Palynological and palaeobotanical investigation of the Carboniferous deposits of the Bristol Coalfield, U.K.; biostratigraphy, systematics and palaeoecology

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Abstract

This multi-disciplinary study of the Pennsylvanian-aged Warwickshire Group of the Bristol Coalfield presents the first secure biostratigraphical dating of this historically contentious sequence. Stratigraphical revisions and reinterpretation also enable accurate infra-basin correlation between the Coalpit Heath Syncline and the southern limb of the Kingswood Anticline. Newly produced palynological miospores and megaspores and palaeobotanical biozonations the inter-borne formation and Dooland Member are mid-to late Bolsovian in age, featuring assemblages corresponding to the Laveineopteris rarinervis palaeobotanical Sub-Zone. The base of the Asturian roughly approximates the base of the OT Biozone, occurring within the lowermost 120m of the Mangotsfield Member, the uppermost division of the Wednesfield Member. A stratigraphical gap is highlighted for the first time between the Wednesfield Sandstone and Grovesend formations, encompassing the early to mid-Asturian absent Linopteris obliqua palaeobotanical Biozone and Lobatopteris micromiltonii palaeobotanical Biozone assemblages. This correlates to similar hiatuses in both nearby coalfields and several European basins related to the Leonian phase of uplift, part of the Variscan Orogeny. Both palynological and palaeobotanical data sets are interpreted within a facies context to highlight a diverse patchwork of plant communities. Bolsovian peat mires were dominated by lepidodendrids and ferns and were replaced by tree fern and fern mires in the late Asturian likely due to uplift-induced alterations in drainage. High diversity pteridosperm-sphenophyte and fern clastic swamps fringed and infiltrated these mires. Early Asturian braided fluvial systems created disturbed riparian niches that were colonised by low diversity pteridosperm-sphenophyte communities and Sigillaria-sphenophyte-fern-cordaitalean communities. High levels of cordaitae pollen adds to the body of evidence that these plants were not merely restricted to upland areas. Evidence suggests that marattial tree ferns may have originated within clastic environments within the Bolsovian. Therefore, re-evaluation of widespread and dominant members of Asturian peat mires.
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1 Introduction

The Bristol Coalfield of southwest Britain, although intensively studied in the early history of palaeobotany, has received little attention for 75 years. This thesis provides the first in-depth and multidisciplinary investigation of the mid-Bolsovian to Cantabrian (Moscovian-Kasimovian) Warwickshire Group of the Bristol Coalfield, which comprises, from base to top, the Winterbourne, Pennant Sandstone and Grovesend formations. A newly produced stratigraphy also allows, for the first time, accurate interpretation of the strata of the southern limb of the Kingswood Anticline and correlation to a revised stratigraphy of the Coalpit Heath Basin to the north. These new and revised stratigraphies are dated using a new miospore, megaspore and palaeobotanical biozonation, allowing the age range of these previously contentious coal measures to be securely constrained. Palynological and palaeobotanical assemblages are interpreted within a facies and stratigraphical context to elucidate a diverse patchwork of plant communities, which shifted and progressively adapted in response to the changing environments of the late Carboniferous.
2 Geological setting

2.1 Introduction to the Carboniferous

The name Carboniferous is derived from the Latin *carbo* (charcoal) or Italian *Carboarium* (charcoal producer) combined with the Latin *ferrous* (bearing). Due to the economic value of the contained coal, the Carboniferous was one of the earliest geological periods classified. Carboniferous rocks outcrop throughout the British Isles (Figure 1), however, little economic mining continues today. Even though earlier coals are known, the late Carboniferous marks the first period of extensive coal deposits. For the purposes of this study, the term “late Carboniferous” is used for the sake of brevity when referring to the Middle to Late Pennsylvanian epoch, when these coal bearing deposits were laid down.

![Figure 1 – Outcrops of Carboniferous rocks (shaded areas) in Britain and Eire. Generated from BGS (Stubblefield and Trotter, 1957; 2008).](image-url)
2.1.1 Late Carboniferous (Middle to Late Pennsylvanian) time scales

2.1.1.1 Most recent stratigraphical framework

Historically a multitude of differing stratigraphical classifications are used in Russia, Europe and North America. The Gradstein et al. (2004) publication presents the current standard chronostratigraphy, and correlates the regional subdivisions commonly used in literature. This study will use the western Europe and British regional unit names, as these overwhelmingly dominate the relevant literature for this topic. The latest version of the International Commission on Stratigraphy geological timescale for the Carboniferous is shown in Figure 2, with a detailed outline of the British and western European stages appearing in Figure 3.

![Figure 2 - Correlation of western European and British regional units to the standard chronostratigraphy and North American stages. Sea level curve are also shown (relative to modern sea level, scale in metres). Chart created using TSCreator by Lugowsk and Ogg (2008) which uses the time scale proposed by Gradstein et al. (2004).](image-url)
Figure 3 – Comparison of the Standard Chronostratigraphy of the Carboniferous with the western European and British regional units. This study will use the Western and British stages and sub-stages. Sub-stages of the Westphalian and Stephanian are defined, as these will be particularly relevant in this study. After Gradstein et al. (2004).

### 2.1.1.2 Global Stratotype Section and Points (GSSP)

Interestingly, the Carboniferous has very few Global Stratotype Section and Points (GSSP): the lower limit of the Carboniferous (base of the Tournaisian) was only ratified in 1990. The location is the base of Bed 89 at La Serre in Monte Noire, France. This is based on the first appearance of the conodont *Siphonodella sulcata*. The bed contains various trilobites, cephalopods, foraminifera, brachiopod and coral fauna. However, reworking often poses a problem in these nearshore fauna and so the first appearance of the *sulcata* conodont is often used for correlation of the boundary (Paproth et al., 1991)
In 1996 the GSSP for the middle Carboniferous boundary was approved. Arrow Canyon in the arid Basin and Range Province of Nevada (U.S.A.) near Las Vegas was selected as the stratotype. In the mid-Carboniferous, the Arrow Canyon region was situated in a subtropical seaway, on the western coast of Euramerica. The base of the Pennsylvanian at Arrow Canyon is taken at the first appearance of the conodont *Declinognathodus noduliferus*, a cosmopolitan species which allows correlation between both deep and shallow water facies. Correlation of this boundary in England is difficult, as there is an apparent hiatus of at least 84 m, indicated by missing conodont zones (Lane et al., 1999). In 2000 this boundary was set as dividing the Mississippian and Pennsylvanian, which were given subsystem ranking.

After originally being set in 1841, the basal Permian boundary has been progressively moved back in time. In 1996 it was set as being in Bed 19 in the Aidaralash Creek region of Aktöbe, in the Ural Mountains of Kazakhstan. The section has abundant conodont, ammonoid and fusinacean foraminifera faunas. Lithologies at the boundary are shallow shelfal fluvial-deltaics. The boundary is taken as the first occurrence of *Streptognathodus isolatus* conodont (within the *S. "wabaunsensis"* conodont zone) (Davydov et al., 1998).

### 2.1.2 Late Carboniferous palaeocontinental reconstructions

Palaeocontinental reconstructions are a vital part in understanding the geology of any region, by allowing the placement of lithologies in their correct palaeogeographical setting. Early Carboniferous (Figure 4) and late Carboniferous (Figure 5) reconstructions were obtained from Blakey (2010), which are colour reproductions of the reconstructions in Blakey (2007).
Figure 4 - Palaeocontinental reconstruction of Earth in the Middle Mississippian (340 Ma) (Blakey, 2010). Britain is outlined in dark green, just to the south of the equator.

Figure 5 – Palaeocontinental reconstruction of Earth in the Late Pennsylvanian (300 Ma) (Blakey, 2010). Britain is outlined in dark green, just to the north of the equator.
2.1.3 Late Carboniferous palaeoclimate, sea level and palaeogeography

2.1.3.1 Palaeogeography

Gondwana moved slowly northward through the Carboniferous, and finally docked with the Old Red Sandstone (Euramerica) continent at the Mississippian-Pennsylvanian boundary (~318 Ma). Large (10 cm) medullosalean pteridosperm seeds of the same species are found in mid-Namurian (320 Ma) rocks from both Gondwana and Euramerica; seeds this big would not be wind transported for more than a few metres, suggesting the seaway between the two continents must have closed sometime in the Visean or early Namurian (McKerrow et al., 2000). Other evidence for the timing of this continental collision are outlined in ‘2.1.3.2 Sea-level and glaciation’.

As the last remnants of the Rheic ocean closed, the Appalachian-Mauretanide-Variscan (or Hercynian) orogenies produced mountainous regions in North America and Europe as the two continents sutured. The mountain ranges collectively formed the Central Pangaea Mountains, and would have towered over 3 km in height, similar to the present day Himalayas (Otto-Bliesner, 1993). Throughout this study this tectonic event will be referred to as the Varsican Orogeny. The effects of this orogeny played an important role in the lithological and vegetational evolution of the Bristol Coalfield, which will be discussed in depth throughout this study.

Edwards (1998) suggests that as the WNW-ESE trending Variscan Deformation Front propagated northwards in the Westphalian a foredeep was produced due to lithospheric flexure, which provided accommodation space in the southern regions of Britain. It was into this subsiding paralic basin that the Westphalian peat mires of southern Britain prograded and retrograded with the glacioeustatic rhythm. A pulse of uplift occurred near the Bolsovian-Asturian boundary, producing a hiatus in all the Euramerica paralic basins known as the Leonian Phase (Opluštíl and Cleal, 2007; Cleal et al., 2009; Cleal et al., 2011).
Basins and emergent areas were produced in Britain in the Devonian and Carboniferous as rifting occurred in a back arc setting to the north of the closing Rheic ocean. This lead to the formation of discrete depocentres, which filled with sediment in the Namurian and Westphalian as the basins thermally subsided after rifting ceased (Waters et al., 2007). In the Carboniferous, the Bristol and Somerset Coalfields were located in a low relief basin on the southern flank of the emergent Wales-Brabant High (Figure 6).

![Figure 6](image)

Figure 6 – Palaeogeographic reconstruction of Great Britain in a) Langsettian-Bolsovian and b) Asturian-Cantabrian times. Basins and highs are show, with depositional facies information. Adapted from Waters et al. (2007).

### 2.1.3.2 Sea-level and glaciation

Southern Hemisphere glaciations of Gondwana occurred from the late Devonian till the late Permian. This late Palaeozoic ice age is generally cited as lasting from 260-360 Ma (Rygel et al., 2008). High latitude fluctuations in ice volume are recorded in cyclic sediments and deep incision surfaces in the low latitudes as sea level fell and rose. Isbell et al. (2003) divided the Palaeozoic glaciation into three parts; Frasnian-Tournaisian (Glacial I), Namurian-Westphalian (Glacial II) and Stephanian-Permian (Glacial III).
Figure 7 – Simplified correlation of the 8 eustatic phases. The main phases are correlated to glaciations episodes in Gondwana, eastern Australia and Siberia, as evidenced by various geological proxies and geochemical data. Figure from (Falcon-Lang, 2004; Rygel et al., 2008).
The whole Tournaisian is regarded as a glacial period, with variations in the Gondwana ice volume causing glacioeustatic fluctuations of up to 60 m (Rygel et al., 2008). The early Visean was generally non-glacial, but sea-levels fluctuations of <25 m may have been produced by small ice sheet fluctuations. Near the end of the Visean large sea level fluctuations of up to 100 m occurred, indicating a large increase in magnitude compared to the early stages (Figure 7). These fluctuations persisted till the start of the Westphalian (around 15 Ma later). Lithological evidence indicates that ice sheet in the Mississippian were relatively small and discontinuous (Smith and Pickering, 2003).

A large global unconformity occurs at the Mississippian-Pennsylvanian boundary, resulting in a gap of 4 Ma due to non-deposition, and palaeovalley incision of up to 150 m in parts of North America (Rygel et al., 2008). It is likely this event was caused by large scale glaciations on Gondwana and eastern Australia. An estimated fivefold increase in ice volume (Smith and Pickering, 2003) occurred at this boundary. In eastern Australia and South America the increase in ice volume is broadly coincident with uplift which likely provided a locus for ice initiation. Evidence for glaciers in these mountains has been recorded (Cleal and Thomas, 2005). It is possible that the tropical forests on the subsequent Namurian-Westphalian deltas helped maintain low CO₂ levels which aided expansion and maintenance of the ice-sheets until the Stephanian. Ice likely retreated from Gondwana at the Westphalian-Stephanian boundary, in a brief interglacial warm-pulse that lasted 2-3 Ma.

Extensive Gondwanan glaciation reoccurred in the early Stephanian, and persisted until the early Permian (289 Ma). The largest glacioeustatic sea-level fluctuations (100-120 m) occurred at this time, at the peak of the Permo-Carboniferous glaciation. Hyde et al., (1999) modelled the end of the Westphalian (306 Ma) using a mass balance model/energy balance model which has proved accurate in matching estimated ice extent and volume for the Pleistocene glaciation. The model showed glaciations initiated in western Australia, before spreading over Gondwana. Ice extended to 45°S, which matches reconstructions from proxy data (Figure 12). However, the model overestimates Africa ice cover and underestimates latitudinal extent of South American ice. Ice was
shown to retreat from the mid-latitudes during Milankovitch precession minimas, which the model showed could be capable of producing the tens to hundreds of metres of sea-level fluctuation estimated from the late Carboniferous cyclothems.

### 2.1.3.2.1 Isotopic evidence

![Phanerozoic CO$_2$ levels for the Phanerozoic, produced by the GEOCARB III model](image)

Figure 8 – Phanerozoic CO$_2$ levels for the Phanerozoic, produced by the GEOCARB III model. From (Royer et al., 2004; Royer, 2006)

A large positive increase in $\delta^{13}$C occurs across the Mississippian-Pennsylvanian boundary; contemporaneous with an estimated increase in atmospheric CO$_2$ (Figure 8). This shift is global, but the values differ greatly on either side of Pangaea (Figure 9). Saltzman (2003) and Grossman et al. (2008) detected shifts in the $\delta^{13}$C in brachiopods from the carbonate platform of Arrow Canyon (Nevada) of +4‰, considerably less than the +6‰ found in Tethys to the east. They concluded that suturing of Euramerica and Gondwana at this time closed the last remnants of the seaway, and deflected the circumequatorial flow of warm water towards the poles (Figure 10). This vapour laden air would have carried the necessary moisture to the southern hemisphere, via high velocity gyres, possibly causing the rapid glaciations seen at the boundary (Smith and Pickering, 2003). Saltzman (2003) also cites the rise of provincialism of Tethyan and non-Tethyan faunas at the time as evidence for the seaway closure at this time.
Figure 9– δC$^{13}$ carbonate values for the Russian Platform brachiopods (Tethys) with mid-continental USA brachiopods and Arrow Canyon micrite (Panthalassa). A sharp positive shift in δC$^{13}$ is seen at the Mississippian-Pennsylvanian boundary at the same time as a large (~200 m) rapid fall of sea-level, inferred as a period of glacial expansion on Gondwana. At the Westphalian-Stephanian (Moscovian-Kasimovian on this scale) a large negative but short lived shift in δC$^{13}$ occurs, implying an increase in atmospheric CO$_2$. This is contemporaneous with a drying out of the low latitudes, a pulse in Variscan uplift and rapid deglaciation on Gondwana. Reprinted from Palaeogeography, Palaeoclimatology, Palaeoecology, 268/1-3, Grossman et al., Glaciation, aridification, and carbon sequestration in the Permo-Carboniferous: The isotopic record from low latitudes, 222-233. Copyright 2008, with permission from Elsevier.

The positive shift in δC$^{13}$ (Figure 11a) could also have been due to, or re-enforced by, enhanced nutrient supply. As sea-level falls in response to glaciation, shelves become exposed and nutrients are washed into the ocean increasing productivity in nearshore settings. Increases in $^{87}$Sr/$^{86}$Sr, indicating increased continental weathering, also supports this (Figure 11b). Productivity is also enhanced in glacial periods by enhanced pole-equator temperature gradients causing increased coastal margin upwelling and ocean mixing (Bruckschen et al., 1999).
Figure 10 – Palaeocontinental maps showing simplified ocean circulation and δC^{13} values for Panthalassa and Tethys for a) late Visean (330 Ma) and b) middle Namurian (320 Ma). Closure of the oceanic gateway by the middle Namurian deflected the circumequatorial currents poleward, transporting moisture to Gondwana that facilitated the rapid glaciations at this time. Divergence of the δC^{13} values between Panthalassa and Tethys at this time provides evidence for this closure. Elevated δC^{13} values in Tethys may have been caused by strong downwellings or nutrient depletion. Numbered red circles indicate key locations; 1-Arrow Canyon (Nevada), 2-Midcontinental America, 3-United Kingdom, 4-Russian Platform. Information and figure adapted from Saltzman (2003).

High δC^{13} in the Bolsovian could have been caused by the burial of vast amounts of organic carbon (rich in C^{12}) in the tropical peat mires of the time. Sea-level fluctuations decreased in the Westphalian, with estimates ranging from 20-40 m. These reduced amplitude fluctuations likely relate to a reduction in the volume of the Gondwana ice sheet. The large drop of 5‰ in δC^{13} at the Westphalian-Stephanian boundary is taken as yet more evidence of the large scale deglaciation at this time, and is further supported by the coeval (minor) positive ^{87}Sr/^{86}Sr shift (Figure 11b). This deglaciation appears to have little effect on the δO^{18} values, which shows only a slight negative shift (Figure 11c). The short lived fall in δC^{13} here likely relates to a brief period of global warming, possibly due to increased CO_{2}.
Figure 11 – Correlation of a) $\delta^{13}C_{\text{b}}$, b) $^{87}\text{Sr}/^{86}\text{Sr}$ and c) $\delta^{18}O$ isotope records for the Carboniferous. All isotope readings are from shell material. The three glacial identified by Isbell et al., (2003) are identified and correlated the isotope record. Yellow areas highlight the Mississippian-Pennsylvanian and Moscovian-Kasimovian (Westphalian-Stephanian) boundaries. Dashed line indicates the start of Glacial II, where the ice caps become more widespread and permanent. Adapted from Chemical Geology, 161 /1-3, Bruckschen et al., Isotope stratigraphy of the European Carboniferous: proxy signals for ocean chemistry, climate and tectonics, 127-163, Copyright 1999, with permission from Elsevier.
2.1.3.2.2 Climate modelling

Otto-Bliesner (1993) modelled the Westphalian (306 Ma) using GENESIS, a fully coupled atmosphere, ocean, land and ice sheet GCM (general circulation model). Sensitivity tests on the effect of the contemporaneous uplift of the Central Pangaean Mountains showed that these Himalayan-sized ranges may have focused precipitation on the equatorial belt year-round which maintained the moisture levels needed for extensive coal formation. This effect was more intense to the north (windward) side of the mountains, which would explain the greater expanse of coal on this side of the mountains. Model simulations which included this 3 km high mountain range had a 20% and 680% increase in precipitation in January and July, respectively. Termination of glaciations at the Westphalian-Stephanian boundary may have combined with a narrowing of the ITCZ (Intertropical Convergence Zone) as uplift proceeded, which may have contributed to rain shadow formation and the inferred drying out at this boundary (Edwards, 1998).

