica Polonica p. 342.

Tuberculatisporites (Ibrahim) Potonié and Kremp 1955. Palaeontographica 88, p. 88, fig. 21.

Valvisporites Ibrahim Sporenformen des Aegirhorizonts des Ruhr-Reviers p. 33, pl. 4, fig. 30.

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Fig. 1 Transect of vegetation in lowland dryland adjacent to the coal swamps. From Thomas and Cleal 2017.

Fig. 2. Correlation between the IUGS global chronostratigraphy for the Pennsylvanian Subsystem and the lowest part of the Permian System, and the European (Heerlen) regional chronostratigraphy. From Cleal and Shute 2012, based partly on Heckel & Clayton (2006). For a discussion about the uncertainty concerning the position of the Moscovian Stage boundary relative to the Heerlen scheme, see Kullmann *et al*. (2007).

Fig. 3. The palaeogeography of Variscan Euramerica showing where coalfields developed during the late Westphalian – early Stephanian (Kasmovian). Modified from Cleal et al. (2009) showing where swamps developed rather than where coalfields are known today. The coalfields studied are indicated on the map.

Fig. 4. Microspores from the South Wales Coalfield. 1. *Cadiospora magna* Kosanke, Llantwit 1 coal seam; 2. *Endosporites globiformis* , (Ibrahim) Schopf, Wilson and Bentall, Llantwit 2 coal seam; 3. *Lycospora pusilla,* (Ibrahim) Somers, Llantwit 2 coal seam; 4. *Cirratriradites saturni,* (Ibrahim) Schopf, Wilson and Bentall, Llantwit 2 coal seam; 5. *Densosporites* spherotriangulus Kosanke, Llantwit 3 coal seam; 6. *Crassispora kosankei* (Potonie and Kremp) Bhardwaj, Llantwit 1 coal seam; 7. *Endosporites globiformis* (Ibrahim) Schopf, Wilson and Bentall, Llantwit 2 coal seam.

Fig. 5. A. North-eastern North America showing the position of Cape Breton and the Sydney Coalfield. B. General Upper Carboniferous stratigraphy of the Sydney Coalfield.

Fig. 6. The stratigraphy of the upper part of the south-eastern South Wales Coalfield.

Fig. 7. The stratigraphy of the coal seams in the Forest of Dean Coalfield, UK.

Fig. 8. The stratigraphy of the Dobrudzha Coalfield.

Fig. 9. Diagrams showing the comparative difference in spores through the coalfields.

Fig. 10. Ecological scenarios for the lycophytes based on assemblages of microspores. See text for explanations

Table 1. Genera and species of lepidophyte spores encountered in this study showing the fructifications they come from and their probable parent plants.

Table 2. Genera of lycophyte spores from boreholes in the Sydney Coalfield, Cape Breton, Canada: as a percentage of total spores; as a percentage of total lycophyte spores; comparison of relative percentages of *Lycospora* and *Densosporites*.

Table 3. Genera of lycophyte spores from sediments above the listed coal seams in the South Wales Coalfield, UK: as a percentage of total spores; as a percentage of total lycophyte spores; comparison of relative percentages of *Lycospora* and *Densosporites*.

Table 4. Genera of lycophyte spores from coal seams in the Forest of Dean Coalfield, UK. as a percentage of total spores; as a percentage of total lycophyte spores; comparison of relative percentages of *Lycospora* and *Densosporites*.

Table 5. Genera of lycophyte spores in the Gurkova Formation in the Dobrudzha Coalfield, Bulgaria, plotted against depth of sample: as a percentage of total spores; as a percentage of total lycophyte spores; comparison of relative percentages of *Lycospora* and *Densosporites*.

Table 6. Genera of lycophyte spores in the Krupen Formation of the Dobrudhza Coalfield, Bulgaria, plotted against depth of sample: as a percentage of total spores; as a percentage of total lycophyte spores; comparison of relative percentages of *Lycospora* and *Densosporites*.

Table 7. Genera of lycophytes encountered in this study together with their fertile organs, spores and their palaeoecology.

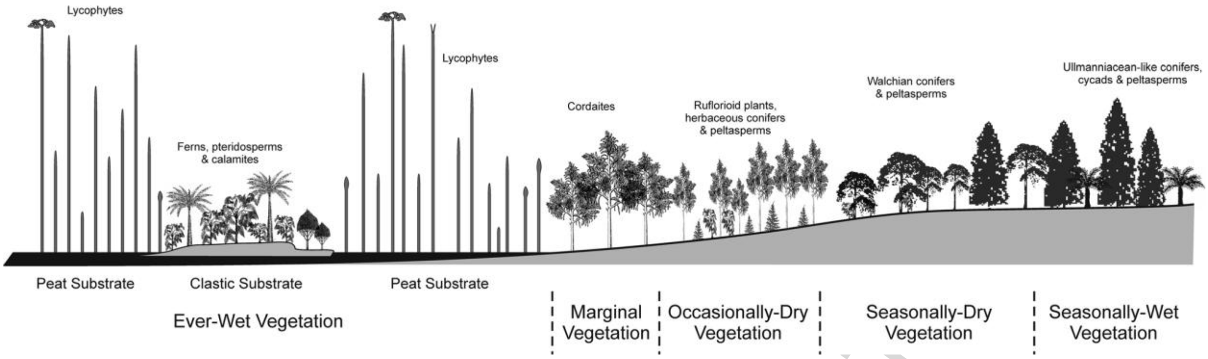
Lycophytes
Lycophytes
Ferns, pteridosperms
& calamites
Cordaites
Rufloroid plants,
herbaceous conifers
& peltasperms
Walchian conifers
& peltasperms
Ullmanniacean-like conifers,
cycads & peltasperms
Peat Substrate
Clastic Substrate
Peat Substrate
Ever-Wet Vegetation
Marginal
Vegetation
Occasionally-Dry
Vegetation
Seasonally-Dry
Vegetation
Seasonally-Wet
Vegetation