Ziegler et al. (1987) and Peyser and Poulsen (2008) proposed that the Gondwana ice, which extended to around 40°S, may have produced a semi-permanent polar high pressure zone which would have focused the ITCZ over the equatorial zone. This would have a similar effect to the Central Pangaean Mountains in keeping the equatorial zone warm and wet all year, which would have aided coal formation in the Westphalian (Tabor and Poulsen, 2008).

An increase or 3-4x modern pCO₂, inferred to represent the Permian, was found to produce a reduction in ice volume in the Permian and a final total deglaciation in the modelling runs by Hyde et al. (1999). This rapid deglaciation seems to be representative of the speed of ice loss inferred from proxy data.
2.1.3.3 Other climate indicators

Figure 12 – Proxy evidence for glaciations of Gondwana in the Westphalian (306 Ma). Navy circles indicate locations where tillites have been found, which suggest glaciations of the region. Glaciers likely extended to around 45°S, but extended to nearly 30°S in South America. Coals were formed between 30°S and 30°N (grey circles). An equatorial belt of evaporates were forming through Euramerica and in northern Gondwana. Evaporites were also present in Siberia and North China (red circles). Distribution from Hyde et al. (1999).

Coals formed between 30°S and 30°N in the Westphalian, and occur in Gondwana and Euramerica (Figure 12). Generally wood associated with the Westphalian peat mires has faint or no growth rings, which indicate the climate at this time was equable with adequate water and other growth related factors (Otto-Bliesner, 1993). The top (lowstand) coal underclays of middle Pennsylvanian coal bearing cyclothems are typically highly weathered and rich in aluminium oxide and kaolinite, indicating a wet climate with deep leaching (Frakes et al., 1992). It is thought that the Namurian and Westphalian were ever-wet periods which allowed the lush tropical vegetation to thrive (Opluštil and Cleal, 2007). Towards the end of the middle Pennsylvanian, coal seams become thinner and reduce in quality, indicating that coal-favourable humid conditions were becoming shortened in duration (DiMichele et al., 2009).

In the late Pennsylvanian, coals are far less common and vertisols become dominant with red argillaceous rocks appearing at this time. Calcisols/caliche palaeosols also appear which indicate intense evaporation drawing moistures up through the soil profile (Opluštil and Cleal, 2007). These lithologies indicate a strongly seasonal semi-arid climate, but where evaporation generally exceeds precipitation fluxes. Stomatal
densities were seen to decrease in examined medullosalean seed fern cuticles, which indicates a rise in CO$_2$ levels in the Stephanian (Cleal et al., 1999).

2.1.4 Late Carboniferous vegetation

2.1.4.1 The tropical forests of Euramerica

A global expansion of vascular plants, particularly the lycopsids, occurred between 360 and 286 Ma. This was accompanied by development of more complex stele, increasing efficiency of resource exploitation, and increased complexity of rooting systems. Arborescence was aided by formation of secondary cortex (‘inner bark’) in the lycopsids, and trunks covered with root mantles in the tree ferns (Cleal and Thomas, 1999a).

As the Namurian deltas formed in the Variscan foreland basin, the first arborescent lycopsids appeared in the tropical regions. There are several possible reasons for the appearances of forests at this time, one being that the increase in polar ice volume at this time deflected ocean currents, increasing precipitation on the low latitudes (Frakes et al., 1992). The newly forming delta substrates may have also offered the lycopsids a new niche to exploit. However, the decrease in albedo and input of moisture via evapotranspiration caused by the newly forming forests may have acted to cause the inferred increase in precipitation (Cleal and Thomas, 2005).

For over 9 million years (DiMichele and Phillips, 1996) in the middle Pennsylvanian, peat mires (which gave rise to the abundant coal measures) formed on delta lobes where moisture input was sufficient to overcome evaporation and maintain waterlogged conditions all year round. It was these waterlogged conditions that caused the low oxygen levels needed to prevent bacterial decay of the plant material. As lobes switched and/or seasonal moisture supply fluctuated, vegetation types changed. This change in vegetation can be seen from palynological and macrofossil assemblage changes between the coal beds and their roof clay and seat earth.
2.1.4.1.1 Lycopsids (giant ‘club mosses’)

Westphalian peat mires were dominated by giant lycopsid (lycophyte) trees, such as *Lepidodendron* and *Sigillaria*, which reached a staggering 40 m tall with 1 m basal trunk diameters. These are informally known as the club-mosses. The first lycopsids appear in the fossil record in the Lower Devonian (~410 Ma) and gradually increased in abundance, representing nearly two-thirds of the late Carboniferous forests (Willis and McElwin, 2002). Most arborescent lycopsids were heterosporous, and their 10-100 cm cones contained mega and microspores (monoecious) or just one type (dioecious) (Cleal and Thomas, 1999a). Megaspores are typically about 1-2 mm in diameter and can be smooth or spinose, and typically have a triangular projection on the proximal pole. Microspores are trilete with granular distal surfaces, such as *Lycospora*. All lycopsids which survived beyond the Jurassic are herbaceous varieties (Figure 13d); like the extant *Isoetes*, *Lycopodium* and *Selaginella*.

*Lepidodendron* is the most well-known arborescent lycopsid, with its long straight trunk and simple branching crown with grass-like leaves. Simple microphyll leaves grew out of the trunk, producing the characteristic snake-like scale scars (‘leaf cushions’) on the trunks (Figure 13a). Unlike modern angiosperms, lycopsids produce little wood and gained their structural strength from their bark-like covering. They reproduced via spores which were produced in cones. *Lepidodendron* was shallow rooted, with simple bifurcating root patterns mimicking the crown morphology. It is thought that *Lepidodendron* and the other Lepidodendracean lycopsids was adapted to water logged conditions, and thrived in the wet parts of the peat mires (direct in-situ stump evidence presented in DiMichele and DeMaris, 1987). The roots of these lycopsids are preserved as the fossils known as *Stigmaria* (Figure 13b). The roots could several metres in length, and even extend vertically into the water. *Stigmaria* fossils are usually in the form of casts, as the root system was filled with sediment as the plant rotted away. Density of these lycopsids is estimated as 500-1800 trees per hectare, based on in-situ fossilised stumps (DiMichele and DeMaris, 1987).
Figure 13 – a) The scale-like leaf scars of *Lepidodendron*, a common Coal Measures fossil in Euramerica. Specimen is 19 cm long, with the 2 cm wide rhomboidal leaf scars. From Winterbourne Down. b) The shallow rooting system of *Lepidodendron* is known as the fossil *Stigmaria*. This example in the Botanical Gardens in Sheffield is 2.3 m wide. c) *Sigillaria*, the bark imprint of a Late Carboniferous lycopsid. Specimen is 5 cm tall. From Winterbourne Down. d) All extant lycopsids are herbaceous, like this *Selaginella*. Specimen 10 cm tall.

It is thought that genera such as *Lepidodendron, Lepidophloios* and *Diaphorodendron* were monocarpic. These genera therefore produced crown foliage and cones only towards the end of their life cycles. (DiMichele and Phillips, 1985; Kenrick and Davis, 2004; Opluštil, 2010). The lycopsid forests would have therefore looked like a collection of bare poles for their estimated 10-15 year growth, and then repeatedly divided apically to form the crown foliage (Phillips and DiMichele, 1992; Cleal and Thomas, 1999a). Spores were released from the crown cones prior to plant death. This would have meant that the modern dense canopy of tropical rainforests was absent in the Carboniferous analogues, even though in-situ stumps show a greater density of trees compared to modern day tropical forests. Lycopsids would have been efficient photosynthesisers due to their large leaf-rich crown and photosynthetic leaf cushions adorning the trunk (Phillips and DiMichele, 1992). See section ‘2.1.3.2.1 Isotopic evidence’ for implications on the lycopsids and the carbon cycle.
Although most arborescent lycopsids preferred water-logged and undisturbed substrates, species of *Sigillaria* could tolerate drier conditions, and are thought to have lived on the fringes of the peat mires (Phillips and DiMichele, 1992). *Lepidophloios* had horizontally elongated leaf cushions and favoured the wettest swamp areas. *Lepidophloios* spores also had physical features consistent with dispersal and fertilisation in water (DiMichele and Phillips, 1996). It appears that some *Lepidophloios* species, particularly the ones with *Lepidocarpon* cones, had ‘female’ cones with sporangium that contained only one megaspore. This shows a development of reproductive strategy which is approaching that in seed plants.

Other lycopsid families were smaller; these are termed herbaceous lycopsids. These are traditionally interpreted as being <0.5 m in size, forming part of the understory. More recent studies demonstrate some species had a liana-like habit and grew on their arborescent cousins, and could reach up to 10 m length as they grew upwards towards the crown of the arborescent lycopsid (Opluštil et al., 2006). *Selaginellites, Lycopodites* and *Paurodendron* are examples of herbaceous lycopsids: small-bodied recumbent lycopsids (Bateman et al., 1992).

Genera such as *Chaloneria* and *Omphalophloios* (cones= *Sporangiostrobus*) are thought to have been somewhere in between; shorter than the large arborescent, but definitely not recumbent/liana-like herbaceous forms (Thomas, 1997). These are commonly referred to as the sub-arborescent lycopsids.

### 2.1.4.1.2 Sphenopsids (giant ‘horse-tails’ and allies)

Ancient relatives to modern day horsetails (*Equisetum*, Figure 14a) were the sphenophytes such as *Calamities* (Figure 14b). These first appear in the rock record in the early Carboniferous (~350 Ma) (Willis and McElwin, 2002). Unlike their extant relatives, some of these were large arborescent plants which grew up to 10 m tall. Sphenophytes have characteristic segmented stems with prominent vertical ribbing, and grew in disturbed substrates on the margins of streams and lakes. Spores were produced.
in cones which, like the leaves and branches, formed whorls around the main stem. Although the sphenopsids are considered to have been predominantly homosporous, evidence for heterospory is seen in the Westphalian (Willis and McElwin, 2002). The specialised sporangiophores which bore the cones were distinct from the sterile foliage (Cleal and Thomas, 1999a). The most common fossilised remains are *Calamities*, internal moulds of these giant horsetail stems, which formed when the central air filled chamber filled with sediment upon burial. Of all the Carboniferous flora, only *Calamites* grew in groups of clones borne from an extensive rhizome (Kenrick and Davis, 2004). The sphenophylls, such as *Sphenophyllum*, were herbaceous unlike the arborescent members such as *Calamities*. These scrambling plants lived in open and disturbed ground.

Figure 14 – a) Modern *Equisetum* at the Botanical Gardens in Sheffield, they stand around 1.5 m tall. This photograph was taken in November, so the specimens lack the distinctive foliage. b) Casts of sphenopsids form the common Late Carboniferous *Calamites* fossils. Specimen is 5.5 cm tall. From Winterbourne Down.

Sphenopsid cone clusters have been assigned to several genera (*Calamostachys, Palaeostachya, Macrostachya* and others) which are differentiated based on the position of the sporangiophores in relation to the sterile bracts. Most cones are homosporous, but a few were heterosporous. Like some of the lycopsids, some sphenopsid cones contained just one megaspore which indicates a development nearing the seed-based methods of reproduction (Cleal and Thomas, 1999a).
2.1.4.1.3 Filicopsids (ferns)

Tree ferns in the Carboniferous canopy were represented by members of the Marattiales family, and look superficially like extant *Dickinsonia* (Figure 15a) and *Cyathea* (Figure 15a and b). Tree ferns inhabited levees and other clastic lowlands from the Bolsovian period. The trunks (*Psaronius*) consisted of a narrow cylinder, which was surrounded by a mantle of roots which grew down the trunk from the crown vegetation.

When a frond dies it is shed from the plant, leaving a characteristic circular scar and can be used to assign the fossil to a genera based on shape and distribution (Willis and McElwin, 2002). The detached fronds usually belong to *Pecopteris, Cyathocarpus, Polymorphopteris* and *Lobatopteris* form genera. The *Cyathocarpus arborescens* groups are well known Asturian fossils, with specimens up to 3 m long with small tooth-like pinnules and simple veining. Most Carboniferous tree ferns were homosporous. In the Stephanian, tree ferns were responsible for the majority of the peat production (Cleal and Thomas, 1999a).

![Figure 15 – a) Dickinsonia Antarctica (left half of photograph) and Cyathea medullaris (two smaller specimens on the right half of the photograph) in the Winter Gardens, Sheffield. b) Cyathea latibrosa in the Botanical Gardens, Sheffield.](image)
Other types of ferns were adapted to a variety of ecological settings, mostly forming a low-level ground cover and flourishing in areas where disturbance and/or fire remove other types of vegetation (DiMichele and Phillips, 2002). Sphenopteroid, tedalaceous and gleichenaceous are the most common small/scrambling fern groupings used in the literature. Epiphytic species of ferns like *Botrypteris* have been found to root into this root mantle of *Psaronius* (Cleal and Thomas, 1999a).

### 2.1.4.1.4 Gymnosperms: Pteridospermopsids (‘seed ferns’)

The seed ferns (pteridosperms) reproduced via seeds, making them more similar in reproductive habit to modern conifers. They also had much more woody material than the true ferns. The pteridosperms lived on mineral rich substrates, instead of the organic rich peat mire sediments, and seem to have lived in fire-prone regions of the mires (DiMichele and Phillips, 1996; Kenrick and Davis, 2004).

Most late Carboniferous pteridosperms belonged to the medullosalean group, consisting of small trees with fronds of around a metre long. Fronds could grow up to 7 m long (in *Alethopteris lonchitica*), and seeds up to 10 cm have been recorded. The large 0.3 mm pollen grains are postulated to have been carried by insects. Common genera include *Neuropteris, Laveineopteris* and *Macroneuropteris*. Smaller, possibly scrambling species appear in the Stephanian. From the lower to middle Westphalian, a gradual increase in vein anastomisation occurs in *Neuropteris*. This genus also had pore-like openings on the leaf margin, which is seen in extant plants as an adaption to humid climates.

Seed anatomy and structure in preserved specimens is seen to be similar to modern cycads, suggesting a possible relationship. Medullosalean pre-pollen are monolette, and likely produced motile sperm in its microgametophytes, like extant cycads (Figure 16). Medullosalean ferns are common in the Westphalian, and die out in the early Permian.
Lagenostomacean pteridosperms occur in the early Carboniferous and are lost in the early Stephanian. Late Carboniferous varieties are vine-like (*Mariopteris*), and were likely epiphytes on lycopsids. The much less common callistophytes include foliage of *Dicksonites* and the seeds *Callospermarion*. This group was similar to the medullosaleans, but had bisaccate pollen similar to cordaites and conifers, which suggests a windblown method of dispersal. This group is common in Asturian and Stephanian times.

![Figure 16 - Modern cycads, such as this Cycas revoluta at the Winter Gardens (Sheffield), are thought to be the closest analogue for the extinct pteridosperms.](image)

### 2.1.4.1.5 Gymnosperms: Cordaites

Members of the corditales, an extinct group similar to conifers, are thought to have had a mangrove-like habit, with stilt-like roots in some cases. Originally this group were thought to have lived in upland alluvial fans, on alluvial gravel substrates and thin soils, often being found in coastal deposits after river transportation. Given the size of some of these trunks (Falcon-Lang, 2004; Falcon-Lang and Bashforth, 2004) it seems unlikely that they would have been transported over vast distances from these ‘upland‘ areas. Many authors now stress that the ‘dry-tolerant‘ nature of this group is not necessarily synonymous with ‘upland‘, and that levees and sand banks with an elevation of as little
as 1-2 metres would be enough to produce sufficiently drained substrates (Dimitrova et al., 2011). It is now accepted that cordaites were a significant component within the lowlands, often inhabiting well-drained levees adjacent to active braided fluvial systems channels or even on the margins of peat mires (DiMichele and Phillips, 1994; Bashforth et al., 2011).

While this group reproduced via seed and pollen like modern conifers, they lack the scale/needle-like leaves. Their strap-like leaves have parallel veins along their length and were helically arranged on the stems. Branches had a central pith zone surrounded by secondary wood, a feature seen in many conifers. Cones were aggregated into inflorescences and were borne on the most distal branches, and contain an ovule or several pollen sacs. Pollen was saccate, which likely aided wind dispersal. Very similar foliage is found in northern temperate regions today, such as Rufloria. The closely related Voltziales were more like modern Pinaceae and Araucariaceae conifer families.

2.1.4.1.6 Other gymnosperms

Megafossils of other gymnosperms are very rare in Carboniferous aged rocks. Bisaccate pollen, which were likely produced by gymnosperms, are however found in rocks of Middle and Upper Pennsylvanian age. These types of pollen are easily transported by wind and water over very large distances, and may illustrate gymnosperm-dominated ‘upland’ areas outside the peat-generating areas of the peat mires (Chaloner, 1958; Frederiksen, 1970). There is, however, a new school of thought that proposed that our entire view of the ecology of the Carboniferous peat mires is the product of a huge taphonomic bias (Falcon-Lang et al., 2009). These authors suggest that there were long periods of time in the coastal mires when a more dry-tolerant gymnosperm flora dominated, but due to the facies association these ecosystems were only very rarely preserved (e.g in incised channel fills during glacial lowstands).
2.1.4.1.7 Vegetation and the glacial-interglacial rhythm

The lycopsid-dominant peat mires occurred in the lowlands during late transgressive (deglaciation) and highstand (interglacial) periods (Figure 18a) when the climate was typically warm and humid (Figure 17). Low diversity *Lepidodendron* and *Lepidophloios* occurred in the late transgressive stages (Figure 18a), which gave way to a much greater diversity during the highstand periods (Figure 18b). Short-lived mires were dominated by *Lepidodendron* and *Lepidophloios*, with *Sigillaria* in the more ephemeral mires. Tree ferns, seed ferns, horsetails and cordaites dominated the mineral substrates of levees and the prograding deltas (Falcon-Lang, 2004). Cordaites were likely present all-year in the well-drained and marginal areas.

Glacial periods (Figure 18c) are characterised by river incision, and the palaeovalleys produced by this contain cordaites which were washed down from their upland habitat. Small lycopsid (typically the more tolerant *Sigillaria*) pods formed in rare isolated peat mires in the palaeovalleys, where wetland habitats persisted during the cool and dry glacial periods (Figure 17). Generally cordaites, tree ferns and seed ferns dominated during glacial intervals, with horsetails and lycopsids occurring as riparian vegetation (Falcon-Lang, 2004). Alternate diagrammatic representation of the relationship between the transgressive-regressive cycle and plant assemblage can be seen in Figure 19.

![Figure 17](image-url) - Diagrammatic representation of typical Carboniferous lithologies and how they can be used to place the unit within sequence stratigraphy and glacial-interglacial cycles. Adapted from Falcon-Lang (2004)
Figure 18 – Pennsylvanian tropical forests and their response to the glacial-interglacial cycles. Adapted from (Falcon-Lang, 2004).
Figure 19 – Alternate view of vegetation changes related to the transgressive-regressive sea-level cycle. Lycopsid-dominated peat mires can again be seen to dominate transgressive (deglaciation) and highstand (glacial) intervals. As glaciation occurs, regression causes drying out on the alluvial plain, with a reduction in lycopsids (to only the more tolerant *Sigillaria* types) and an increase in cordaites and pteridosperm occurrence. Adapted from Falcon-Lang (2003).
These theories and models explain the changes in vegetation and the glacial-interglacial cycle, but do little to explain why the same coal forest flora managed to colonise such vast areas after each glacial episode. Falcon-Lang and DiMichele (2010) suggest that coal measures flora would have had to retreat into large or well-connected refugia to enable re-colonisation by a broadly similar vegetational assemblage. Constriction and fracturing of these refugia towards the end of the Westphalian and into the Stephanian may have been a contributing factor to the floral turnover event evident near this boundary (see ‘2.1.4.1.9 The Westphalian-Stephanian turnover event’).

2.1.4.1.8 Late Bolsovian and middle Asturian diversity changes

During the late Bolsovian, a widespread reduction in macrofloral species diversity occurs across a geographically broad area of Euramerica; evident in the Ruhr, Pennine, South Wales, and Saar-Lorraine coalfields (Cleal et al., 2009; Cleal et al., 2011). The synchronous nature of this turnover over widespread geographic area suggests a climatic trigger, such as a reduction in temperature and/or rainfall in the late Bolsovian (Cleal et al., 2012). An synchronous and geographically widespread increase in species diversity occurs in the middle Asturian of the South Wales, Saar-Lorraine and Sydney coalfields suggests an possible increase in temperature and/or rainfall at this time (Cleal et al., 2012).

2.1.4.1.9 The Westphalian-Stephanian turnover event

The Mid-Late Pennsylvanian transition saw a drastic change in wetland vegetation types in tropical Euramerica. The lycopsid, seed fern and subordinate tree fern forests were rapidly replaced by tree ferns and subdominant seed ferns (DiMichele and Phillips, 2002; DiMichele et al., 2009) and the equatorial forests contracted in size by around 53% (Cleal and Thomas, 2005). Approximately 67% of the Westphalian peat-mire species disappeared from the coastal systems (DiMichele et al., 2009). The
reproductively edaphic varieties of lycopsids were most affected by this event. Only the more tolerant species of *Sigillaria* (such as *Sigillaria brardii*, the only known arborescent lycopsid from the Permian) persisted on beyond the Stephanian (Edwards, 1998). Whereas the lycopsids required wet and soft substrates to establish and reproduce, the opportunistic tree ferns were likely able to colonise a much wider variety of substrates. Tree ferns likely had rapid growth rates, thanks to their ‘cheaply’ constructed air-sac filled stems, and highly dispersible spores (Gastaldo *et al*., 1996; DiMichele *et al*., 2009).

Trees in the lycopsid forests are thought to have been widely spaced, creating little canopy cover over the ground. The post-turnover tree fern forests may have produced ground shielding canopies with their large fronds and closer spacing. This would decrease the land albedo, as evapotranspiration was greater from the canopy, which would have maintained a locally wetter climate which may have enabled peat mires to persist into the late Pennsylvanian even as the climate began to become drier (DiMichele *et al*., 2009). Reduction of the extent of the palaeotropical forests by half would also have increased the surface albedo of the Earth, increasing reflection of heat back into the atmosphere as land heating is reduced. This may have contributed to the early Stephanian warm pulse.

The lycopsids and other coal measures flora were likely displaced into large and well-connected refugia during Westphalian glacial periods, which enabled their widespread re-colonisation during the subsequent interglacials. Increased intensity of glaciations, and/or shifts in drainage patterns related to uplift, near the Westphalian-Stephanian boundary may have acted to constrict and fracture these refugia. As the refugia became more isolated, the lycopsids became unable to recolonise the interglacial peat mires due to their comparatively low dispersal potential. The ferns and tree ferns were then able to occupy the vacated niches in the interglacial peat mires due to their relative ease of dispersal and more adapted physiology. Higher palynological species turnover is seen from coal-to-coal in Stephanian assemblages when compared to the Westphalian.
examples, which seems to support the idea of increasing isolation of glacial refugia as possible contributor to the floral turnover (Falcon-Lang and DiMichele, 2010).

A basin inversion event in the late Westphalian-Stephanian occurred in the Variscan foreland, as basin subsidence was replaced by compression and uplift. A pulse of tectonic uplift at the Westphalian-Stephanian boundary would have eliminated the accommodation space in the foredeep of the northward advancing Variscan Deformation Front. This loss of accommodation space, combined with increased sandy sediment sourced from the uplifting Central Pangaean Mountains and local uplift, may have contributed to the drying out as the water table level fell and the area became better drained (Kerp, 1996; Cleal et al., 2004; Cleal and Thomas, 2005). Evidence for an uplift is seen across Euramerica as a hiatus referred to as the Leonian Phase, but is early Asturian and therefore predates the boundary by 1-2 Ma (Opluštil and Cleal, 2007). Alternatively, Edwards (1998) suggests that the foredeep may have become filled with clastics by the end of the Westphalian, and this may have caused or contributed to lowering the water table and drying out the mires. DiMichele et al., (2009) suggest that as Pangaea began its final phase of assembly here, the mega-monsoon initiated and shifted rainfall away from the tropics.

An interesting feature of the extinction event is that it was time transgressive across Euramerica. The turnover is seen at the Westphalian-Stephanian boundary in the intramontane basins of eastern Euramerica, but lycopsid-dominated vegetation is still dominant in the Stephanian of the Interior Province of North America. Westphalian-type mire biomes are recorded in the Permian of China (DiMichele and Phillips, 1996; Edwards, 1998), suggesting wet conditions were still dominant here in the Permian. This non-synchronous but latitudinally persistent vegetation turnover therefore was likely not caused by a single event, such as a large scale deglaciation and climate change. No modelling, as yet, can reproduce this relative timing of drying out at the low latitudes.

This growing body of evidence suggests that a pulse of uplift near the boundary shifted drainage patterns and altered sediment influx; causing substrates to become better
drained, facilitating the floral turnover. The time transgressive nature of the turnover would favour a tectonic induced mechanism over the traditional purely climatic hypothesis (see Cleal et al. (2009; 2011).

A typical hectare of lycopsids would have been capable of removing 160-578 tonnes of carbon from the atmosphere each year, of which 108-390 tonnes per annum would have been sequestered into coal formation (Cleal and Thomas, 2005). These estimates are based on a 10-year life span. Beerling and Woodward (2001) and Cleal and Thomas (2005) estimate that the Westphalian Euramerica peat mires would have been capable of drawing down 93-108 megatonnes of carbon per year in their global coverage of approximately 2395x10^3 km^2 in Asturian.

The transition from lycopsids-dominance to dominance of slower growth ferns would have resulted in a reduction in productivity, reducing the drawdown capability of this important carbon sink. The 53% contraction of the forests and change in dominant taxa in the Stephanian could have caused an increase in atmospheric CO_2 of 2-5ppm per annum (Cleal and Thomas, 2005) or 50-60 megatonnes of carbon per annum (Cleal and Thomas, 1999b). This increase in carbon dioxide would likely have been enough to produce the observed lower δ^{13}C values, and also trigger the deglaciation event evident in the geology on Gondwana. The most compelling conclusion from the currently available body of data is that the increase it atmospheric CO2 may in fact be a by-product of the tropical forest collapse, rather than the cause.
2.2 The late Carboniferous of the Bristol Coalfield

2.2.1 Introduction

The Bristol and Somerset Coalfield is situated in the south west of Britain (Figure 20a). The Coalfield consists of three main basins; Bristol, Pensford and Somerset; which lie between Cromhall and the Mendips. The area covers around 100km², with the coalfield continuing for another 320km² under the surrounding Mesozoic cover. The Cotswold Hills bound the area to the west, with an escarpment of Mesozoic deposits. Although the basins form three distinct outcrop areas, they are all part of the same continuous coal field which now appear separated due to more recent geological activity. There are several inliers to the west of the main coalfield outcrop: (1) the Nailsea Syncline, which is structurally distinct but in continuity with the Somerset Coalfield; (2) the Severn Coalfield, which is considered an extension of the Forest of Dean Coalfield (Cleal, 1986); and (3) the Clapton-in-Gordano and Barrow Gurney inliers, which are structurally separate from the Bristol Coalfield (Green, 1992; Kellaway and Welch, 1993). A small outcrop of lowermost Downend Member within Golden Valley near Bitton is included as part of the Bristol Coalfield, due to its close proximity.

The Bristol Coalfield occurs in an area of low relief postulated to have been produced by Permo-Triassic erosion that removed part of the Warwickshire Group sequence, and culminated in the formation of a peneplain (Kellaway and Welch, 1993). The Coalfield consists of two outcrops of Warwickshire Group lithologies, which are separated by the east-west trending Kingswood Anticline (Figure 20b). The northern portion, the roughly triangular-shaped Coalpit Heath Basin extends for roughly 40km² and was heavily economically exploited in the past. South of the anticline, the Warwickshire Group outcrops in another ~5km² area straddling the River Avon. The small isolated outcrop within Golden Valley is included within this southern portion. These now distinct areas were laid down as a continuous unit, but have been separated by subsequent deformation and erosion (Figure 21).
Figure 20 – a) Location of Bristol in south west Britain. b) Simplified geological map of the Bristol Coalfield. Warwickshire Group formations/members are in bold. SWLMCMG= South Wales Lower and Middle Coal Measures Group. Simplified from online 1:10000 maps on Digimap and paper copies of BGS 1:10000 series sheets ST67NE and ST68SE. See Figure 21 for a cross section along the line marked N-S.

Figure 21 – Cross section of along the line of section in Figure 20.
2.2.2 Structural evolution

Deposition of the coal measures in the Bristol region was constrained by two pre-existing structures; the north-east trending Lower Severn Axes to the west and the north-south Malvern Axes to the north of the basin. During the Bolsovian, the first pulse of Variscan orogenic movement produced folding parallel to these pre-existing structures and uplift on the northern margins of the coalfield (Green, 1992). This uplift, likely centred around the Usk Anticline, produced the localised red bed at the top of the Winterbourne Formation in the northern portion of the basin. The Coalpit Heath and Pensford-Radstock synclines may have been partially initiated at this time (Moore and Trueman, 1942; Mykura, 1952; Trueman, 1954). This pulse of uplift slightly pre-dated the Leonian Phase (early-mid Asturian) of uplift, and is coincident with a change in sedimentation in the southern British coalfields from coastal plain deposits to the coarse lithic arenites of the Pennant Sandstone Formation.

The main phase of Variscan folding and faulting occurred in this region during the Stephanian and earliest Permian. This phase produced the north-directed, east-west trending faults in the south of the region as well as the Mendip Hills; 4 periclones in en echelon formation, with the large Beacon Hill pericline forming the southern limit to the Radstock Basin. The structural trend rotates anticlockwise as the distance from the Variscan front increases; having a north-south alignment in the Coalpit Heath area and a north-east to south-west alignment in the west of the region. This deviation from an east-west trend may have been in part due effects of the pre-existing Lower Severn and Malvern axes (Green, 1992). These structural pattern changes may also be, in part, due to a later period of east-west compression during the final stages of the Variscan orogeny (Peace and Besly, 1997).

2.2.3 History of research

The Bristol and Somerset coalfields contain some of the earliest exploited fuel sources in the world, with evidence for use in the Neolithic period. There are even records of
extraction by the Roman and Tudor empires. Mining exponentially increased in the late eighteenth century during the Industrial Revolution, as new industries and transport mechanisms put pressure on fuel reserves. By 1920 the older Bristol pits were nearing exhaustion and by 1973 the last colliery at Kilmersden closed its doors.

John Strachey (1671-1743) was the first to describe and illustrate the Bristol coal seams, along with the shells and fossilized fern-like plants contained within (Kellaway and Welch, 1993). He was the first to name and describe the Pennant Sandstone. His study highlighted the regions patterns of faulting and the angular unconformity between the Upper Carboniferous and Permo-Triassic strata above. Strachey, like many early workers, was unsure of the nature of the relationship between the Dinantian Limestone, Namurian Millstone Grit and the Coal Measures due to the contact being obscured by Mesozoic deposits (Kellaway and Welch, 1993).

William Smith (1769-1839) was the first to map the geology of the eastern edges of the Bristol and Somerset Coalfield, in a five mile area surrounding Bath in 1799. What started as a survey of underground mines in Stowey (Somerset) in 1791 soon produced this earliest colour coded recording of the surface geology of the district. The recycled Carboniferous material in the Blue Lias lead Smith to incorrectly place the Coal Measures stratigraphically below the Dinantian Limestone in 1817 (Kellaway and Welch, 1993).

In 1822 Conybeare and Philips officially classified the Carboniferous System which, at the time, consisted of: the Old Red Sandstone (now classed as Devonian), Carboniferous or Mountain Limestone, Millstone Grit and Coal Measures (Gradstein et al., 2004). In 1824, Buckland and Conybeare produced the paper “South-Western coal district of England and Wales”. In this paper the first division of strata into the Upper Coal Shale, Pennant Grit and Lower Coal Shale was proposed. Greenwell and McMurtrie's classification was complete in 1869, and is outlined in Table 1.
This was followed by mapping of the first versions of the Geological Survey Old Series, sheets 19 and 35 which were completed in 1845. A memoir to accompany these sheets was published by H.D Woodwards in 1876 (Kellaway and Welch, 1993). Woodward’s memoir, however, contained little structural information. It was not until 1901 that McMurtrie produced the first generalised structural map of the coalfield (Moore and Trueman, 1939). The 1901 classification was adopted but partially altered by Moore and Trueman (1937) (see Table 1). In 1865, Crossham’s studies showed that the “Millstone Grit” shown on maps of the Kingswood Anticline was in fact part of the Coal Measures.
(Pennant Sandstone Formation). In 1947 Truman discarded the Vobster and New Rock Groups divisions of the Lower Coal Series.

The first published descriptions of the lowest marine bands, the Ashton Vale Marine Band and Croft’s End Marine Band, appeared in 1907 and 1937 respectively. Boreholes were drilled between 1912 and 1920 and 1949 and 1954 at Coalpit Heath, Winterbourne, Yate and Harry Stoke. These boreholes enabled the four main marine band marker beds to be classified. The positions of the Winterbourne and Croft’s End marine bands were not found in Radstock till 1968, along with a marine shale thought to correlate to the Harry Stoke Marine Band.

Many notable palaeobotanists worked on the Bristol Coalfield in the 19th and 20th century, such as; Arber, Brongniart, Crookall, Kidston, Lillie, Moore and Sternberg. See Pendleton et al. (2012) for a details of historic palaeobotanical work.

2.2.4 Bristol stratigraphy

Building on earlier work, Kellaway and Welch (1993) provided a detailed review of the stratigraphy of the Bristol-Somerset Coalfield. Recently, Waters et al. (2007; 2009; 2011) emended the stratigraphical terminology based on lithostratigraphical correlation of mapable geological units, as opposed to the broadly chronostratigraphical system of Kellaway and Welch (1993). The Lower to Upper Coal Measures are now collectively known as the Coal Measures Supergroup. They defined the South Wales Coal Measures Group, containing coal-bearing sequences with marine bands (Langsettian to mid-Bolsovian; Bashkirian-lower Moscovian), overlain by the Warwickshire Group, characterized by coarse-grained sandstone, red mudstone and an absence of marine bands (mid-Bolsovian to upper Asturian; mid- to upper Moscovian). The junction of the two groups is positioned at the Cambriense (Winterbourne) Marine Band, the youngest marine incursion in the British Isles (Waters et al., 2009), which historically served as the boundary between the now-redundant Middle Coal Measures and Upper Coal Measures. The Warwickshire Group features three formations recognised in current
stratigraphical nomenclature, from base to top, the Winterbourne, Pennant Sandstone and Grovesend formations.

### 2.2.4.1 South Wales Coal Group

The South Wales Lower Coal Measures Formation at Bristol is around 230 m thick (Kellaway and Welch, 1993) and consists of largely argillaceous lithologies. The base of this unit is taken as the Ashton Vale Marine Band (where *Gastrioceras subcrenatum* gonitaites occur). The upper limit is taken as the Harry Stoke Marine Band, with its associated *Anthracoceratities vanderbeckei*. This band is also thought to approximate to the Langsettian-Duckmantian boundary (Kellaway and Welch, 1993). These units are incompetent, and are heavily folded at Radstock between the more competent strata above and below. The lower coals contain much of the higher rank coals found in this region.

The South Wales Middle Coal Measures Formation occur stratigraphically above the Harry Stoke Marine Band, and range up to the Croft’s End Marine Band (*Donetzoceras* or ‘*Anthracoceratities*’ *aegiranum* zone). This argillaceous unit is around 300 m thick at Bristol and contains the Kingswood Great Coal, an important horizon for correlation to other areas (Kellaway & Welch, 1993). The top of the South Wales Middle Coal Measures Formation and transition to the Warwickshire Group is marked by a band of *Donetzoceras* or ‘*Anthracoceratities*’ *cambriense*, known as the Winterbourne Marine Band. At Radstock these units are folded to such a degree that beds can become inverted (Moore and Trueman, 1942).

The South Wales Lower and Middle Coal Measures formations, collectively referred to as the South Wales Coal Measures Group, reduce in thickness northwards though the coalfield. This attenuation may be an original depositional feature, attenuation due to tectonic events before deposition of the Warwickshire Group and/or due to Mesozoic denudation (Kellaway and Welch, 1993).
2.2.4.2 Warwickshire Group – Winterbourne Formation

The Winterbourne Formation is a 120 – 180 m thick unit whose distribution is restricted to the Coalpit Heath Syncline region of the northern part of the Bristol Coalfield (Green, 1992; Kellaway and Welch, 1993; Waters et al., 2009). The Winterbourne Marine Band (also known as the Cambriense Marine Band) defines the base of the Winterbourne Formation in the Coalpit Heath Syncline region, although this marine marker bed has not been found in the adjacent Kingswood Anticline region (Waters et al., 2009), likely reflecting a topographic high in this area. The top of the Winterbourne Formation is taken to be the base of the first major (> 3 m thick), coarse-grained sandstone bed of the Pennant Sandstone Formation (Waters et al., 2009).

Only two limited surface exposures are known of the Winterbourne Formation; one is adjacent to a Coombe Brook in a wooded area between Fishponds and Speedwell (OS ST 632748), and the other comprises various outcrops along the disused railway line between Staple Hill and Fishponds, specifically near the Staple Hill tunnel (OS ST 651756). However, the Winterbourne Formation is much more thoroughly known from British Geological Survey (BGS) borehole cores including Harry Stoke B and C, Stoke Gifford 3, Yate Deep and Winterbourne (Kellaway and Welch, 1993), demonstrating its distribution over about 20 km². The Winterbourne Formation is also known from Stoke Gifford 2, and Westerleigh 1 and 2 boreholes, but due to the absence of the Winterbourne Marine Band in these areas only an estimated position base of this formation is possible.