Fig. 1

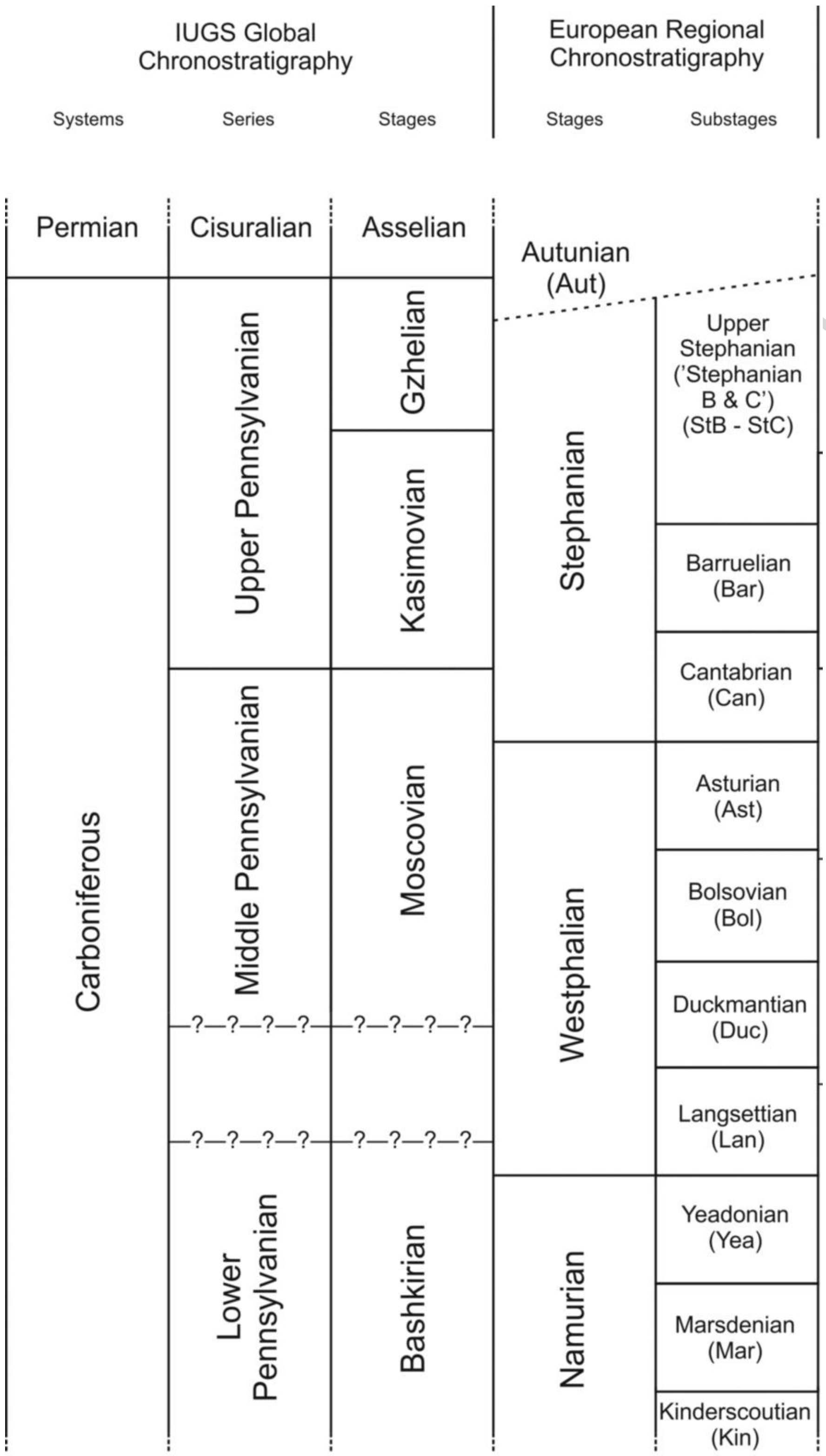
IUGS Global Chronostratigraphy
Systems
Series
Stages
European Regional Chronostratigraphy
Stages
Substages
Permian
Cisuralian
Asselian
Autunian (Aut)
Carboniferous
Upper Pennsylvanian
Gzhelian
Kasimovian
Middle Pennsylvanian
Moscovian
Lower Pennsylvanian
Bashkirian
Stephanian
Westphalian
Namurian
Upper Stephanian ('Stephanian B & C') (StB - StC)
Barruelian (Bar)
Cantabrian (Can)
Asturian (Ast)
Bolsovian (Bol)
Duckmantian (Duc)
Langsettian (Lan)
Yeadonian (Yea)
Marsdenian (Mar)
Kinderscoutian (Kin)
?—?—?—?

Fig. 2

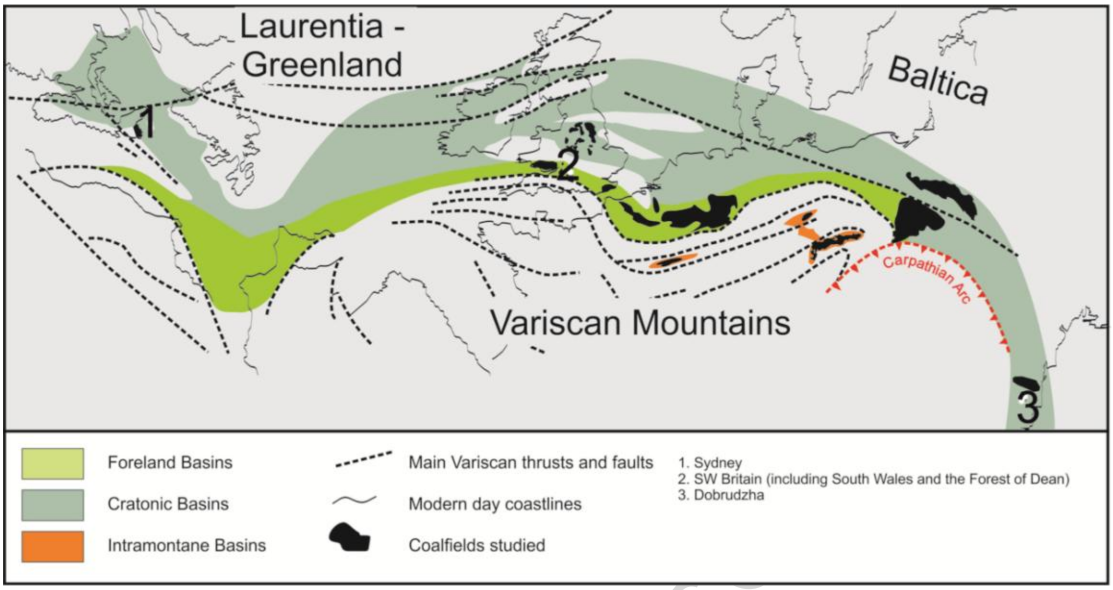
Laurentia - Greenland
Baltica
1
2
3
Carpathian Arc
Variscan Mountains
Foreland Basins
Cratonic Basins
Intramontane Basins
Main Variscan thrusts and faults
Modern day coastlines
Coalfields studied
1. Sydney
2. SW Britain (including South Wales and the Forest of Dean)
3. Dobrudzha