The lower part of the Winterbourne Formation comprises a single basal marine band (in some areas), grey mudstone, locally containing the non-marine bivalve Anthraconauta phillipsii, a few coals, and channel sandstone bodies (Waters et al., 2009). The uppermost 40 m comprises mostly red mudstones and grey/green mottled mudstone beds and at least three beds of conglomerate containing subangular polymictic clasts. The conglomerate beds are up to 2-3 m thick, fine-upwards into coarse-grained sandstone, and may show rooted upper surfaces, reworked caliche nodules and lithic
clasts with oxidized rims (Falcon-Lang et al., 2011; Falcon-Lang et al., 2012). Pringle (1921) noted that conglomerate beds at the base of the Downend Member generally diminish towards the south-southwest, along with average clast size, suggesting a source region to the north-northeast. These conglomerate beds likely match those which are now designated as part of the uppermost Winterbourne Formation.

2.2.4.3 Warwickshire Group – Pennant Sandstone Formation

The Pennant Sandstone Formation is ~600-950 m thick in the Bristol Coalfield and its base was originally defined as the Cambriense Marine Band (Kellaway and Welch, 1993). This unit thins from its maximum calculated thickness in the southern limb of the Kingswood Anticline as it extends towards its limit on the northern edge of the Warwickshire Group outcrop. However, as already noted, in their lithostratigraphical revision, Waters et al. (2009) transferred the lowermost grey and red argillaceous beds encountered in Coalpit Heath Syncline to the Winterbourne Formation. Consequently they moved the base of Pennant Sandstone Formation to a higher stratigraphical level defined by the lowermost mappable unit of thickly bedded (>3 m thick) “Pennant-type” sandstone. Usually this occurs near the level of the Parrot (=Hen?) Coal in the Bristol Coalfield; however, in the Somerset Coalfield, the base of the Pennant Sandstone Formation is at the level of the Little Course Coal, some 120 m below the Cambriense Marine Band (Stubblefield and Trotter, 1957). Hence, the base of the formation is profoundly diachronous (younging from south to north), and time-equivalent to the Winterbourne Formation in its oldest part (Figure 22).

The top of the Pennant Sandstone Formation is defined at the Rudge Coal in the Somerset Coalfield, and in the Bristol Coalfield, at the High Coal in the Coalpit Heath Syncline (Kellaway, 1970). Due to the confusion regarding the stratigraphy of the southern limb of the Kingswood Anticline, the present author constructed a new stratigraphical interpretation for this area, based on desktop mapping and field
observations (used in Figure 22 and Figure 29). Using this new stratigraphy the Rock Coal is designated as the upper limit of the Pennant Sandstone in this southern region.

Previous authors have used a unified stratigraphy for the entire Bristol Coalfield, superimposing the Salridge Coal of the southern limb of the Kingswood Anticline onto the stratigraphy of the Coalpit Heath Syncline, 150-200 m below the High Coal. There appears to be no sound basis for this, despite this erroneous stratigraphical chart appearing in almost every paper relating to the Bristol Coalfield for the last few decades (Kellaway and Welch, 1993; Waters et al., 2009, 2011). The Mangotsfield coals - Salridge Coal correlation has also been historically displayed in Hawkins and Tomlinson (1987), as well as on the 1-inch scale geological maps.

In the Bristol Coalfield, the Pennant Sandstone Formation is subdivided into the lower Downend Member (~120-450 m thick) and the upper Mangotsfield Member (~450-550 m thick). The junction between the Downend and Mangotsfield members is taken as the lowest of the Mangotsfield coals in the Coalpit Heath Syncline, and its equivalent, the Temple Cloud Coal, in the Somerset Coalfield. At this level, “Pennant-type” sandstone beds of the Mangotsfield Member rest sharply on top of the Mangotsfield coals. The Mangotsfield coals were worked near Shortwood (Church Lane and Wallsend collieries), and can be traced to the north-west through Mangotsfield and Downend on the geological map. These coals disappear against the Whitefaced Fault and overlying Triassic at Bromley Heath. The Mangotsfield coals seem to be absent from the Pennant Sandstone Formation at the north-western side of the Coalpit Heath Basin, based on the geological maps and BGS borehole logs from the Yate area. In this Kellaway and Welch (1993) correlated the Mangotsfield coals to a thick siltstone horizon, around 150 m above the Winterbourne Marine Band. They do not elaborate on the reasons for this seemingly arbitrary correlation. In absence of any data to the contrary, this correlation is considered as accurate for the purposes of this study. The Mangotsfield coals are also not present in the southern limb of the Kingswood Anticline, but based on the newly produced stratigraphy and field observations it is likely that the Salridge Coal may be its equivalent.
The Pennant Sandstone Formation is dominated by thickly bedded units of coarse-grained, feldspathic, lithic arenites organised into large-scale channel bodies. In extensive exposures in South Wales, these bodies typically rest on scours, several metres deep, and may be > 100 m wide (Jones and Hartley, 1993) however, in the Bristol Coalfield, exposure is generally too poor to confirm channel geometry, with channels and scours generally being larger than the outcrop scale. Nonetheless, there is no reason to assume that the channels of the Bristol Coalfield had a different geometry to those of the adjacent South Wales Coalfield. Palaeocurrent current indicators, in the form of large-scale cross bedding and flute marks, indicate flow towards the north and north-west in the Pennant Sandstone Formation (Pendleton and Falcon-Lang, field observations). This switch in source, from northern in the Winterbourne Formation to a southern source in the Pennant Sandstone Formation, is almost certainly linked to the same pulse(s) of uplift along the Variscan Deformation Front which heralded a switch to coarser sediment types in southern Britain.

Channel-fill comprises pebbly sandstone and coarse-grained sandstone, frequently trough cross-bedded, or locally showing tabular cross-stratification several metres high (Waters and Davies, 2006). Rare, fine-grained intervals between the sandstone beds comprise red mottled mudstone with caliche nodules or grey, platy shales with plant fossils and the non-marine bivalves Anthraconauta phillipsii, and a few lenticular coals (Kellaway and Welch, 1993; Falcon-Lang et al., 2012). The roof of the High Coal, which marks the top of the formation, contains the branchiopod crustacean Leaia (Crookall, 1929) in association with the non-marine bivalves, Anthraconauta phillipsii and A. tenuis (Moore and Trueman, 1937).

2.2.4.4 Stratigraphical gap

Pendleton et al. (2012) provided the first evidence of a stratigraphical gap between the Pennant Sandstone and Grovesend formations, due to the absence of the Linopteris obliqua Zone and Lobatopteris micromiltonii Subzone from the produced palaeobotanical biostratigraphy. A similar lower to middle Asturian stratigraphical gap
is also manifested in eastern South Wales as well as the intramontane basins of Europe (Cleal et al., 2009; Cleal et al., 2011). This hiatus appears to be part of the regional tectonic activity referred to as the Leonian Phase of the Variscan Orogeny (sensu Wagner, 1966). However, no significant palaeobotanical assemblages were recovered from the Mangotsfield Member so it is possible that the hiatus may be of a shorter duration than indicated by the floral Biozone gap. Palynological data provides evidence of early Asturian assemblages within the Mangotsfield Member (see ‘3.3.2.2 Biostratigraphic dating of the Bristol Coalfield’), which would diminish the duration of this hiatus in the Bristol Coalfield indicated by the palaeobotanical indicators.

### 2.2.4.5 Warwickshire Group – Grovesend Formation

The Grovesend Formation is the uppermost unit of the Bristol-Somerset Coalfield, resting on top of the Pennant Sandstone Formation, although the formation boundary is currently nowhere exposed, either in outcrop or borehole core. In the Bristol Coalfield, it comprises the lower Farrington Member, < 70 m thick, which is a succession of grey argillaceous strata with productive coal seams (Table 2). The lowest coal seams of the Farrington Member at Parkfield Colliery are the Hollybush and Great Coals, separated by up to 15 m of shales; these two coals coalesce to the north and are represented by a single coal, the High Coal, at Coalpit Heath (Moore and Trueman, 1937). At Parkfield a thin un-worked sulphurous coal, the Stinking Coal, occurs just above the Top Coal. The Hard Coal appears at both pits, and marks the top of the Farrington Member. One notable characteristic of the Hard Coal is the occurrence of coalstones, which consist of an inorganic iron-rich nucleus coated with carbonaceous material. Wethered (1878) believed these were formed when tree branches and roots decayed and filled with debris.
<table>
<thead>
<tr>
<th>Coalpit Heath Colliery</th>
<th>Parkfield Colliery</th>
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<tr>
<td>Hard Coal</td>
<td>Hard Coal</td>
</tr>
<tr>
<td></td>
<td>Stinking Coal (un-worked)</td>
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<tr>
<td>Hollybush Coal</td>
<td>Top Coal</td>
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<tr>
<td>High Coal</td>
<td>Hollybush and Great Coal</td>
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</table>

Table 2 – Correlation of the Farrington Member coal seams present at Coalpit Heath Colliery in the north and Parkfield Colliery to the south.

In the Brislington area the Farrington Member is estimated to be ~100 m thickness with four worked coals; the Rock, Pot, Trench and Trolley. These four Brislington coals were worked to the south east of Brislington (Buckland and Conybeare, 1824). Note that the Brislington Rock Coal is not related to the Rock Coal of the Somerset Coalfield which marks to top of the Farrington Member in that area. The Brislington seam is so named due to the presence of a 6 m thick “rock of paving-stone, call'd Penant” around 6.5 m above (Strachey, 1719; Buckland and Conybeare, 1824).

Based on the stratigraphical work during the course of this study, it would seem likely that the Rock Coal is equivalent to the Great Coal of Parkfield Colliery and the High Coal of Coalpit Heath Colliery, and therefore should be treated as the base of the Farrington Member in this area. This likely stratigraphical correlation was also recognised by Hawkins and Tomlinson (1987), which appears to have either been not recognised or ignored in subsequent stratigraphical work. As mentioned above, the Rock Coal is overlain by a ‘Pennant-type’ sandstone. Kellaway and Welch (1993) note that the Coalpit Heath High Coal is overlain by “a thick current-bedded sandstone” in the Iron Acton and Nibley areas, and the 1 inch-scale geological maps also show a similar sandstone overlying the High Coal in the Frampton Cotterell area. This seems to lend more support to a stratigraphical correlation between the Rock and basal Farrington Member coal; although the lack of reports of an equivalent sandstone at Parkfield and over much of the Coalpit Heath Basin cannot be ignored.
The Farrington Member is overlain by the Barren Red Member, a red mottled mudstone succession, which is <200 m thick in the Coalpit Heath Syncline area (Waters et al., 2009). These units inter-digitate, and are probably coeval, at least in part. Several impersistent sandstone beds appear throughout the Barren Red Measures, as indicated on the 1 inch-scale geological maps, in both the Coalpit Heath Basin and the southern limb of the Kingswood Anticline.

Higher units of the Grovesend Formation do not occur in the Bristol Coalfield; however, in the Somerset Coalfield, the Radstock and Publow members overlie the Barren Red Member (Waters et al., 2009). Relatively little is known of the sedimentary facies and palaeontology of these units, beyond that they are dominated by grey mudstone with non-marine bivalves, “Pennant-type” sandstone bodies, and a few coals (Waters et al., 2009). They probably represent the deposits of poorly-drained coastal plains. The Hursley Hill borehole (OS ST 618 656), drilled just beyond the southern limit of the Bristol Coalfield outcrop, provides access to the Radstock and Publow members in close proximity to the southern edge of the coalfield (Kellaway, 1970).

2.2.5 Biostratigraphy and correlation

2.2.5.1 Biostratigraphy

The Cambriense Marine Band, which marks the base of the Winterbourne Formation (and the Warwickshire Group) in the Bristol Coalfield, is positioned near the lithostratigraphical middle of the Bolsovian succession (Waters et al., 2009). No conodonts have been reported from this unit (Phil Heckel, pers. comm., 2011), so its correlation with successions in the USA and the IUGS global chronostratigraphy is in doubt. The goniatites that are characteristic of this marine band were described as Anthracoceras cambriense Bisat, but were later simultaneously transferred to the genera Weideyoceras (Popov, 1979) and Donetzoceras (Saunders et al., 1979), the latter probably being the more correct name (Phil Heckel, pers. comm., 2011). Davydov et al. (2010), who used the genus, Weideyoceras, positioned their W. cambriense Zone as
mid-Moscovian, which would make it equivalent to the uppermost Bolsovian to lower Asturian in the western European regional chronostratigraphy. However, as all *Donetzoceras cambriense* specimens lack sutures crucial for ammonoid systematics (Saunders *et al.*, 1979), comparison of the Russian and British material is uncertain, and in the absence of sutures also raises the question as to whether the whole taxon is a *nomen dubium* (Phil Heckel, pers. comm., 2011).

As no marine bands occur in the Warwickshire Group, there is considerable difficulty in correlating these beds with the global stratigraphy. However, Moore and Trueman (1937) produced a non-marine lamellibranchs (bivalves) zonal scheme for the Bristol and Somerset Coalfield. Assemblages containing *Anthraconauta phillipsii* occur in the Winterbourne and Pennant Sandstone Formation, with *A. tenuis* occurring in the upper half of the Mangotsfield Member and the Grovesend Formation (Moore and Trueman, 1937; Waters *et al.*, 2009). *A. phillipsii* is generally regarded as an upper Bolsovian index fossil with *A. tenuis* having a first occurrence just below the base of the Asturian Substage (although see Cleal, (1984) for a discussion on the practical problems of using these bivalves as biostratigraphical indices).

Dix (1934) also applied a palaeobotanical zonation to the Bristol area. Pendleton *et al.* (2012) have since produced an updated megafloral biozonation of the Bristol Coalfield, based on reappraisal of historic records, re-identification of museum specimens and collection of new assemblages from previously unsampled localities and facies. Based on this work, the Winterbourne and Pennant Sandstone Formation have megafloral assemblages that belong to the *Laveineopteris rarinervis* Subzone of the *Paripteris linguaefolia* Zone indicating a mid- to late Bolsovian age. Specifically, these formations contain *Laveineopteris rarinervis, Annularia sphenophylloides*, and *Reticulopteris muensteri* which have their lowest stratigraphical occurrences in the mid-Bolsovian, at the base of this subzone. The Farrington to Radstock members of the Grovesend Formation, in contrast, have megafloral assemblages belonging to the *Dicksonites plukenetii* Subzone of the *Lobatopteris vestita* Zone, indicating a late Asturian age. The presence of *Odontopteris brardii* Brongniart, *Lobatopteris viannae* (Teixeira) Wagner
and *Alethopteris pseudograndinioides* var. *subzeillerii* (Wagner) Zodrow and Cleal in the Publow Member suggests the presence of Cantabrian aged rocks (*Odontopteris cantabrica* Zone) at the top of the succession.

### 2.2.5.2 Correlation with other areas

Table 3 correlates the Bristol marine bands to those in other British coal fields, on the basis of the goniatite Biozones. The base of the Warwickshire Group in the Bristol coalfield is taken as the Winterbourne Marine Band, which correlates to the *cambrienne* goniatite Biozone. As mentioned previously, the base of the Pennant Sandstone Formation is profoundly diachronous; younging northwards from the Somerset Coalfield and across the Bristol Coalfield. The base of the Pennant Sandstone Formation in Somerset lies just above the Aegiranum Marine Band, giving a basal age to the Warwickshire Group of basal Bolsovian in this area (Figure 22).

<table>
<thead>
<tr>
<th>Bristol &amp; Somerset marine band</th>
<th>goniatite biozone</th>
<th>Yorkshire marine band</th>
<th>East Midlands marine band</th>
<th>South Wales marine band</th>
<th>Scotland marine band</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winterbourne</td>
<td><em>A. cambriense</em></td>
<td>Top</td>
<td></td>
<td>Upper Cwmgorse</td>
<td></td>
</tr>
<tr>
<td>Croft’s End</td>
<td><em>A. aegiranum</em></td>
<td>Mansfield</td>
<td>Mansfield</td>
<td>Cefn Coed</td>
<td></td>
</tr>
<tr>
<td>Harry Stoke</td>
<td><em>A. vanderbeckei</em></td>
<td>Clay Cross</td>
<td></td>
<td>Amman</td>
<td>Queenslie</td>
</tr>
<tr>
<td>Ashton Vale</td>
<td><em>G. subcrenatum</em></td>
<td>Pot Clay</td>
<td>Pot Clay</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3 – Correlation of Bristol marine bands to those in other Carboniferous basins of Great Britain. After description in Kellaway and Welch (1993).

The Pennant Sandstone Formation (and equivalent Stallion Hill Sandstone Formation) of the Forest of Dead, Severn, Newent and Oxfordshire coalfields to the north are profoundly younger (late Asturian) than the Pennant Sandstone of the Bristol Coalfield (Bolsovian to early Asturian) (Cleal, 1986; Cleal, 1987; Cleal, 1997; Waters et al., 2011; Pendleton et al., 2012; Pendleton and Wellman, 2012). Initiation of coal measures sedimentation in these basins was likely initiated by the Leonian Phase of tectonic
activity; this same tectonic activity is also manifested as a disconformity within the eastern South Wales (Cleal, 1978), Bristol (Cleal and Thomas, 1996; Pendleton et al., 2012) as well as other European coalfields (Cleal et al., 2009; Cleal et al., 2011).

Figure 22 – Correlation of lithostratigraphic units and key coal seams between coalfields in the Bristol and Somerset area. Somerset stratigraphy adapted from Kellaway and Welch (1993) and Waters et al. (2011). Bristol stratigraphy was constructed afresh, as part of this thesis.
2.2.6 Palaeoenvironments

2.2.6.1 Marine conditions

The marine bands represent periods of marine incursion, where a relative rise in sea level (isostatic and/or eustatic) lead to deposition of dark grey-black carbonaceous shales. These widespread swamplands and shallow muddy seas may have persisted over Bristol for long periods of time. Abundant goniatites, bivalves, small crustaceans, Lingula and productid brachiopods colonised these shallow seas. A greater variety of marine faunas occur in Wales, which may suggest incursions entered the Bristol region from the west (Rayner, 1981). The same marine bands can often be traced for several hundreds of square kilometres over Britain, even extending to France and Germany (Rayner, 1981).