Fig. 3

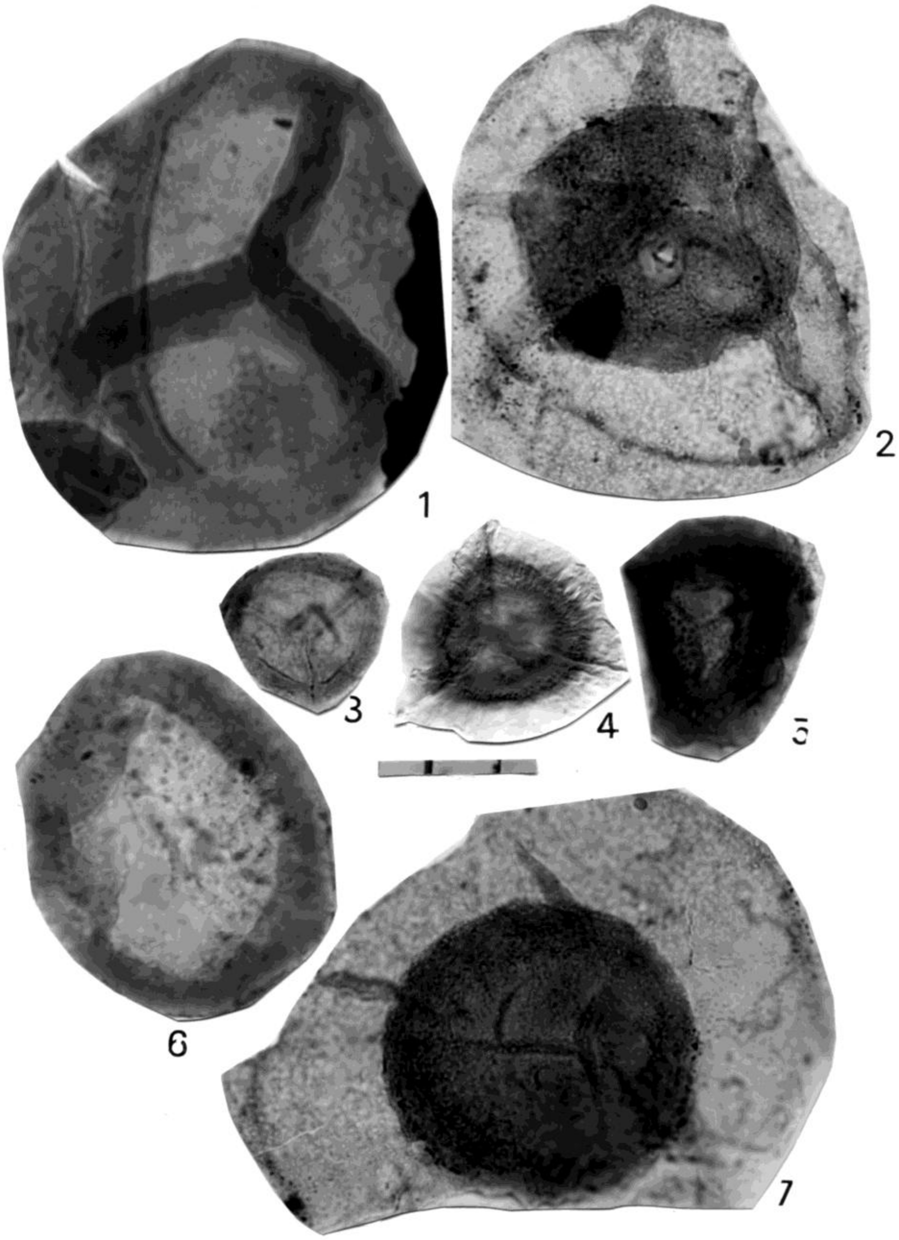

Fig. 4

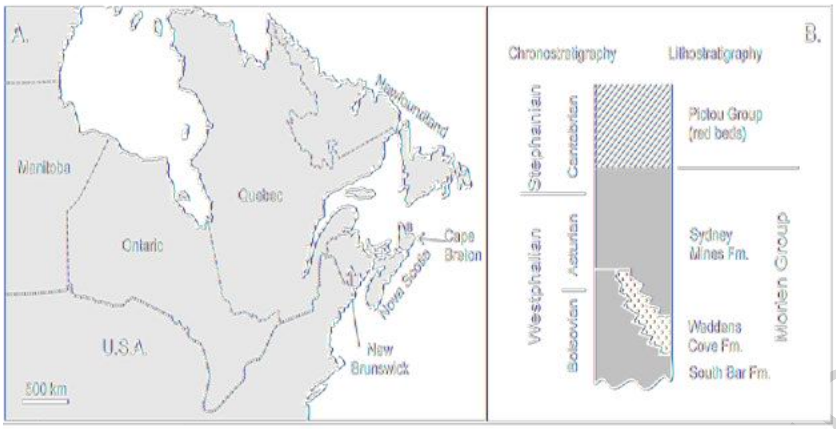
A.
Manitoba
Ontario
Quebec
Newfoundland
Cape Breton
Nova Scotia
New Brunswick
U.S.A.
500 km
B.
Chronostratigraphy
Lithostratigraphy
Stephanian
Cantabrian
Westphalian
Asturian
Bolsovian
Pictou Group (red beds)
Sydney Mines Fm.
Waddens Cove Fm.
South Bar Fm.
Morien Group

Fig. 5

Coal	Stages
Llantwit No 1 Llantwit No 2	Cantabrian
Llantwit No 3 Daren Ddu	Asturian

Fig. 6

Coal	Lithostratigraphical Unit
Woorgreen Coals (Dilke Hospital)	Woorgreen Member
Crow or Dog Seam	Household Coals Member
Twenty Inch Seam	
Starkey Seam	
Rocky Seam	
No Coal Seam	
Brazilly Seam	
Yorkley Seam	Forest of Dean Pennant Formation
Coleford High Delf Seam	
Whittington Seam	

Fig. 7

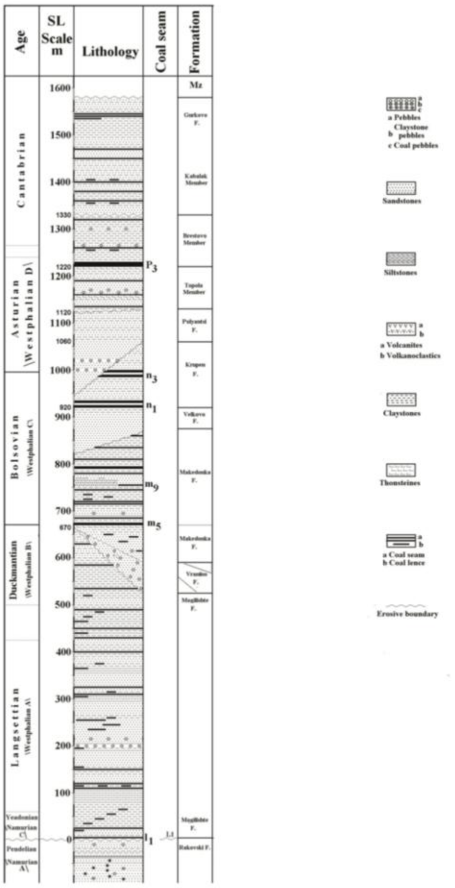
Age
SL Scale m
Lithology
Coal seam
Formation
Cantabrian
Asturian \Westphalian D\
Bolsovian \Westphalian C\
Duckmantian \Westphalian B\
Langsettian \Westphalian A\
Yeadonian \Namurian C\
Pendelian \Namurian A\
1600
1500
1400
1330
1300
1220
1200
1120
1100
1060
1000
920
900
800
700
670
600
500
400
300
200
100
0
P3
n3
n1
m9
m5
l1
Mz
Gurkovo F.
Kabulak Member
Brestovo Member
Tepola Member
Polyantsi F.
Krupen F.
Velkovo F.
Makedonka F.
Makedonka F.
Vrankin F.
Magilishte F.
Magilishte F.
Rakovski F.
a Pebbles
b Claystone pebbles
c Coal pebbles
Sandstones
Siltstones
a Volcanites
b Volkanoclastics
Claystones
Thonsteines
a Coal seam
b Coal lence
Erosive boundary

Fig. 8

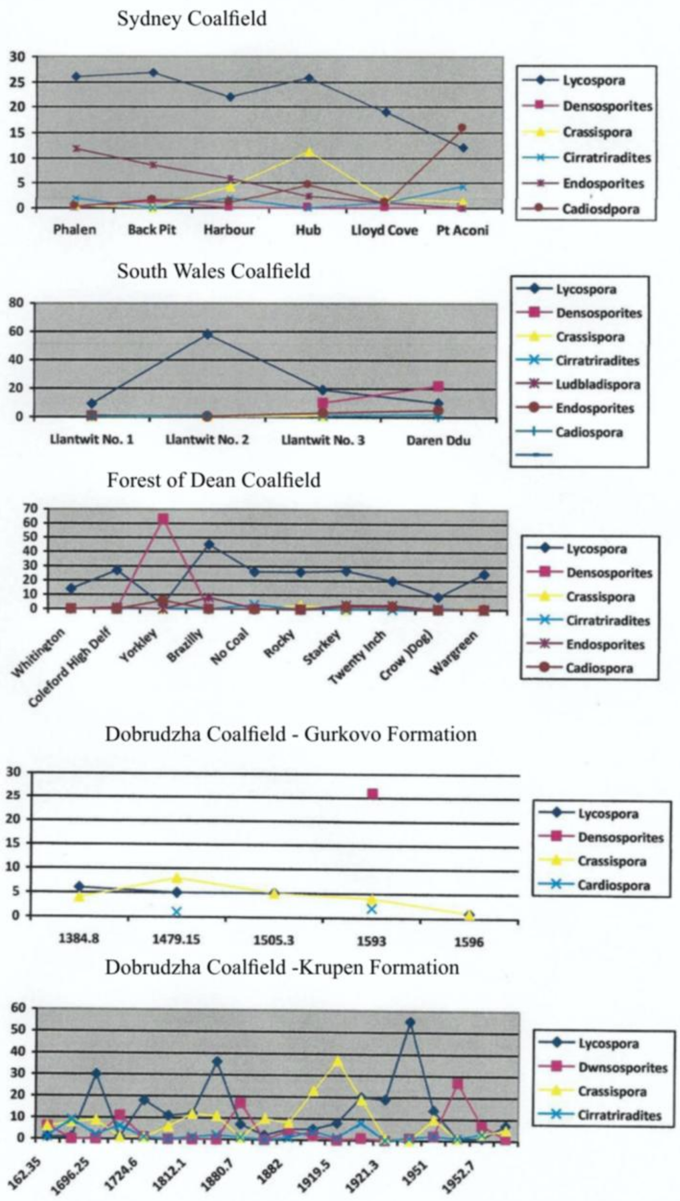
Sydney Coalfield
30
25
20
15
10
5
0
Phalen
Back Pit
Harbour
Hub
Lloyd Cove
Pt Aconi
Lycospora
Densosporites
Crassispora
Cirratriradites
Endosporites
Cadiosdpora
South Wales Coalfield
80
60
40
20
0
Llantwit No. 1
Llantwit No. 2
Llantwit No. 3
Daren Ddu
Lycospora
Densosporites
Crassispora
Cirratriradites
Ludbladispora
Endosporites
Cadiospora
Forest of Dean Coalfield
70
60
50
40
30
20
10
0
Whitington
Coleford High Delf
Yorkley
Brazilly
No Coal
Rocky
Starkey
Twenty Inch
Crow)Dog)
Wargreen
Lycospora
Densosporites
Crassispora
Cirratriradites
Endosporites
Cadiospora
Dobrudzha Coalfield - Gurkovo Formation
30
25
20
15
10
5
0
1384.8
1479.15
1505.3
1593
1596
Lycospora
Densosporites
Crassispora
Cardiospora
Dobrudzha Coalfield -Krupen Formation
60
50
40
30
20
10
0
162.35
1696.25
1724.6
1812.1
1880.7
1882
1919.5
1921.3
1951
1952.7
Lycospora
Dwnsosporites
Crassispora
Cirratriradites