2.2.6.2 Winterbourne Formation

Falcon-Lang et al. (2011) interpreted this succession as the deposit of a poorly-drained coastal plain, overlain by the deposits of a (periodically) well-drained alluvial plain subject. The alluvial plain deposits consist of predominantly grey clastics, which give way to increasingly persistent red beds and conglomerates towards the base of the Pennant Sandstone Formation above. Suppressed water table in these upper deposits was also likely linked to the first pulses of Variscan uplift, which centred on the Usk Anticline, and initiated the deposition of the closely associated conglomerates. It has also been suggested that the well-drained alluvial plain may have also been subjected to a seasonal (subhumid) tropical climate (Falcon-Lang et al., 2011). The relative importance of climatic and tectonic influence on red bed formation at this time, which is widespread across Britain and northwest Europe is debated (Besly and Turner, 1983; Besly and Fielding, 1989; Glover et al., 1993; Pagnier and van Tongeren, 1996; Pierce et al., 2005; Bertier et al., 2008).
2.2.6.3a Braided fluvial system – riparian communities

The Pennant Sandstone Formation represents the remains of large-scale braided fluvial systems that were deposited on an alluvial braid plain (Brenchley and Rawson, 2006). Coarse grained sandstones with large-scale cross bedding were laid down in these braided river channels (Figure 23 a-c). The metre scale unidirectional cross bedding in the Pennant Sandstone Formation indicate these rivers flowed from the south, likely from the uplifting Central Pangaean Mountains just beyond the south coast of Britain. Localised conglomerate horizons occur throughout the sequence. Lenticular horizons of conglomerate occur also which likely represent channel lags (Figure 23d). Sandstone casts of stems (Figure 23e) and trunk imprints (Figure 23f) are the only type of plant megafossil preserved in this depositional setting, due to the coarse nature of the sediment and high energy of the system. These sandstone cast assemblages are dominated by Calamites and Sigillaria, likely represent the flora that flourished on well drained riparian niches on the margins on the fluvial system and around the peat-forming wetlands. See Pendleton et al. (2012) for a more detailed account of these sandstone cast floras. Isolated fragments of calcified wood are also found to be locally abundant in the Pennant Sandstone Formation but these are typically located in beds with rounded reworked clasts of clay and mudstone, and are not typically found in association with the plant sandstone casts.
**2.2.6.3b Braided fluvial system – channel abandonment**

Several ‘leaf beds’ (Figure 24) have been found in the coarse fluvial Pennant Measures sandstones at Bristol (Pendleton *et al.*, 2012). These lenticular beds are usually less than a metre thick, and only a few metres wide. These beds contain blocky mudstone and/or siltstone, and may contain fairly abundant leaf and frond fossils. The sandstone above these lenticular shales often features a prominent erosive basin, with flute marks which indicate flow from the south of the coalfield. These lenticular mudstones and siltstones
were likely deposited in abandoned channels, with floral assemblages that feature one dominant pteridosperm taxon with rare *Calamites*. These parautochthonous assemblages record pteridosperm-calamitalean stands living within the active channel belt directly comparable to communities reported from similar contexts and ages elsewhere in tropical Euramerica (Bashforth *et al.*, 2010; Bashforth *et al.*, 2011).

Figure 24 – a) A leaf bed on the south bank of the River Frome at The Dingle. These lenticular beds of mudstone and/or shale occur sporadically in the Pennant Sandstone Formation b) Close up of the same leaf bed, where the flute marks on the sole of the over-riding Pennant Sandstone Formation sandstone can just be made out. These unidirectional current indicators suggest a this portion of the fluvial system flowed from the south. c) *Macroneuropteris scheuchzeri* leaf, from the Dingle lead bed. d) *Neuropteris dussarti* pinna, from Bluebell Wood Quarry.

### 2.2.6.4 Floodplains and clastic swamps

Floodplains are areas outside of the fluvial channels, beyond the river bank and levees. These flat lying areas adjacent to the fluvial system were periodically inundated by
water and fine grained sediment which breached the river channel during periods of peak discharge. Extensive floodplain facies were deposited in the Grovesend Formation, particularly (Figure 25). The Barren Red Member features red floodplain mudstones, indicating prolonged periods of enhanced drainage. Although there is an excellent palaeobotanical record of the Grovesend Formation, all these assemblages are from roof shales which predominantly reflect clastic swamps in close proximity to peat-generating environments. While no putative floodplain floral assemblages are known from the Bristol Coalfield, it can be assumed that this facies would contain broadly similar assemblages to the roof shales (clastic swamps).

Figure 25 – The Grovesend Formation (Barren Red Member), exposed in the old Ibstock Brick Pit next to the site of the old Brandy Bottom Colliery, Pucklechurch. The Barren Red Member consists of red mudstones and shales, deposited on extensive floodplains.

The origin of roof shales has been debated (Gastaldo et al., 1995), but they probably represent parautochthonous assemblages preserved during the final stages of peat mire drowning (DiMichele et al., 2007; DiMichele and Falcon-Lang, 2011) or plants that grew in clastic swamps that replaced the mires (Falcon-Lang, 2009). The roof shale assemblages reported by Pendleton et al. (2012) consistent with other studies of Middle Pennsylvanian wetlands, indicate these areas of clastic sediment attracted a much greater abundance and diversity of pteridosperms and other plants than the peat mires, perhaps reflecting input from a variety of somewhat heterogeneous sub-environments (e.g.
levees, swamps, coasts) and soil chemistries (DiMichele and Phillips, 1994; DiMichele et al., 2001; DiMichele et al., 2007; Bashforth et al., 2010; Bashforth et al., 2011).

### 2.2.6.5a Peat mires – economic scale

Peat is the partially decayed remains of plants, where anaerobic and acid conditions prevent full decay of the organic matter by inhibiting the action of bacteria and other organisms which aid decomposition. These peats formed in mires and bogs in the Carboniferous, likely in similar depositional environments to the modern age. Generally thick and laterally continuous coal seams, such as the Salridge Coal in Figure 26a, are thought to have been generated in peat mires which can be related to two modern analogues: topogenous (or planar) peat mires form where the land lies below the ground water table (ground water fed), and tend to infill the topography; ombrogenous (or domed) peat mires usually succeed topogenous mires, where peat domes up above the surrounding landscape and water saturation is maintained by high levels of rainfall (meteoric water fed). Whereas large lycopsids dominate the topgenous mires, stunted vegetation is found in ombrogenous mires due to the lower nutrient levels and absence of standing water (Greb et al., 2006). Sub-arborescent lycopsids, such as Omphalophloios (Sporangiostrobus) and Chaloneria, and their associated palynomorphs, are therefore more common at the top of thick coal seams where ombrogenous mire developed as a climax community (Phillips and DiMichele, 1994).

These autochtonous coals typically sit above a thick mudstone layer, called a seat earth, which represents the soil and sediment which the peat mire flora was anchored to. These seat earths typically contain the rooting structure of arborescent lycopsids (Stigmaria, Figure 26e) as well as finer rootlets from various other plants Figure 26d. Typically these sediments have been extensively bioturbated by the peat mire flora, and contain little or no fossilised plant material (other than roots and rootlets).
2.2.6.5b Peat mires – within braided fluvial system

Thin lenses of coal are often found in the Pennant Sandstone Formation, Figure 26b, which likely represent localised peat generating areas within the braided fluvial system. These lenses are typically only 1-2 m wide and <1 m thick with a lenticular shape, so it is possible they also represent small scale peat generating areas within abandoned channels.
3 Palynology - miospores

3.1 Materials and methods

3.1.1 Sampling and samples

See Appendix 1 for full details of all samples.

3.1.1.1 Field site sampling

The bulk of the material for the palynological part of this study was acquired from outcrop in the field area (Figure 27). The vast majority of the exposed Warwickshire Group in the Bristol coalfield are massive coarse grained fluvial sandstones. Fine-grained clastics (mudstones, shales and siltstones) and coals are very scarce in outcrop, and typically occur as thin lenticular beds less than 1 m thick and only a few metres wide. Palynomorphs are typically only found in these fine-grained clastics.
Figure 27 – Location of the two main study areas of Warwickshire Group near Bristol (divided by the South Wales Coal Measures Group exposed in the Kingswood Anticline). Locality 20 (Hursley Hill borehole) is located beyond the southern limit of the coalfield outcrop.
Figure 28- Detailed map of localities. Locality 20 (Hursley Hill borehole) is shown in Figure 27. Geology maps simplified from online 1:10000 maps on Digimap and paper copies of BGS 1:10000 series sheets ST67NE and ST68SE.
Fourteen field sites and four boreholes (Figure 28) provided material suitable for palynological investigations, providing two hundred and five samples in total, which covered the entire range of the Warwickshire Group stratigraphy (Figure 29). Of these 205 samples, 63 were of sufficiently preserved for semi-quantitative counting, and 58 were logged for presence-absence data. When a fine-grained clastic bed less than 25 cm was located, a single rock sample from an un-weathered representative central location was taken. Most of the fine-grained clastic beds were between 0.3-1 m thick, and were sampled at the top, middle and base. Two fine-grained clastic beds, each over 6 m thick, were found. In these cases the aim was to acquire 1 sample per metre, with un-weathered and finest grained areas of the bed being sampled wherever possible. Where heterogeneous regions occurred, samples were taken from these sedimentologically different areas in order to maximise potential palynomorph recovery.

Coal seams in outcrop are either only a few centimetres thick, or only a few centimetres of the full bed thickness is exposed. A representative fist-sized lump of coal was taken from outcrop where possible. In several locations where a coal seam has been historically known, only small flakes of coal was recovered from the soil by digging or from scree piles. This is not an ideal sampling method, and was only done where ex-situ coal could be matched to a named seam with a high level of certainty. One large coal seam was sampled more extensively based on slight variations in the appearance and nature of the coal seam in the accessible portions. A specimen catalogue is included in Appendix 1.
Figure 29 – Stratigraphy of the Warwickshire Group, detailing relative stratigraphical positions of field sites and borehole material.
Locality 1: Harry Stoke B; Winterbourne Formation (ST 632 782)
Although several BGS boreholes penetrate the Winterbourne Formation, only Harry Stoke B and Harry Stoke C have surviving borehole material at British Geological Survey (Keyworth). A full summary log of the boreholes are in Kellaway and Welch (1993), and a more detailed log of the lower portion of the Harry Stoke C borehole is in Falcon-Lang et al. (2011), based on original borehole log records (BGS). National Coal Board coal residues from Harry Stoke B were discovered at MB Stratigraphy Ltd (Sheffield), who kindly donated sub samples. Only 5 of the coal samples contained depth information; it was not deemed useful to reprocess other coals which had no stratigraphical information attached. 25 mudstone samples and 2 coal samples were kindly supplied from the remaining Harry Stoke B material by British Geological Survey. The Harry Stoke B borehole was drilled in 1950 at location near Hambrook, between the University of the West of England campus and Junction 1 of the M32. The Winterbourne Formation is exposed through 145 m of the borehole section. A sparse megaspore assemblage was also recovered from one coal (Pendleton and Wellman, 2012).

Locality 2: Coombe Brook; Winterbourne Formation (ST 632 748)
Several small isolated exposures of apparently in situ Winterbourne Formation mudstones are present in Coombe Brook: a small stream in a wooded area between Fishponds and Speedwell. One mudstone specimen was kindly donated by Nick Chidlaw, who collected during May 1993. As Harry Stoke B provided a continuous and measurable sequence of samples over almost the entire thickness of the Winterbourne Formation, it was not deemed necessary to obtain more samples from this locality.

Locality 3: Staple Hill Dramway; Winterbourne Formation (ST 651 756)
Patchy Winterbourne Formation mudstones are present adjacent to the eastern entrance to the long tunnel between Staple Hill and Fishponds, which carries the Dramway beneath the A4017. These dark grey mudstones outcrop on the southern bank of the Dramway cutting over a distance of around 150 m. A large spoil tip of coal intermixed
with dark mudstones was found around 150 m east of the tunnel entrance, resting directly on this southern retaining wall.

**Locality 4: Grove Cottage; Pennant Sandstone Formation, Downend Member (ST 640 772)**

Only one Downend Member siltstone lens was discovered during the course of this study. Grove Cottage is located in Frenchay, to the east of where Frenchay Bridge crosses the River Frome. Two small (<5 cm thick, ~1 m wide) lenticular coal seams occur in a disused quarry, which forms the garden behind this cottage. The sedimentology of the outcrop is typical of the Pennant Sandstone Formation with a series of channel scours with patchy channel-lag conglomerates at the bases of metre-scale cross-bedded fluvial-deposited sandstones. Lateral accretion surfaces, festoon bedding and convolute bedding are also common, and are seen at the base or near the top of the larger sandstone beds. A bright coal caps one of the lateral accretion surfaces, and a dull coal appears to be filling a small conglomerate-filled scour, forming a lenticular bed with opposing inflexes (‘S’-shaped). This small scour appears at the base of same lateral accretion surface packet as the previous coal. These thin lenticular coals likely represent short-lived and localised peat generating environments in close proximity to the braided fluvial system, possibly in a point bar-type or levee setting. Alternatively, it is possible that mats of peat were dislodged from larger mires and transported within the fluvial system, where they came to rest within this point bar-type setting. A sparse megaspore assemblage was also recovered from the dull coal (Pendleton and Wellman, 2012).

**Locality 5: Mangotsfield coals at Church Lane Colliery; Pennant Sandstone Formation, Mangotsfield Member (ST 668 763)**

Two collieries, Church Lane and Wallsend, worked the Mangotsfield seams between Staple Hill and Shortwood. The Mangotsfield coals are stratigraphically important, as they represent the division between the Downend and Mangotsfield members of the Pennant Sandstone Formation. Fragments of coal from spoil tips near the location of
Locality 6: Red Pool; Pennant Sandstone Formation, Mangotsfield Member (ST 652 791)
Large disused Mangotsfield Member quarry on the west side of Bury Hill, to the south of Winterbourne Down. This disused quarry features good exposure partially encircling the north and eastern side of the equestrian school. There are several lenticular and several thin but laterally extensive conglomeritic bands within the lower ~3.5 m of Pennant Sandstone visible in the northernmost wall. Around 3.6 m up the north quarry wall, a ~1 m metre thick siltstone bed is partially exposed. These lenses are likely related to channel lag/channel abandonment events. All samples recovered from this locality were devoid of palynomorphs.

Locality 7: 3 Frome Bank Gardens; Pennant Sandstone Formation, Mangotsfield Member (ST 652 791)
Large disused Mangotsfield Member quarry surrounding the residential properties of Frome Bank Gardens, at the south western limit of Winterbourne Down. Along the north western exposed quarry face of number 3 Frome Bank Gardens a 6.5 m thick siltstone bed is exposed. The exposure starts in the overgrown portion at the west of the quarry face, and occupies nearly the full length of the garden. The unit is represented by alternating centimetre-scale beds of blocky and laminated grey siltstones. This siltstone bed likely represents and abandoned channel, with dimensions greatly exceeding the scale of this outcrop.

Locality 8: Winterbourne Down railway cutting; Pennant Sandstone Formation, Mangotsfield Member (ST 651 798)
SSSI site and type section for the Mangotsfield Member. This site was assessed during the early 1980s as part of the Geological Conservation Review (Cleal and Thomas, 1996) and designated as a SSSI in 1990. Around 75 m of cross bedded Pennant sandstone is well exposed in the London-Cardiff railway cutting which runs east-to-west
through Winterbourne Down. A 3.5 m siltstone bed occurs between Chainage Marks 110.9 and 110.11 on the south side of the cutting. On the northern side of the cutting the siltstone bed thins and it only 0.5 m thick. This outcrop is also mentioned in Kellaway and Welch (1993). Like the large siltstone lens at Frome Bank Gardens, this likely represents an infilled abandoned channel.

Locality 9: The Dingle leaf beds; Pennant Sandstone Formation, Mangotsfield Member (ST 653 794)
Numerous quarries litter the Mangotsfield Member of the southern bank of the Frome in the south east of Winterbourne Down. An unusually well exposed quarry lies ~130 m to the east of the Frome Way footbridge, just to the south of The Dingle. This horizon lies ~160 – 200 m above the Mangotsfield coals, roughly in the middle Mangotsfield Member. At the base of the quarry is a lenticular siltstone band, which infills the undulating topography of the Pennant Sandstone below. The Pennant Sandstone above has an erosive base, and features flute marks at its base which indicate a palaeocurrent flow roughly towards the north-west. The siltstone bed has a maximum thickness of ~75 cm, although this is very variable due to the undulating upper and lower surfaces. The bedding at the edge of the siltstone lens truncates and converges against the Pennant Sandstone below. The bed geometry suggests that the siltstone is likely infilling an old channel. Another siltstone lens appears at a stratigraphically similar position on both sides of the quarry.

The siltstone varies in colour from grey, purple, red or brown. Sporadic plant fossils are found in the siltstone bed, mostly in the form of isolated or damaged pinnules of *Macroneuropteris* (Pendleton et al., 2012). This locality likely represents an abandoned channel.

Locality 10: 65 The Dingle; Pennant Sandstone Formation, Mangotsfield Member (ST 656 794)
A ~0.75 m thick coal appears at the top of an old Mangotsfield Member quarry, to the rear number 65 on the Dingle. The Dingle is a narrow residential road in the south east
of Winterbourne Down, lying on the north bank of the River Frome. Stratigraphically this locality is just above the middle of the Mangotsfield Member, and features quite high levels of clastics (fine sand and silt) throughout the coal. At the western side of the outcrop the coal is split into two leaves by a coarse sandstone bed. This sandstone bed has a maximum thickness of 20 cm and thins and dips to meet the sandstone at the base of the coal seam towards the east of the 4 m wide coal seam. Exceptionally well preserved and abundant miospores, and a stratigraphically important and ecologically interesting megaspore assemblage were also recovered from this locality (Pendleton and Wellman, 2012).

The coal seam samples split into 1 mm thick sheets when they are dried, with plant debris concentrated on these surfaces. From close inspection of the samples, it appears that the plant debris layers also have higher levels of clastics. Given the regularity of these layers throughout the 0.75 m thick coal, it is likely this reflected a climatic or seasonally-induced cyclicity. The regularity of these couplets is attributed to seasonal cyclicity in hydrology due to their consistently thin nature. Periods of forest fire would also result in periods of increased run off, due to vegetation loss, and therefore could contribute to the plant debris and clastic-rich layers between the more coaly layers.

There are several lines of evidence against a fire-driven cyclicity for these couplets, most notable of which is the apparent lack of charcoal fragments within the palynological samples and the un-charred nature of the palynomorphs. Charcoalification during forest fires often leads to low compression of palynomorphs (Scott et al., 2010), whereas all the miospores and megaspores from this locality are highly compressed. The thin but consistent thickness of the couplets throughout the coal would also require fires to occur on a regular, possibly annual, time scale in the surrounding area.

Locality 11: Huckford Quarry Nature Reserve; Pennant Sandstone Formation, Mangotsfield Member (ST 656 799)
Designated as a Local Nature Reserve in 1993, this long disused quarry lies to the south west of the Winterbourne Viaduct on the west bank of the River Frome. Cross bedded
Pennant Sandstone of the Mangotsfield Member was quarried here 65 years ago, and used in construction of the railway line as well as local buildings.

Three siltstone beds occur in the coarse sandstone; to the south (25 cm thick), north (15 cm thick) and north west (25 cm thick) in stratigraphically ascending order. The three siltstone beds are separated by no more than 5-10 m in vertical distance.

**Locality 12: Farrington Member coals and shales; Grovesend Formation, Farrington Member**

These seams range from 0.5-1.5 m in thickness, and extend across 60-70 m of stratigraphy. These coals represent widespread and well-developed mire communities.