Fig. 9

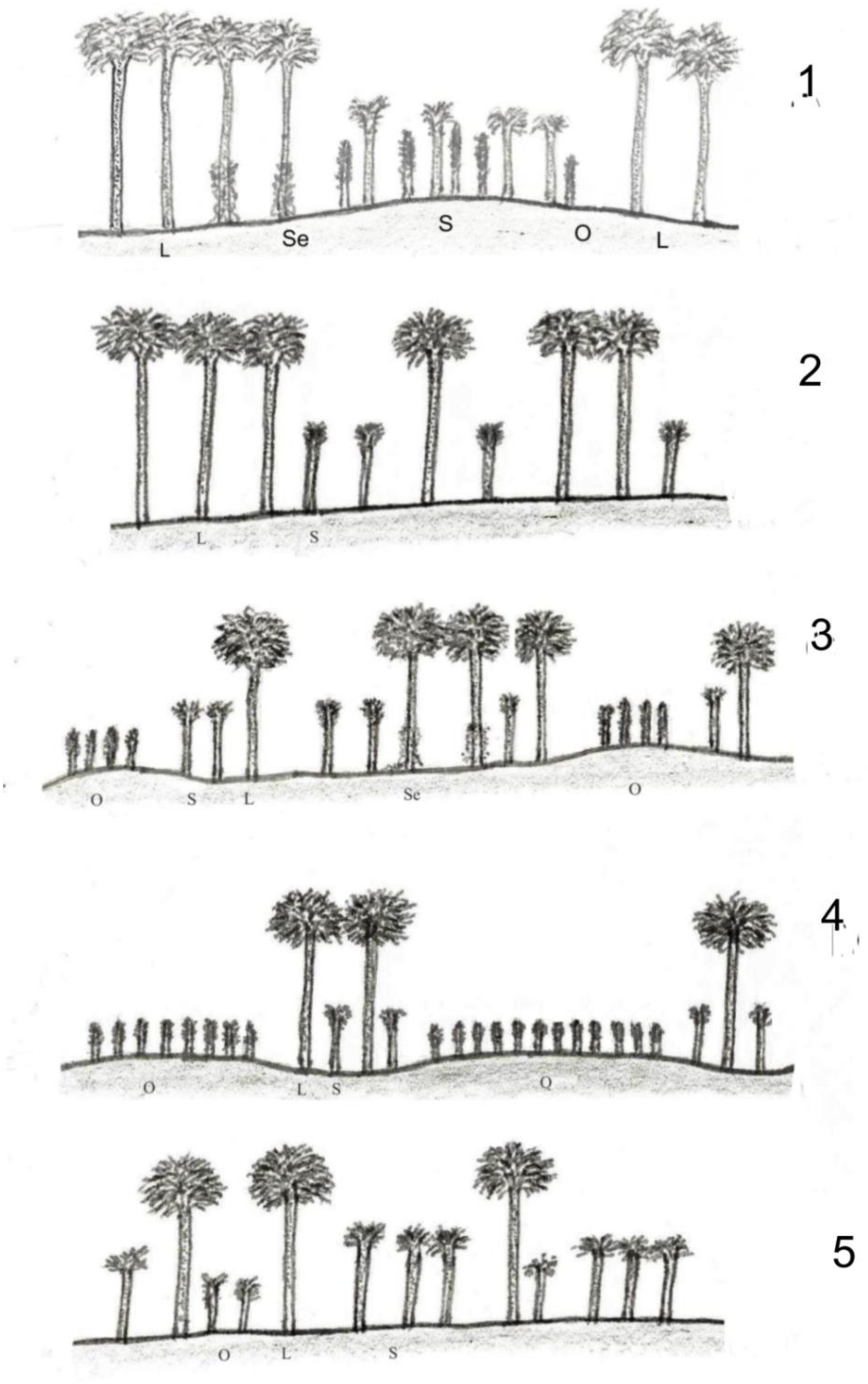

Fig. 10

Table 1

Microspore genus	Species	Fructification	Parent plant
Lycospora Schopf, Wilson and Bentall 1944 Spores with cingulum *Lycospora micropapillata* Group	*Lycospora parva, L. micropapillata, L. pusilla, L. rugosa, L. granianellatus, L. rugulosa*	*Lepidostrobus* Brongniart emend . (Brack-Hanes and Thomas 1980)	*Lepidophloios* Sternberg
Lycospora Schopf, Wilson and Bentall 1944 Spores with cingulum and zona *Lycospora brevijuga* Group	*Lycospora brevijuga, L. brevis, L. denticulata, L. micrograna, L. punctata, L. subjuga, L. triangulata, L. clavata, L. perforata, L. contacta*	*Lepidostrobus* Brongniart emend. (Brack-Hanes and Thomas 1980)	*Lepidophloios* Sternberg
Lycospora Schopf, Wilson and Bentall 1944 Spores with cingulum and zona *Lycospora pellucida* Group	*Lycospora pellucida, L. pseudoannulata, L. intermedia, L. loganii*	*Lepidostrobus* Brongniart -	*Lepidophloios* Sternberg
Lycospora Schopf, Wilson and Bentall 1944 Spores with cingulum and zona *Lycospora uber* Group	*Lycospora noctuina, L. noctuina* var. *reticulata, L. uber, L. nitida, L. uzunmehmedii, L. tenuireticulatus*	*Dtto*	*Lepidophloios* Sternberg
Lycospora Schopf, Wilson and Bentall 1944 Spores with cingulum and zona *Lycospora rotunda* Group	*Lycospora rotunda, L. subtriquetra, L. curtata*	*Dtto*	*Lepidophloios* Sternberg
Microspinosporites Pseudosaccate spores with microspinate distal surface	*Microspinosporites orbiculus, M. chaloneri*	*Flemingites* Carruthers emend (Brack-Hanes and Thomas 1980; *Moscvostrobus* Naugolnykh and Orlova 2006 (*Sublepidodendron songziense*-China-Famennian*)*	*Lepidodendron* Sternberg
Densosporites (Berry) Butterworth, Jansonius, Smith and Staplin 1964	*Densosporites* spp. (extremely variable genus, specific classification has no use	*Porostrobus* Nathorst (Bharadwaj 1958; Chaloner 1958a) *Omphalophloios* White (Chaloner 1962; Bek & Opluštil 1998; Bek & Strakova 1996, Bek et al., 2015).	*Selaginella* Beauvoir *Omphalophloios* White
Cingulizonates	*Cingulizonates*	*Porostrobus*	*Porostrobus* Mayjprst
Cristatisporites	*Cristatisporites* spp.	*Omphalophloios*	*Omphalophloios* White

Cadiospora	*Cadiospora magna*	*Thomasostrobus* Opluštil, Bek & Drábková 2009	Possibly *Sigillaria brardii*
Crassispora (Bhardwaj) Sullivan 1964	*Crassispora kosankei*	*Sigillariostrobus* Schimper ex Feistmantel; *Mazocarpon* Benson1918	*Sigillaria* Brongniart
Cirratriradites Wilson and Coe 1940	*Cirratriradites anulatus* *Cirratriradites annuliformis* *C. saturni*	*Selaginella (*Chaloner 1954; Leisman 1960); Thomas 2005)	*Selaginella* Beauvoir
Lundbladispora Balme 1963	*Lundbladispora gigantea* (Alpern) Doubinger 1968	*Selaginellites*	*Selaginella*-like herb
Endosporites Wilson and Coe 1940	*Endosporites zonalis* *E. globiformis, E. ornatus*	*Polysporia* Newberry (Chaloner 1953, 1958b) *Chaloneria* Pigg and Rothwell 1983	*Chaloneria* Pigg and Rothwell
Cappasporites	*Cappasporites distortus*	*Achlamydocarpon*	*Paralycopodites?* Morey and Morey,
Calamospora Schopf, Wilson and Bentall 1944	*Calamospora* spp.	*Eleutherophyllum drepanophyciforme* Remy and Remy 1960	
Spencerisporites	*Spencerisporites radiatus, S. gracilis, S.striatus, S. karczewskii*	*Spencerites insignis, S. leismani, S. moorei, S. havlenae, S. chaloneri*	*Spencerites*Scott
Paleospora	*Paleospora fragile* Habib 1966	*Spencerites majusculus* Scott 1897	*Spencerites* Scott
Anapiculatisporites	*Anapiculatisporites minor*	*Carinostrobus foresmani* Baxter 1971	*Selaginella*-like herb
Indotriradites (Permian)	*Indotriradites splendens* Balme and Hennelly	*Selaginella harrisinana* Townrow 1968	*Selaginella*-like herb
Dictyotriletes (Permian)	*Dictyotriletes* sp.	*Collinsonostrobus*	*Selaginella*-like herb
Dictyotriletes sp.	*Dictyotriletes* sp.	*Kladnostrobus psendae, K. clealii* Libertín, Bek and Dašková 2005	

Table 2

Genus	**2** **(Phalen)**	**6** **(Backpit)**	**10** **(Harbour**	**12**	**14** **(Hub)**	**18** **(Lloyd Cove)**	**2** **(Pt Aconi)**
Lycospora	25.9	26.91	22.0	19.84	25.57	18.99	11.99
Densosporites	0	1.40	0	0	0	0	0
Cadiospora	0.28	1.63	1.20	0.60	4.68	1.19	15.89
Cirratriradites	1.87	0	2.00	1.17	0	0.99	4.33
Crassispora	0.57	0	4.28	0	11.29	1.75	1.21
Endosporites	11.19	8.63	6.00	0	2.40	1.19	0

Genus	**2** **(Phalen)**	**6** **(Backpit)**	**10** **(Harbour**	**12**	**14** **(Hub)**	**18** **(Lloyd Cove)**	**2** **(Pt Aconi)**
Lycospora	66	70	62	92	58.2	78.8	36
Densosporites	0	3.6	0	0	0	0	0
Cadiospora	0.7	4.2	3.4	2.6	10.6	5	47.69
Cirratriradites	3	0	5.6	5.4	0	4	13
Crassispora	1.3	0	12	0	25.7	7.2	3.4
Endosporites	28	22.2	17	0	5.5	5	0

Genus	**2** **(Phalen)**	**6** **(Backpit)**	**10** **(Harbour**	**12**	**14** **(Hub)**	**18** **(Lloyd Cove)**	**2** **(Pt Aconi)**
Lycospora	100	95	100	100	100	100	100
Densosporites	0	5	0	0	0	0	0

Table 3

Genus	Daren Ddu	Llantwit No. 3	Llantwit No. 2	Llantwit No. 1
Lycospora	10	19	58	9
Densosporites	22	10		<1
Cadiospora	<1		1	<1
Crassispora		1	<1	<1
Cirratriradites	2	1		1
Lundbladispora				<1
Endosporites	5	3	<1	1
Total lyophytes	39	34	60	13

Genus	Daren Ddu	Llantwit No. 3	Llantwit No. 2	Llantwit No. 1
Lycospora	25.6	55.9	96.5	69.2
Densosporites	56.4	29.4		<7.6
Cadiospora	<1		1.5	<7.6
Crassispora		2.9	1	<7.6
Cirratriradites	5.1	2.9.		7.6
Lundbladispora				<7.6
Endosporites	12.8	8.9	1	7.6

Genus	Daren Ddu	Llantwit No. 3	Llantwit No. 2	Llantwit No. 1

Lycospora	31	62	100	99
Densosporites	69	38		1

Table 4

Genus	Pennant Formation									
	Whittington Member			Household Coals Member						Woorgreen Member
	14	Coleford High Delf Seam	Yorkley Seam	Brazilly Seam	No Coal Seam	Rocky Seam	Starkey Seam	Twenty Inch	Crow or Dog Seam	Woorgreen Coals (Dilke
Lycospora		27	3	45	26	26	27	20	9	25
Densosporites			63							
Cadiospora	14		6					2		>1
Crassispora		>1				2	2		>1	1
Cirratriradites					2				1	
Endosporites		1		8	>1			3		
Total lycophytes		29	72	53	29	28	29	25	11	27

Genus	Pennant Formation									
	Whittington Member			Household Coals Member						Woorgreen Member
	14	Coleford High Delf Seam	Yorkley Seam	Brazilly Seam	No Coal Seam	Rocky Seam	Starkey Seam	Twenty Inch	Crow or Dog Seam	Woorgreen Coals (Dilke
Lycospora		91.3	4	85	92.8	92.9	93.1	80	81	93
Densosporites			88							
Cadiospora	100		8					8		3.