**Locality 12a: Coalpit Heath Colliery (ST 697 815)**

Coalpit Heath Colliery is general considered synonymous with Frog Lane Pit, although a second and much older pit occurs to the north east called Mayshill Pit. The latter is reported to have been connected to Frog Lane Pit, and used as a ventilation shaft (Kellaway and Welch, 1993). It is likely all material labelled as being sourced from “Coalpit Heath Colliery” in museum collections refers to Frog Lane Pit specifically. The colliery was abandoned in the 1950s as the seams became exhausted. Reports indicate that the thickness of the Farrington Member here is around 53 m; taking the distance between the Hard and High Vein at Frog Lane Colliery.

Coalpit Heath Colliery roof shale sub-samples were obtained from megafloral specimens from Bristol City Museum and Art Gallery and the Moore Collection at the University of Bristol. Megasporeres were recovered from a specimen originally collected by Crookall (Crookall, 1925a; Crookall, 1925b) and are discussed in (Pendleton and Wellman, 2012).

**Locality 12b: High Coal at Serridge Adit (ST 668 796)**

The High Coal of Coalpit Heath was accessed via a drainage adit locally referred to as the Serridge Adit, beneath the Kendleshire golf course to the south-west of Frampton Cotterell. This adit drains westward and enters the River Frome south of Huckford.
Quarry. At this partially flooded exposure the High Coal, the lowest of the Farrington Member coals in this area, was measured as 1.7 m thick. The roof shale at this locality is red-stained, almost certainly of secondary origin. The High Coal of Coalpit Heath represents a merging of two Parkfield coals: the Hollybush and Great Coals. At this exposure, the High Coal clearly consists of 1.1 m of a more fissile coal that easily breaks into <5 mm angular to sub-angular fragments, with 60 cm of more massive and hard coal above with numerous brown and red streaks (almost certainly produced by oxidation of pyrite).

**Locality 12c: High Coal at Old Vicarage (ST 673 807)**
The same coal seam was also accessed 1.25 km to the northeast, where it was briefly exposed during the summer of 2011 during building work in the basement of the Old Vicarage in Frampton Cotterell. Here 50 cm of a soft black coal was exposed, which contained relatively high levels of pyrite compared to other Bristol coals investigated. The visual appearance of the coal combined with high pyrite levels are similar to the coal exposed in the Serridge Adit, suggesting that the coal represents the upper portion of the High Coal and is equivalent to the Hollybush Coal of Parkfield.

**Locality 12d: Hard Coal at Westerleigh railway cutting (ST 696 796)**
The Hard Coal, the uppermost coal of the Farrington Member, can be seen to cross a railway line to the south of Westerleigh. This line represents a semi-disused spur departing from the main Bristol-Birmingham line, which serves a CPL Petroleum Ltd. depot to the south. This spur was original part of the Dramway which connected Coalpit Heath Colliery in the north to Parkfield in the south.

At around Chainage 56, ~160 m south of the bridge crossing the railway at Westerleigh, a small talus slope of brown mudstone was sampled. As the railway cutting in this area is totally overgrown, it was not possible to locate in-situ material but it does not seem likely that this freshly fallen material could be sourced from outside the locality.
Roughly 180 m south of the bridge, a sample of mineral rich coal was recovered from a lenticular lens. The lens is estimated to be around 3 m wide and around 1 m thick; almost certainly representing an abandoned channel based on the visible geometry. The high mineral content of this coal suggests a high level of clastic input into this peat-generating area. In this area Pennant-type sandstone can be seen on either side of the lens.

In this location no outcrop of the Hard Coal was found, however, between Chainage 58 and 59 the railway cutting embankments become both lower and reduced in angle. A large amount of ex situ dark mudstone and coal in overgrown talus slopes is visible. Several lumps of coal were recovered from this area, which probably represent fragments of the Hard Vein.

Locality 12e: Parkfield Colliery (ST 690 777)
Parkfield Colliery to the north west of Shortwood worked the four economical coals of the Farrington Formation in this area between 1853 and 1936. The colliery closed in 1936 due to substantial water incursion. Workings from this colliery extended to the west and north-west, following the coals as they dip towards the centre of the basin. Here the Farrington Formation is represented by the Great, Hollybush, Top and Hard coals. Parkfield Colliery roof shale sub-samples were obtained from megafloral specimens from Bristol City Museum and Art Gallery and the Moore Collection at the University of Bristol.

Locality 12f: A4174 road cutting at Shortwood bridge (ST 674 762)
In the past the Parkfield coal seams were exposed in a now disused railway cutting that is now part of the Dramway cycle path. Original measurements along this section were made by Green and Kellaway in 1948 and reported in Kellaway & Welch (1993). These were all made using the northern side of the bridge, which now carries the B4465 over the A4174 at Shortwood, as a marker. Using these measurements, it was possible to measure out the section and locate the four Farrington Member coals: the Great, Hollybush, Top and Hard coals. Fragments of coal and shale were found in localised
landslippages at the reported locations of the Great, Hollybush and Top Coals. The outcrop of the Hard Coal was the only in situ coal found, but more recently even this seam has been completely obscured by overgrowth. Several siltstone samples were obtained from small sections, exposed by digging, just below and above the locality of the Hard Vein. No trace was found of the two Rag Coals and the Stinking Coal, which occur stratigraphically above the four major seams.

**Locality 12g: Shortwood brickpit (ST 682 768)**
A specimen of an unmapped coal from an portion of the A4174 near Stonehill was kindly donated by Nick Chidlaw. This coal was exposed ca. April 1993, and is estimated to be several metres above the Buff Coal.

**Locality 13: Golden Valley, Painters Pit (ST 690 711)**
Several pits worked the basal Pennant Sandstone Formation coal seems in the Golden Valley area, near Bitton. This outcrop has become isolated from the main coalfield outcrop due to subsequent tectonics and sediment deposition. Several mudstone and coal fragments were obtained from minor spoil tips surrounding a ventilation chimney, which served Painter’s Pit.

**Locality 14: A4174 at Stonehill (ST 646 709)**
During the widening of the A4174 ca. 1993, Nick Chidlaw (local geologist) collected several coal seams which were exposed between Stonehill and the A4174 terminus on the southern bank of the River Avon. One of these came from a coal exposed in bank cuttings, where a bridge now carries the A431 over the A4174. This 0.5 m thick coal, and surrounding clastics, was noted as being sheared and lying several metres above the Buff Coal. From photographs taken at the time this seam was exposed, it also appears to have frequently clastic rich layers (mainly at the upper and lower limits of the coal).

**Locality 15+16: Bickley Wood (ST 643 706 and ST 641 704)**
A large disused quarry occupies an area between Hanham Green and Hanham Abbots, on the northern bank of the River Avon, to the west of where the A4174 crosses the
river. The Elm Tree Pub, on Abbots Road, is located at the northern edge of the wooded area, which continues south to the bank of the river. This 9.5 hectare wood was notified as a SSSI in 1988. This site has been previously described by Cleal and Thomas (1996) and Moore and Trueman (1937), and was also collected by Fry (ca. 1920s). Pendleton *et al.*, (2012) review the megafloral collections from this locality.

Two siltstone lenses were investigated as part of this study. The first is located ~290 m south of the Elm Tree pub; a small stream terminates in a boggy ~15 m broad depression, with the siltstone lens outcropping in the walls on the west and south of clearing. It is likely that these exposures represent the same large siltstone lens, suggesting that this lens is at least 15 m wide. The second siltstone lens occurs ~165 m to the south west, at the base of an east/north east facing wall. This lens is ~1 m thick and at least 3 m wide. The second locality contains the megafloral assemblage Both localities are grey siltstone lens within a coarse-grained sandstone channel complex, likely representing areas of channel abandonment.

**Locality 17: Salridge Vein near Keynsham (ST 642 701)**

The Salridge Coal is exposed at the top of a north-facing quarry wall, on the western side of the A4174 road as it crosses the River Avon to the north west of Keynsham. The Great Western Railway runs just the south of the Salridge Coal for its entire outcrop length on the geological map. This locality likely represents a similar horizon to the “Chandos Lodge” site of Moore and Trueman (1937). The quarry features Pennant-type channel sandstone bodies containing three siltstone lenses; the latter likely representing periods of channel abandonment. This is overlain by 1.75 m of alternating, thinly bedded (0.2 – 0.3 m) mudstone and coal, developed on top of a 7.3 m thick seat earth. The sequence is capped by a 0.85 m thick coal with a pale beige/ light brown roof; this likely represents the Salridge Coal proper. The beige colour of the roof rock does not appear to be the result of modern weathering, as this uniform colour was seen in fresh excavations of ~1 m into the outcrop made during two abseil runs. A substantial talus slope beneath the coal also yielded a moderately well-preserved megafloral assemblage, sourced from the beige Salridge Coal roof shale (Pendleton *et al.*, 2012)
Locality 18+19 – Brislington School 3 and 1 boreholes (ST 629 696)

The Brislington School 1-3 boreholes penetrated around 35 m of Farrington Member between Brislington and Keynsham, on the southern bank of the Avon. These boreholes provide the only material from the Farrington Member from the southern limb of the Kingswood Anticline, and therefore provide vital information about the stratigraphy in this area. A log of the Farrington Member, produced from the Brislington boreholes, appears in Price et al., (1969) which enabled more accurate stratigraphical placement of the Brislington 1 and 3 boreholes; above and under the Trench Coal, respectively.

Locality 20 - Hursley Hill (ST 618 657)

The Hursley Hill borehole was sunk for the National Coal Board in 1951, 3.3 km south south-east of the southern limit of the Bristol Coalfield outcrop. This borehole penetrated 730 m of Grovesend Formation, including, from base to top, the Barren Red, Radstock, and Publow members. This borehole provides the only material from the Radstock and Publow members, which do not appear within the stratigraphy of the Bristol Coalfield outcrop. In this borehole the Radstock Member and Publow Member are 275 m and 305 m thick, respectively (580 m in total). The megafloras of the Hursley Hill Borehole were studied in the 1960s and 1970s by Robert Wagner, who did not publish this work at the time, and are detailed in (Pendleton et al., 2012).

Twenty four Hursley Hill slides were processed by Maeve Hegarty, as part of an MSc at University College Cork (Eire) with Dr Kenneth Higgs, in a predominantly palynofacies-based study. Two of these slides were deemed suitable for semi-quantitative counts, and four were used for presence-absence logging. An additional specimen, a coaly shale from near the top of the Radstock Member, was processed and counted semi-quantitatively for this study. This specimen also yielded megaspores, as reported by Pendleton and Wellman (2012).
3.1.1.2 British Geological Survey borehole cores

All the Bristol borehole cores are now stored at BGS Keyworth. Most of the boreholes referred to in Kellaway and Welch (1993) have no surviving lithological material. Material from several useful boreholes still remain, although most of the core material has not stored for space reasons. Samples from various depths are available along with original logs and borehole drilling information. The most complete Winterbourne Formation borehole core available is from Harry Stoke B borehole, from which 25 mudstones and 2 coals were sampled. In this case, samples were taken from the remaining borehole material with increased frequency at the top and bottom of the cored Winterbourne Formation. As one of the aims of this study is to date the age ranges of the units, this method was deemed the most efficient. Material was also taken from Brislington 1 and 3, and Hursley Hill boreholes which provide material from Grovesend Formation of the southern limb of the Kingswood Anticline.

It is British Geological Survey policy that only 1/3 of the material can be taken from each sample. As some of the samples were already very small, this further reduced the depths from which useful amounts of material could be obtained. Where other samples from similar depths were available, these were preferentially chosen in order to obtain a sample with a weight would provide the preferred 20g for clastic palynological analysis. Even with being very flexible with sample intervals, a preparation of less than 10g of rock had to be done on several samples.

3.1.1.3 National Coal Board residues

Several thousand of the National Coal Board (NCB) vials are now stored at MB Stratigraphy Ltd in Sheffield. Although most of the material is not applicable, five coal residues from Harry Stoke B exist in this collection. Most of the vials only have an NCB sample number and borehole name. Where depths were recorded, or could be found from NCB literature sourced from BGS, a sub-sample of these residues were taken. Original workers likely didn’t use potassium hydroxide to remove the oxidation
productions produced by macerating in Schulze solution, and so the samples were treated with combined ultrasonic and potassium hydroxide treatment. In all cases this removed much of the palynodebris, resulting in a much cleaner preparation.

3.1.1.4 Sub-samples from museum collections

Numerous plant megafossils were collected while the Coalpit Heath and Parkfield collieries were operational. These are now housed in the Bristol Museum, University of Bristol, British Geological Survey in Keyworth and the Natural History Museum in London. Where the megafossil had a reasonable amount of rock attached, small pieces were carefully removed to be palynologically processed.

Only roof shale specimens, which had seam and colliery information recorded were used. Specimens without stratigraphical information were not used for palynology, as several coal seams were usually worked in each colliery contemporaneously.

3.1.2 Preparation for palynological investigation

3.1.2.1 Mudstones and shales

Samples were taken from the rock store to the preparation room, where they were crushed to pea sized clasts using a cast iron mortar and pestle. Care was taken to thoroughly wash and dry samples before crushing to remove any modern pollen, oils and other contamination. The mortar and pestle were also cleaned between each sample use to prevent cross contamination between samples.

20g of crushed sample was added to a clean polythene jar with some water to prevent any dust mobilization which could contaminate the samples during the processing stages. The polythene jar was then sealed and marked with the sample number of each specimen. All sample information was entered into an Excel spreadsheet.
In the processing room, 20ml of 35% hydrochloric acid was added to each sample to dissolve any diagenetic carbonates. After settling for 24 hours as much hydrochloric acid and water was decanted off as possible without losing sediment. This was repeated 4 times, in order to remove as many of the freed calcium ions as possible. Calcium ions combine with hydrofluoric acid to produce calcium fluoride, and insoluble ‘jelly-like’ precipitate. Calcium fluoride can impede sieving by causing the residue to clump together, as well as causing potential loss of palynomorphs during the heavy liquid separation stages of processing.

35ml of 40% hydrofluoric acid was then added, with 1% hydrochloric acid, which was left to dissolve the silicates over a period of days. The sample was agitated twice a day to ensure maximum digestion of the rock occurred. This was repeated until samples were fully macerated, which usually took about a week. Samples where maceration was slow or incomplete after a week underwent a second hydrofluoric acid treatment. After digestion, the samples were decanted and refilled with water and left to settle. This was repeated for each sample until the pH was neutral when tested with litmus paper (around 8-12 decants).

Once neutral, the sample was sieved with a 20 μm sieve with plenty of warm water. The sieve was disassembled and cleaned between each preparation stage to avoid contamination. A small, well mixed, volume was then sampled with a pipette and put onto a slide for inspection. A 180 μm top sieve was taken if there was a high amount of coarse material that could hide palynomorphs. Minerals and precipitates were removed (see 3.1.2.3 Removal of minerals and calcium fluoride) before slide mounting (see 3.1.2.4 Slide mounting and residue storage). See Figure 30 for a simplified flow chart of the key steps used in the palynological preparations of clastic material.
Figure 30 – A flow chart illustrating the generalised process of palynologically processing a clastic sample to produce light microscope slides.
Figure 31 - A flow chart illustrating the generalised process of palynologically processing a coal sample to produce light microscope slides.
3.1.2.2 Coals

A large representative lump of coal was washed prior to preparation to remove any surface contamination. Any large pyrite fragments were also removed. The lump was crushed in a mortar and pestle to roughly 1 cm clasts. See Figure 31 for a simplified flow chart of the key steps used in the palynological preparations of coal material.

3.1.2.2.1 Miospore preparation (traditional method)

A random sample of the 1 cm clasts were taken, and further crushed to 500 µm in an agate mortar and pestle. A heaped spatula of this sub-500 µm powder was then added to a beaker, and oxidised for 20 minutes in 99-100% nitric acid. After oxidation, the sample was washed to neutral in a 20 µm sieve. The residue was transferred to a beaker with 2% potassium hydroxide (with the volume of potassium hydroxide exceeding that of the residue and water). This beaker was then placed in an ultrasonic bath for 2 minutes. The ultrasonic aids the breakdown of oxidation components by the potassium hydroxide. The sample was then washed again in a 20 µm sieve, and then inspected for mineral and calcium fluoride. If mineral and/or calcium fluoride were present in the residue, these were removed before slide mounting.

3.1.2.2.2a Megaspore preparation

A random sample of the 1 cm clasts were taken and placed into a beaker. The coal clasts were then oxidised for 20 minutes using Schulze solution; concentrated (65%) nitric acid supersaturated with potassium chlorate. After oxidation was complete, the oxidation products were removed using potassium hydroxide in combination with ultrasonics.

The megaspores were winnowed out from the residue by repeatedly filling the beaker with water and agitating the residue into the water column. The heaviest material was left to settle out for a few seconds, and the suspended material was poured into an 180
µm sieve. This was repeated several times until very little light organic matter remained in the water column for more than a few seconds upon agitation. The >180 µm fraction was stored in a vial, and then picked for megaspores.

3.1.2.2.2b Megaspore picking

Coal samples which yielded abundant and well-preserved megaspores were placed into a Petri dish and viewed under a binocular microscope. Megaspores were then extracted from the residue using a thinned-out paint brush and several pipettes of varying diameters. The megaspores became very brittle if allowed to dry out, so they were picked straight out of water and put into a storage vial of water. Megaspores were not analyses from set volumes of coal, and all megaspores liberated from the coal clasts during oxidation were examined and counted. As such, quantitative comparisons between assemblages derived from different samples cannot be accurately made. However, megaspore dominance and diversity patterns between samples will still reflect original ecological patterns and are therefore still highly useful (specifically, when considered alongside miospore assemblages from the same sample). The megaspores were then ready for light and scanning electron microscopy.

3.1.2.2.3 Combined megaspore and miospore preparation

Standard miospore preparations were first done on ten of the coals collected from the field. Interestingly, eight of these appeared barren or were of very low palynomorph abundance with very poor preservation. The same ten coals were then prepared using standard megaspore preparation techniques, with a slight difference. Instead of discarding the <180 µm fraction, this was retained and sieved at 20 µm to form a miospore preparation. With this method, all ten coals produced abundant and moderate to well-preserved palynomorphs. After this initial finding, performing a separate miospore preparation on subsequent coals was abandoned in favour of taking the 20-180 µm fraction from the megaspore preparation.
It is well known that palynomorph abundance in coal varies greatly, even on a millimetre scale through a coal seam. It may be the case that the layers with abundant palynomorphs are rare and comparatively widely spaced in the Bristol coals, and the small amount of sub-500 µm fraction sampled using a standard miospore preparation doesn’t allow these abundant horizons to be sampled efficiently. Using the revised combined miospore and megaspore preparation, a much greater amount of raw coal is sampled which increased the probability of sampling these layers of coal where abundance and preservation of palynomorphs is greatest (Figure 32).

Figure 32- Collection of photomicrographs of representative fields of view of 3 samples. An example of the field of view after a standard miospore preparation is compared to that of the fine fraction (20-180 µm) from a megaspore preparation. In all three cases some increase in the abundance and/or quality of palynomorphs is seen with the megaspore preparation.

### 3.1.2.3 Removal of minerals and calcium fluoride

Even after acid digestions, small fragments of minerals can persist in the residues. If mineral fragments were visible in the residue after maceration, then heavy liquid separation was used. 5ml of the neutral residue was pipetted off into the centrifuge tubes (any more water than this would affect the density of the heavy liquid, and may cause...
loss of palynomorphs due to sinking). The tube was topped up to 45ml with zinc chloride solution, with a specific gravity of 1.95. The tubes (in batches of 4) were spun at 2000rpm for 10 minutes in the centrifuge. After spinning, palynomorphs and organic matter (low density) floated as a black layer at the top, with minerals and other dense material forming a pellet at the bottom of the tube. The top material was carefully poured off, and the waste pellet disposed of.

Calcium fluoride is a common precipitate formed when free calcium ions are present in the sample when hydrofluoric acid is added. It is usually apparent under the light microscope as a translucent grey ‘jelly-like’ substance with minute dark flecks. If calcium fluoride precipitate forms discrete lumps and does not entrap palynomorphs, then the calcium fluoride would sink with the rest of the mineral fraction during heavy liquid separation. In these cases, the mineral will be removed in the process of a normal preparation.

If the calcium fluoride was seen to be attached to, or to entrap palynomorphs, the sample could not simply be centrifuged to remove it. Calcium fluoride is much denser than the organic material, and would cause the palynomorphs to sink during heavy liquid separation. This would cause loss of palynomorphs and bias the samples. In these cases the sample was boiled in 35% hydrochloric acid for a minute to dissolve this mineral and free the palynomorphs. After neutralisation, the residue can be centrifuged as normal.

### 3.1.2.4 Slide mounting and residue storage

The residue was then mixed with 1% PVA (polyvinyl alcohol) to emulsify the organic matter, and ensure palynomorphs are evenly spread and do not stick together. This was then strewn onto a 22x32 mm cover slip in an even layer going all the way to the edges. This was left on a warmplate for around 45-60 minutes, to allow the PVA to evaporate off and stick the distributed spores onto a cover slip. The cover slip with attached palynomorphs was then attached to a glass slide with Petroxy 154 mounting resin, and
left to cure on a hotplate at 120°C for 30-40 minutes to cure. This resin does not deteriorate much with age, and has a refractive index of 1.54 which is close to that of glass. Three slides were taken initially for each sample, or less slides for less productive samples, and clearly labelled with the University of Sheffield style numbering system of year, initials and sample number. An extra number was added for individual slide identification to aid later work.

All vials which had residue remaining after slide mounting were acidified using a few drops of hydrochloric acid. This inhibits mould and bacterial degradation of the residues in case further material is required.

Repository information for each sample is included in Appendix 1.

### 3.1.3 Light microscope analysis and image capture

#### 3.1.3.1 Miospore slides

Most of the analysis of miospore slides from coals and clastics was done using a standard light microscope (Olympus BH-2). The taxonomic part of the thesis was constructed from observations and measurements done with the Olympus BH-2. Photographs were taken with a Lumenera Infinity 5 megapixel camera attached to a Meiji MT500 series binocular biological microscope. Lumenera Infinity Analyze software package was used to capture the images, and Adobe Photoshop CS5 was used for fine adjustments and post-processing of the files. Lumenera Infinity Analyze is capable of stacking images; creating a single in focus image from several photographs at different focal depths. This was used on many of the photographs to produce representative images.
3.1.3.2 Megaspores

After megaspores were picked from a sample and placed in a vial of water, they were pipetted out onto a slide in a droplet of water. Placing a cover slip over the megaspore and water droplet was found to improve the optics on the microscope. The megaspores were photographed, described and identified in this state using the equipment mentioned in the previous section. The same spores were then prepared for scanning electron microscopy.

3.1.4 Scanning electron microscope (SEM) analysis

3.1.4.1 Equipment

All SEM work was carried out using the Phillips XL-20 set-up, housed in the Department of Biomedical Science at the University of Sheffield. SEM stubs were coated with gold using a sputter coater. This produces a high topographic contrast and resolution for microphotography. The SEM beam was set to 20kV for all work in this study.

3.1.4.2 Miospore strew mounts

Samples with the most abundant and well preserved miospores were identified using a light microscope. Of these samples, SEM stubs were prepared where residue or sample was still available. A sample of residue was spread onto a circular class cover slip. This was inspected under the microscope to ensure the specimens were well spread and that there abundant enough to warrant expensive SEM analysis.

Cover slips that were deemed suitable were then fixed to an SEM stub using Araldite epoxy resin. SEM images were taken of miospores, and these were matched to species found in the same samples during the light microscope analysis. Due to the expensive nature of SEM work, very few miospores were imaged under SEM for this study.
3.1.4.3 Megaspor es

Double-sided circular adhesive tabs were placed on the top of SEM stubs as these provide a better background for photographing megaspores than the glass cover slips used for the miospore strew mounts. Megaspores, after being photographed with the light microscope set up, were picked off the microscope slide with a moistened thinned-out paint brush or pipette. These were then carefully placed onto the adhesive tab onto the SEM stub.

3.1.5 Data collection and analysis

3.1.5.1 Logging miospores (semi-quantitative counts)

All available slides of non-barren samples were logged, and the palynomorph species present were recorded in an Excel spreadsheet. With this taxa list, random counts of 200 palynomorphs were made to form the basis of the semi-quantitative data that would be used in identifying Biozones and vegetational assemblages. In poorly preserved or low-yielding samples, only presence/absence data were recorded so as not to skew the semi-quantitative data set. In poorly preserved assemblages only presence-absence data were recorded; in these cases any quantitative counts would be skewed by preservational bias, as the more fragile palynomorphs are typically absent, for example.

3.1.5.2 Biostratigraphy

A high proportion of clastic field samples contained only poorly preserved or a low abundance of palynomorphs, and so most of the biostratigraphic inferences on the Bristol Coalfield were on the basis of first and last occurrences of taxa. General observations on increases or decreases in abundance of stratigraphically important taxa will be included, but as many of the field samples were not deemed suitable for palynological counts detailed species abundance curves have not been constructed alongside the biostratigraphic charts. Biostratigraphic charts were constructed from a
species presence-absence matrix of all the available samples. This matrix was imported into the biostratigraphic software package StrataBugs.

3.1.5.3 Vegetation assemblage reconstruction

3.1.5.3.1 Relating palynological and vegetation assemblages

For decades, palaeobotanists and palynologists have been extracting palynomorphs from in-situ reproductive organs of fossil plants. Much of this work is catalogued in publications such as Balme (1995) and Traverse (2008); and a spate of publications based on more recent work are beginning to emerge (Bek et al., 2009a; Bek et al., 2009b; Bek et al., 2009c; Bek and Libertín, 2010). These records provide a way to assign palynomorphs, particularly at a generic level, to a broad parent plant group which produced them.

Several plant groups are typically used in this type of vegetational reconstruction from palynological counts, which represent much of the botanical and ecological diversity of the coal measures flora (Dimitrova et al., 2005; Dimitrova and Cleal, 2007; Dimitrova et al., 2009; Dimitrova et al., 2010; Jasper et al., 2010). Using this literature, each palynomorph genus was assigned a parent plant group affinity. For problematic genera which have been found in-situ in several differing plant groups, such as Punctatisporites, affinity was listed as “unknown” for the purposes of this study. Generic counts, along with parent plant affinities used in this study, are included in Appendix 6 and Appendix 7.

Palynological assemblages, even those based on quantitative data, should never be used as a direct proxy for absolute proportions of plant groups. Several caveats must always be kept in mind when interpreting vegetational patterns from palynoflora;

a) Miospore production of different plant group was also likely widely different, for
example it is likely that lycopsids would be overrepresented in palynological assemblages due to the vast amounts of miospores produced by this group (DiMichele and Phillips, 1994).

b) Miospore ornamentation, which can affect species or rarely genus classification, can also alter with maturity (Pšenička et al., 2005). Typically this is minor and will have little effect on the broad-scale groupings of plants used in this study. For example, immature *Punctatosporites* lack ornamentation and would therefore be included in *Laevigatosporites*; both of these genera are attributed to tree ferns, however

c) There is also a substantial taphonomic bias towards more robust miospores, whereas thin-walled forms such as *Calamospora* are less likely to be preserved in some depositional settings. This was partially circumvented by only making counts in samples which visually appeared to contain well-preserved assemblages.

d) Transportability of palynomorphs also plays an important factor. Saccate pollen, and possible pseudosaccate miospores, may be transported vast distances by both water and wind vectors. This gives these groups of palynomorphs a much greater dispensability.

**3.1.5.3.2 PAST: PAlaeontological STatistics**

For the purposes of this study, generic counts of palynomorphs were used from productive samples. A generic count vs. sample number matrix was constructed for applicable samples. This matrix was imported into the palaeontological statistical analysis software package PAST, which is freely available online (Hammer et al., 2001). Only Harry Stoke B was selected for seriation/cluster analysis/DCA, allowing detailed study of how the vegetational assemblages varied during deposition of the Winterbourne Formation within a small geographical area. These types of statistical
analysis, specifically DCA, work to highlight ecological gradients. Therefore, these analytical methods were not deemed appropriate for the geographically scattered and lithologically varied nature of the field outcrop samples. The other borehole cores, Brislington School 1 and 3 and Hursely Hill, did not feature enough samples to warrant analysis via cluster analysis/DCA.

The palynological assemblages defined by these analyses were then described in terms of the vegetational assemblage that they represent. These vegetational assemblages were interpreted in conjunction with published models of coal measure flora ecology; such as Phillips and DiMichele (1994), Greb (2006) and many others.

Seriation and cluster analysis
One method that was used to highlight samples with similar palynological assemblages was cluster analysis, using the unconstrained cluster analysis algorithm. Similar dendrograms were obtained using the Pearson’s correlation (Figure 38a), Bray-Curtis (Figure 38b), cosine (Figure 38c) and Euclidean (Figure 38d) similarity measures. Samples with similar generic compositions diverge nearer the top of the y-axis (shallower), whereas samples with very different generic compositions diverge nearer the base of the y-axis (deeper). As the order of the samples in the data matrix can affect the position of the nodes on the dendrogram, the data set was standardised using the order generated by unconstrained seriation analysis (Cleal, 2008a; Cleal, 2008b).

Unconstrained seriation is a graphical technique where presences are concentrated along the diagonal. Cluster analysis was useful in highlighting discontinuities in the data, which were useful in beginning to classify the samples into differing palynological assemblages. For this study, the correlation coefficient with an unconstrained paired group algorithm was used. Due to the complex nature of the extinct ecosystem, specifically the gradational nature of the ecosystems and their influencing variables, this basic type of analysis was used in tandem with ordination analysis.
Detrended Correspondence Analysis (DCA)

Detrended Correspondence Analysis (DCA) is a form of multivariate ordination analysis which is used extensively in modern ecological studies, where gradients exist in the data. Recently, this ordination analysis has been applied to palaeobotanical (Cleal, 2008a; Cleal, 2008b) as well as similar palynological (Dimitrova and Cleal, 2007; Jasper et al., 2010) studies. This method of data analysis arranges data along linear axes which account for the most of variation between the data points; which can be interpreted to reflect the ecological gradients which were the most important in the ecosystem (such as drainage, topography, substrate type etc). The first axis therefore represents the majority of the variation in the data, with the second axis accounting for most of the rest of the variation in the data. The third axis was also plotted for completeness, but most of the data variation is accounted for in the axis 1-axis 2 plot. The end result is a plot where samples with similar generic compositions cluster together. The basic palynological assemblages from the cluster analysis were then highlighted, and their boundaries reinterpreted in gradational space.

It is noted that DCA can distort the relative distances between data points (i.e Bush and Brame (2010), but does not distort relative arrangement and ordering of the points within the plot. For this study, it is the relative arrangement of data points and which palynomorph genera lay at the extremes of the data axes which are of interest, therefore the use of DCA is still deemed valid.

Species diversity and origination/extinction rates

Species diversity plots were also made for the Coalpit Heath stratigraphy. As well as total species diversity, two other plots are available in PAST. These allow the comparison of species origination and species extinction rates, which are vital to understanding the changes in total species diversity.

Extinction and origination curves where produced for the Coalpit Heath Basin; the southern limb of the Kingswood Anticline was deemed to contain too few data points to produce meaningful results. These curves plot the number of first taxa occurrences
(origination curve) and last taxa occurrences (extinction curve), which can be outputted by PAST as part of the Diversity Curve calculations. Extinction-origination curves were constructed for coal and clastic samples separately, in order to better understand any facies controls on the patterns observed. A curve was also produced for all specimens, both coals and clastics.

A species presence–absence matrix by locality was used to plot these curves. Where multiple samples were taken from a single locality, the species lists were merged to create a unified entry for the locality within the presence-absence matrix. Coals and clastics were, however, kept as separate entries for each locality. Uncertain identifications, spp. entries and reworked taxa were omitted from the matrix. Harry Stoke B data were assembled into 10 m bins for plotting.

A null hypothesis model (Olszewski and Patzkowsky, 2001) was included with each curve, which assumes a constant/uniform turnover (time-homogenous model). This was calculated by simply dividing the total number of first or last occurrences over the entire stratigraphy by the total number of occurrences, as below;

\[
null \ reference \ model \ (p) = \frac{total \ number \ of \ first \ or \ last \ occurrences}{total \ number \ of \ occurrences}
\]

This figure is the expected proportion of first or last appearances under a model of constant background turnover (p), which is converted to a raw number by multiplying by the total number of taxa.;

\[
null \ reference \ model \ (raw \ number) = p \times t
\]

\[
where \ t = total \ number \ of \ taxa
\]

This number is included as a vertical line on the curves. Binomial confidence intervals (95%) can be calculated for this null model using the following formula;
\[ 95\% \text{ bionomial confidence interval (proportional)} = 1.96 \times \sqrt{\frac{p(1-p)}{n}} \]

Like the null reference model, this yields a proportional figure which can be converted to a raw number by multiplying by the number of taxa;

\[ 95\% \text{ bionomial confidence interval (raw number)} = \left(1.96 \times \sqrt{\frac{p(1-p)}{n}}\right) \times t \]

Adding and subtracting this number to the null model figure gives a lower and upper value of the 95\% confidence interval, which were also plotted on the diversity curves along with the null model. Where curves deviate outside this 95\% confidence windows, they can be recognised as significant (Olszewski and Patzkowsky, 2001).
3.2 Systematic part

This section features detailed systematics of all Carboniferous miospores recovered from the Warwickshire Group of the Bristol Coalfield. Suprageneric classification follows that introduced by Potonié and Kremp (1954), including modifications by Dettmann (1963). Descriptive terms used in this section are chiefly those utilised in Smith and Butterworth (1967), which reflected earlier works of Erdtman (1952), Harris (1955), Potonié and Kremp (1955) and Couper and Grebe (1961). Additional terms were also sourced from Punt et al. (2007), where appropriate. Miospores interpreted as being generated by vegetation contemporaneous with the formation of the Warwickshire Group are discussed, as are miospores which are likely reworked from previous stages of the Carboniferous. Species which are likely reworked are highlighted within their systematic entry, as well as in ‘3.3.4 Reworked taxa’ where they are discussed with other pre-Carboniferous reworked taxa. Parent plant affinities are from Traverse (2008) and Balme (1995), unless otherwise noted.

Anteturma SPORINITES (Potonié) Ibrahim 1933

Genus TRIHYPHAECITES Peppers 1970

Type species: T. triangulatus Peppers 1970.

Description: Alete miospores with a distinctly triangular amb. Interradial margins straight. Apices are typically rounded, with a septate hyphae originating at each apex.

Discussion: Peppers (1970) states these are probably fungal spores.

Affinity: Fungi.
Trihyphaecites triangulatus Peppers 1970

Plate 1, Figure 1-2

**Holotype:** Peppers (1970), pl. 14, fig.13.

**Type locality:** uncorrelated coal between Cardiff and No. 2 (Colchester) Coal, Carbondale Group, Illinois, U.S.A; Asturian.

**Description:** Alete miospores with a distinctly triangular amb. Interradial margins straight. Apices are typically rounded, with a septate hyphae originating at each apex. Hyphae 18-24 µm long and 10-12 µm wide.

**Dimensions:** Body 34 (1 specimen; HF). Body 31-33 (2 specimens; Schulze and 2% KOH).

**Discussion:** Isolated hyphae of comparable geometry and size are occasionally found in the Bristol assemblages.

**Occurrence:** Harry Stoke B borehole to Grove Cottage (Winterbourne Formation to Downend Member).

**Known range:** Asturian (Peppers, 1970), but almost certainly have a wider stratigraphical range.
Anteturma SPORITES Potonié 1893

Turma TRILETES (Reinsch) Dettmann 1963

Suprasubturma ACAVATITRILETES Dettmann 1963

Subturma AZONOTRILETES Dettmann 1963

Infraturma LAEVIGATI (Bennie and Kidston) Potonié 1956

Genus LEIOTRILETES (Naumova) Potonié and Kremp 1954

Type species: L. sphaerotriangulus (Loose) Potonié and Kremp 1954.

Description: Trilete miospores with a distinctly triangular amb. Interradial margins variable; may be slightly concave, straight or convex. Apices are typically rounded, but may occasionally be truncated to concave. Laesurae exceed half the length of the radius, with some species laesurae reaching up to four fifths of the way to the equator. Exine is laevigate, or rarely infrapunctate.

Comparison: A consistently triangular amb differentiates this genus from other trilete laevigate miospores.

Discussion: Smith and Butterworth (1967) and Playford (1963) maintain that Palaeozoic miospores of this form should be retained in the genus *Leiotriletes*, whereas Staplin (1960) refers to the post-Palaeozoic form genus *Deltoidaspora*. The author will use the former form genus for the Bristol coalfield miospores, in keeping with the overwhelming majority of publications.

Affinity: Ferns.
**Leiotriletes levis** (Kosanke) Potonié and Kremp1955

Plate 1, Figure 3

1955  *Leiotriletes levis* (Kosanke); Potonié and Kremp, p. 38.

**Holotype:** Kosanke (1950), pl. 3, fig.10.
**Type locality:** McCleary's Bluff, McLeansboro Group, Illinois, U.S.A.; Asturian to Cantabrian.

*Description:* Trilete miospores with a triangular amb. Amb may be slightly convex, but more commonly slightly concave. Apices rounded. Laesurae generally exceeds three fifths of the radius, and may slightly exceed four fifths of the radius and are commonly seen to be open. Laesurae bounded by dark lips 3-4 µm wide which occur along the length of the laesurae in the contact area. Exine laevigate and thin.

*Dimensions:* Body 27 (31) 39 (3 specimens; HF). Body 28-32 (2 specimens; Schulze and 2% KOH)

*Discussion:* The Bristol representation of this species seems to be smaller than the holotype, and the 32.5-41.8 µm size range seen by Ravn (1979). *Latipulvinites kosankei* Peppers 1964 may be synonymous.