Crassispora		>3.5				7.1	6.9		>1	4
Cirratriradites					6.9				9	
Endosporites		3.5		15	>1			12		

Genus	Pennant Formation									
	Whittington Member			Household Coals Member						Woorgreen Member
	14	Coleford High Delf Seam	Yorkley Seam	Brazilly Seam	No Coal Seam	Rocky Seam	Starkey Seam	Twenty Inch	Crow or Dog Seam	Woorgreen Coals (Dilke
Lycospora		100	4.5	100	100	100	100	100	100	100
Densosporites			95.5							

Table 5

Genus	Gurkova Formation				
	Depth of samples [m]				
	1384,80	1479,15	1506,30	1593,00	1596,00
Lycospora	6	5	5	-	1
Densosporites	-	-	-	26	-
Cadiospora	-	1	-	2	-
Crassispora	4	8	5	4	1
Total lycophytes	10	14	10	32	2

Genus	Gurkova Formation				
	Depth of samples [m]				
	1384,80	1479,15	1506,30	1593,00	1596,00
Lycospora	60	5	50	-	50
Densosporites	-	-	-	81.25	-
Cadiospora	-	1	-	6.25	-
Crassispora	40	8	50	12.5	50
Total lycophytes	10	14	10	32	2

Genus	Gurkova Formation				
	Depth of samples [m]				
	1384,80	1479,15	1506,30	1593,00	1596,00
Lycospora	100	100	100	-	100

Densosporites	-	-	-	100	-

Table 6

Genus	Krupen Formation																			
	Depth of samples, [m]																			
	1954,30	1952,70	1951,60	1923,00	1921,30	1920,75	1920,20	1919,50	1919,30	1882,00	1881,75	1880,70	1854,20	1812,10	1725,25	1724,60	1722,70	1696,25	1695,80	1626,35
Lycospora	7	1	1	14	55	19	20	8	5	5	2	7	36	12	11	18	1	30	1	1
Densosporites	1	7	27	2	1	-	1	-	2	4	-	17	-	-	-	1	11	-	-	6
Crassispora	5	3	1	10	-	1	19	37	23	8	10	1	11	12	6	1	1	9	8	6
Cirratriradites	1	3	1	2	1	-	8	1	4	1	-	1	2	1	-	1	6	2	9	1
Total lycophytes	14	14	30	28	57	20	48	46	34	18	12	26	49	25	17	21	19	41	18	14

Genus	Krupen Formation																			
	Depth of samples, [m]																			
	1954,3	1952,7	1951,6	1923,00	1921,30	1920,75	1920,20	1919,50	1919,30	1882,00	1881,75	1880,70	1854,20	1812,10	1725,25	1724,60	1722,70	1696,25	1695,80	1626,35
Lycospora	50	7.1	3.3	50	96.5	95	41.6	17.4	14.7	27.7	16.6	26.7	73.5	48	64.7	85.7	5.3	73.2	5.5	7.2
Densosporites	7.1	50	90	7.1	1.75	-	2.1	-	5.9	22.2	-	65.4	-	-	-	4.7	57.9	-	-	42.8
Crassispora	35..7	21.4	3.3	35.7	-	5	39.6	80.5	67.6	44.4	83.3	3.8	22.5	48	35.2	4.7	5.3	21.9	44.5	42.8
Cirratriradites	7.1	21.4	3.3	7.1	1.75	-	16.6	2.1	11.8	0.45	-	3.8	4	4	-	4.7	31.6	4.9	50	7.2
Total lycophytes	14	14	30	28	57	20	48	46	34	18	12	26	49	25	17	21	19	41	18	14

Genus	Krupen Formation																			
	Depth of samples, [m]																			
	1954,3	1952,7	1951,6	1923,0	1921,3	1920,7	1920,2	1919,5	1919,3	1882,0	1881,7	1880,7	1854,2	1812,1	1725,2	1724,6	1722,7	1696,2	1695,8	1626,3
Lycospora	88	12	4	88	9 8	100	95	100	71	55	100	7	100	100	100	95	8	100	100	14
Densosporites	12	88	96	12	2	-	5	-	29	45	-	17	-	-	-	5	92	-	-	86

Table 7

Stem genus	Character of fertile organ	Spore genus	Paleoecology
Lepidodendron	Bisporangiate cones *Flemingites*	Microspores – *Microspinosporites* Megaspores – *Lagenicula* or *Lagenoisporites*	Wet swamp forests often dominating the vegetation
Lepidophloios	Unisporangiate cones: *Lepidostrobus*, *Lepidocarpon* or *Achlamydocarpn*	Microspors – *Lycospora* Megaspores: *Cystosporites*	More open areas of the wetter parts of the swamp forests
Ulodendron	Possibly bisporangiate cones	Microspores – *Microspinosporites* Megaspores – *Lagenicula* or *Lagenoisporites*	Areas subjected to flooding and sediment incursion
Sigillaria	Unisporangiate cones - *Sigillariostrobus*	Microspores – *Crassispora* Megaspores – *Tuberculatisporites* or *Laevigatisporites*	Channel margins or on wet floodplains fringing channels in the swamp forests
Omphalophloios	Fertile zones (*Sporangiostrobus*)	Microspores - *Densosporites*	On slightly elevated parts of the swamp forests. Most successful when competition was low
Chaloneria	Fertile zones (*Polysporia*)	Microspores – *Endosporites* Megaspores -*Valvisisporites*	In mixed communites, but not in the wetter parts of the swamp forests. Occasionally dominant
Selaginella	Bisporangiate ones	Microspores – *Cirratriradites* Megaspores - *Triangulatisporites*	Scrambling or epiphytic plants in mixed communities