*Comparison:* The broad low lips of this species are distinctly different from the prominent folds which accompany the laesurae of *L. tumidus.* Although this species is a similar size to *L. parvus,* the latter species does not have lipped laesurae.

*Occurrence:* Harry Stoke B borehole to roof of Parkfield Hard Coal, Bickley Wood to Hursley Hill borehole (Winterbourne Formation to Radstock Member).

*Known range:* Bolsovian to Asturian (Kosanke, 1950; Peppers, 1964; Potonié and Kremp, 1955; Ravn, 1979).
**Leiotriletes parvus** Guennel 1958

Plate 1, Figure 4


_Type locality:_ Outcrop coal, Pottsville Series, Indiana, U.S.A.; Early to Middle Pennsylvanian.

_Description:_ Trilete miospores with a triangular amb. Amb may have slightly concave to straight interradials with truncate apices, or rarely slightly convex interradials with broadly rounded apices. Laesurae fairly distinct and extend between half and three fifths of the way to the equator. Laesurae may be open. Exine laevigate and thin.

_Dimensions:_ Body 30 (32) 33 (5 specimens; HF)

_Comparison:_ The similarly sized _L. levis_ features distinct lips bordering the laesurae. _L. sphaerotriangulus_ is bigger (>35 µm) and is more has more consistently convex interradials.

Occurrence: Harry Stoke B borehole to below Westerleigh Hard Coal and siltstones above Shortwood Hard Coal, Bickley Wood to roof of Hursley Hill borehole (Winterbourne Formation to Radstock Member).

_Known range:_ Duckmantian-Asturian.

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**Leiotriletes sphaerotriangulus** (Loose) Potonié and Kremp 1954

Plate 1, Figure 5

1933 _Laevigali-sporites sphaerotriangulus_ (Loose); Ibrahim, p. 20.
1944 _Punctati-sporites sphaerotriangulatus_ (Loose); Schopf _et al._, p. 31.
1950 _Plani-sporites sphaerotriangulatus_ (Loose); Knox, p. 316.
1950 _Leiotriletes sphaerotriangulus_ (Loose); Potonié and Kremp, p. 120.
**Description:** Trilete miospores with a triangular amb with straight to slightly convex interradials, and broadly rounded apices. Laesurae distinct, between three fifths and three quarters of the radius of the miospore. Laesurae commonly open, and may rarely have a slight darkening in the contact area. Exine laevigate and thin.

**Dimensions:** Body 39 (38) 46 (7 specimens; HF). Body 39 (1 specimen; Schulze and 2% KOH).

**Comparison:** *L. parvus* is smaller (<35 µm), and rarely seen to have convex interradials. *L. cf. sphaerotriangulus* is bigger, has a thicker exine and consistently concave interradials.

**Occurrence:** Harry Stoke B borehole to roof of Parkfield Hard Coal, Stonehill unnamed coal to Hursley Hill borehole (Winterbourne Formation to Publow Member).

**Known range:** Langsettian to lower Bolsovian.

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*Leiotriletes cf. sphaerotriangulus* (Loose) Potonié and Kremp 1954  
Plate 1, Figure 6

**Description:** Trilete miospores with a triangular amb with convex interradials, and broadly rounded apices. Laesurae distinct, between two fifths and four fifths of the radius of the miospore. Exine laevigate and relatively thick for the genus.

**Dimensions:** Body 52 (58) 59 (6 specimens; HF).

**Comparison:** *L. sphaerotriangulus* is typically smaller, and features a thinner exine and may have straight interradials.
Occurrence: Harry Stoke B borehole to shales associated siltstones above Shortwood Hard Coal (Winterbourne Formation to Farrington Member).

**Leiotriletes tumidus** Butterworth and Williams 1958

Plate 1, Figure 7

*Holotype:* Butterworth and Williams (1958) pl. 1, fig.5-6.

*Type locality:* Cawder Cuilt borehole, Central Coalfield, Scotland; Namurian A.

*Description:* Trilete miospores with a triangular amb. Amb may be slightly convex, but more commonly slightly concave. Apices rounded. Laesurae a third to four fifths of the radius. Laesurae bounded by prominent folds, 3-4 µm wide, which give the appearance of lips. Exine laevigate and thin.

*Dimensions:* Body 28 (37) 40 (4 specimens; HF). Body 37 (1 specimen; Schulze and 2% KOH)

*Comparison:* *L. levis* has broad low lips, which are very different to the folds of this species.

*Occurrence:* Harry Stoke B borehole to Huckford Quarry (Winterbourne Formation to Mangotsfield Member).

*Known range:* Viséan-Namurian. Reworked.

**Genus Punctatisporites (Ibrahim) Potonié and Kremp 1954**

*Type species:* *P. punctatus* Ibrahim 1933.

*Description:* Trilete miospores. Amb is almost always circular or only slightly oval, but some species may have a tendency towards a slightly more triangular amb. Laesurae generally exceeds half of the radius of the miospore, but may reach four fifths in some
species. Exine is generally laevigate, but some species may have very subtle punctuation or a scabrate ornament. Exine very variable among species, may be moderately thin to very thick.

**Comparison:** This genus typically has thicker exine and less folds than most *Calamospora* species. Laesurae in *Punctatisporites* are also generally longer and no contact area is recognisable.

**Discussion:** Most of the species listed below are recorded from the Namurian by Smith and Butterworth (1967), who exclusively examined coals. These species are more typically recorded from the siliclastics, than coals of the Bristol coalfield. This may suggest the parent plant groups were more typical of clastic swamps than peat generating areas. It is also possible that these taxa are reworked, but given their consistent stratigraphical coverage in the Bristol Coalfield, this is deemed less likely.

**Affinity:** Ferns and marattialean tree ferns, also sphenophylls.

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**Punctatisporites aerarius** Butterworth and Williams 1958

*Plate 1, Figure 8*

**Holotype:** Butterworth and Williams (1958), pl.1, fig. 17.

**Type locality:** Lower Garscadden Ironstone Seam, Central Coalfield, Scotland; Namurian A.

**Description:** Trilete miospores with a circular amb. Some specimens have an elongate amb, with a slightly convex or rounded triangular shape. Laesurae distinct and exceed half the miospore radius, and may reach just short of three quarters of the way to the equator. Exine is laevigate, with some specimens showing localised development of minute granulation. Exine moderately thick, 3-5 μm.

**Dimensions:** Body 55 (59) 75 (5 specimens; HF). Body 55 (58) 59 (3 specimens; Schulze and 2% KOH).
Comparison: *P. minutus* is smaller (<55 µm).

Occurrence: Harry Stoke B borehole to Westerleigh Hard Coal, Bickley Wood (Winterbourne Formation to Farrington Member).

Known range: Viséan to Asturian.

*Punctatisporites minutus* Kosanke 1950

Plate 1, Figure 9

Holotype: Kosanke (1950), pl. 16, fig. 3.

Type locality: Woodbury Coal, McLeansboro Group, Illinois, U.S.A; Asturian-Cantabrian

Description: Trilete miospores with a circular amb. Laesurae distinct, usually between two thirds and three quarters of the miospore radius in length. Exine punctate, which may only be visible in localised areas. Exine moderately thin for the genus, around 2 µm thick.

Dimensions: Body 30-31 (2 specimens; HF).

Comparison: May look similar to thick walled *Calamospora*, but can be distinguished by their longer laesurae. Can be distinguished from *P. nitidus* by its punctate ornament. *P. punctatus* is larger (>35 µm) and has a more distinct punctate ornamentation.

Occurrence: Harry Stoke B borehole to siltstones above Shortwood Hard Coal (Winterbourne Formation to Farrington Member).

Known range: Viséan to Asturian.
**Punctatisporites nitidus** Hoffmeister et al., (1955)

Plate 1, Figure 10

*Holotype:* Hoffmeister et al. (1955), pl. 36 fig. 4.

*Type locality:* Carter No. 3 borehole (TCO-82), Hardinsburg Formation, Kentucky, U.S.A; Viséan-Namurian.

*Description:* Trilete miospores with a typically circular amb, with occasional specimens showing a slight tendency to a subtly convex triangular amb. Laesurae usually distinct, extending between three fifths and four fifths of the way to the equator. Exine laevigate, with some specimens showing scabrate ornament locally. Exine around 2 µm thick.

*Dimensions:* Body 31 (41) 55 (6 specimens; HF). Body 31 (42) 48 (5 specimens; Schulze and 2% KOH).

*Comparison:* Usually slightly larger than *P. minutus*, which has a similar exine thickness and laeurae length. *P. minutus* is also subtly punctate. Smith and Butterworth (1967) also noted *P. nitidus* from British coals has a larger size range than that given by Hoffmeister et al., (1955).

*Occurrence:* Harry Stoke B borehole to Huckford Quarry, Salridge Coal (Winterbourne Formation to Mangotsfield Member).

*Known range:* Namurian to Bolsovan.

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**Punctatisporites obesus** (Loose) Potonié and Kremp 1955

Plate 1, Figure 11

1932 *Sporonites obesus* Loose in Potonié et al., p. 451.
1934 *Laevigatisporites obesus* Loose, p. 145.
1944 *Calamospora obesus* (Loose); Schopf et al., p. 52.
1955 *Punctatisporites obesus* (Loose); Potonié and Kremp, p. 43.


**Holotype:** Loose (1932), pl. 19, fig. 49.

**Type locality:** Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

**Description:** Trilete miospores. Amb varies between round and rounded triangular, with the later morphology being slightly more common. Laesurae extremities not always distinct due to the thick nature of the exine, but usual can be seen to extend to between three fifths and three quarters of the way to the equator. Exine laevigate and very thick, usually 6-8 μm.

**Dimensions:** Body 96 (98) 104 (5 specimens; HF). Body 98 (102) 115 (6 specimens; Schulze and 2% KOH).

**Comparison:** Exine is thicker than most other species within this genus. *P. cf. obesus* has a similar exine thickness, but is smaller (<100 μm) and has longer laesurae.

**Occurrence:** Harry Stoke B borehole to siltstones above Shortwood Hard Coal (Winterbourne Formation to Farrington Member).

**Known range:** Upper Langsettian to Asturian.

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**Punctatisporites cf. obesus** (Loose) Potonié and Kremp 1955

Plate 2, Figure 1

**Description:** Trilete miospores with a generally circular to rounded triangular amb. Laesurae not distinct, owing to thickness of the exine. Laesurae extend around four fifths of the way to the equator. Exine laevigate and very thick, 4-9 μm.

**Dimensions:** Body 45 (61) 85 (4 specimens; HF).

**Comparison:** Smaller and with longer laesurae than *P. obesus*, which it otherwise closely resembles.
Occurrence: Harry Stoke B borehole to Huckford Quarry (Winterbourne Formation to Mangotsfield Member).

**Punctatisporites punctatus** Ibrahim 1932

Plate 2, Figure 2

1933 *Punctati-sporites punctatus* Ibrahim, p. 21.

*Holotype:* Ibrahim (1932), pl. 15, fig. 18.
*Type locality:* Ägir Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

**Description:** Trilete miospores, with a circular to slightly rounded triangular amb. Laesurae fairly distinct, between two thirds and four fifths of the radius. Exine punctate, with depressions around 0.5 µm in diameter, which gives the amb a distinctly roughened appearance. Exine 2 µm thick.

*Dimensions:* Body 39 (44) 48 (4 specimens; HF).

**Discussion:** Slightly smaller than the size ranges quoted in Smith and Butterworth (1967), which are typically in the range of 50-60 µm. However, all the size ranges in Smith and Butterworth (1967) were made on specimens macerated using oxidation, often with KOH washes, which may account for the comparatively smaller size of the Bristol representative of this species.

**Comparison:** Exine thinner and laesurae longer than similarly sized *P. aerarius*. *P.minutus* has a finer punctate ornament and is smaller (<35 µm).

**Occurrence:** Harry Stoke B borehole to Dingle leaf bed (Winterbourne Formation to Mangotsfield Member)

*Known range:* Langsettian to lower Bolsovian
Genus CALAMOSPORA Schopf et al. 1944

Type species: C. hartungiana Schopf et al. 1944. May be synonym of C. mutabilis Loose 1932 (Smith and Butterworth, 1967).

Description: Trilete miospores. Amb more or less circular, but often heavily distorted by numerous prominent folds. Laesurae generally fairly short, generally extended for roughly half of the spore radius. Laesurae variable and often of unequal lengths. Although the trilete mark is actually very distinct, it is often partially or even totally obscured by the folding. Some species may have folds on the laesurae which superficially resemble lips, and/or a small darkened region in the centre of the contact area. Exine laevigate, and very thin.

Comparison: Differs from Punctatisporites in possessing typically much thinner and heavily folded exine. Laesurae in this genus are typically also much shorter, and some species may show darkening of contact areas or curvaturae development.

Discussion: Size limits suggested in Smith and Butterworth (1967) will be used to differentiate some morphologically similar species where large size ranges are present.

Affinity: Sphenophytes typically. Also noeggerathialeans, sphenophylls and probably some ferns.

Calamospora breviradiata Kosanke 1950

Plate 2, Figure 3

Holotype: Kosanke (1950), pl.19, fig. 4.
Type locality: No. 2 Coal, Carbondale Group, Illinois, U.S.A.; Asturian.

Description: Trilete miospores with circular amb. Laesurae distinct, with a prominent ridge emphasising the trilete mark. There is a fairly distinctive darkening of the contact
area, which occurs at the proximal pole and extends for almost the entire length of the 
laesurae. Laesurae two thirds to a little over half of the radius. Exine laevigate and thin. 
Folds are usually towards to edge of the miospore and run parallel to the amb, causing 
minimal modification to the amb shape.

*Dimensions:* Body 41 (47) 55 (5 specimens; HF). Body 42 (1 specimen; HF).

*Comparison:* The ridged laesurae and darkened contact area make this species readily 
distinguishable from other members of the genus.

*Occurrence:* Harry Stoke B borehole to 65 The Dingle, Bickley Wood to below Salridge 
Coal (Winterbourne Formation to Mangotsfield Member). Possibly in shales associated 
with Shortwood Top Coal and Coalpit Heath High Coal (Farrington Member).
*Known range:* Namurian A to Bolsovian.

**Calamospora microrugosa** Schopf *et al.* 1944

Plate 2, Figure 4

1932 *Sporonites microrugosus* Ibrahim, p. 447.
1933 *Triletes microrugosus* (Ibrahim); Waltz in Luber and Waltz, p. 10.
1938 *Calamospora microrugosus* (Ibrahim); Schopf *et al.*, p. 52.
1944 *Leiotriletes microrugosus* (Ibrahim); Ishchenko, p. 15.
1952 *Calamotriletes microrugosus* (Ibrahim); Luber, p. 36.
1955 *Laevigati-sporites microrugosus* (Ibrahim); Ibrahim, p. 18.

*Holotype:* Ibrahim (1931), pl. 14, fig. 9.
*Type locality:* Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

*Description:* Trilete miospores. Variable amb shape; may be round if folding is minor, 
or very irregular if folding is pervasive. Laesurae fairly distinct in most specimens, 
usually occupying just less than half of the radius. Laesurae may be partially hidden by 
folding. Laesurae are rarely ridged, and when this occurs there is usually some form of 
darkening of the contact area at the proximal pole. Exine laevigate, and thin.
Compression folding is usually very common, but occasional specimens show a lesser degree of folding.

*Dimensions*: Body 89 (102) 139 (5 specimens; HF). Body 95 (1 specimen; Schulze and 2% KOH).

*Comparison*: This species is separated from the smaller, but otherwise indistinguishable *C. pallida*, by exceeding 75 µm.

*Occurrence*: Harry Stoke B borehole to siltstones above Shortwood Hard Coal, Stonehill unnamed coal to below Salridge Coal (Winterbourne Formation to Farrington Member).

*Known range*: Viséan to upper Bolsovian.

**Calamospora pallida** (Loose) Schopf *et al.* 1944

Plate 2, Figure 5

1934 *Punctati-sporites pallidus* Loose, p. 146.
1944 *Calamospora pallidus* (Loose); Schopf *et al.*, p. 52.

*Holotype*: Loose (1932), p. 18, fig. 31.
*Type locality*: Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

*Description*: Trilete miospores, with an originally round amb. Amb is usually heavily modified by folding, giving the miospores a more irregular shape. Laesurae are distinct to indistinct, and may be partially or totally obscured by folding. Laesurae often unequal in length, and range from just short of half to around two thirds of the miospore radius. Exine is laevigate and thin. Compression folding is common and pervasive.

*Dimensions*: Body 63 (66) 69 (4 specimens; HF). Body 60 (68) 77 (4 specimens; Schulze and 2% KOH).
Comparison: The size limits of 55 to 75 µm will be used to separate this species from the smaller *C. parva* and the larger *C. microrugosa* (as proposed in Smith and Butterworth, 1967).


Known range: Viséan to Asturian.

**Calamospora parva** Guennel 1958

Plate 2, Figure 6

**Holotype:** Guennel (1958), text fig. 16.

**Type locality:** Outcrop coal, Pottsville Series, Indiana, U.S.A; Early to Middle Pennsylvanian.

Description: Trilete miospores, with a circular amb. Laesurae distinct, either just shorter or just longer than half of the miospore radius. Exine is laevigate, and thin. Compression folds tend to be towards the equatorial margin, and follow the outline of the amb.

Dimensions: Body 34 (42) 50 (5 specimens; HF). Body 42 (45) 49 (4 specimens; Schulze and 2% KOH).

Comparison: Similar to *C. pallida* and *C. microrugosa*, but considerably smaller. An upper size limit of 55 µm is suggested in Smith and Butterworth (1967) to differentiate *C. parva* from the former miospores. The folding pattern of this species is most similar to *C. breviradiata*, in that they often follow the shape of the amb.

Occurrence: Harry Stoke B borehole to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Stonehill unnamed coal to Hursley Hill borehole (Winterbourne Formation to Publow Member).
Known range: Viséan to Asturian.

Calamospora straminea Wilson and Kosanke 1944

Plate 2, Figure 7

1958 Punctatisporites stramineus (Wilson and Kosanke); Guennel, p. 68.

Holotype: Wilson and Kosanke (1944), pl.1, fig. 1.
Type locality: Angus Coal Company Mine, Des Moines Series, Iowa, U.S.A.; Asturian.

Description: Trilete miospores, with a circular amb. Laesurae distinct, ranging from just short of half of the radius up to around three fifths. Exine is laevigate, and fairly thick for the genus.

Dimensions: Body 35-37 (2 specimens; HF). Body 40 (53) 60 (3 specimens; HF).

Comparison: This species has a thicker exine and is less folded than the similarly sized C. parva.

Occurrence: Harry Stoke B borehole to Parkfield Great Coal (Winterbourne Formation to Farrington Member.

Known range: Duckmantian to Asturian.

Genus TRINIDULUS Felix and Paden 1964

Type species: T. diamphidios Felix and Paden 1964.

Description: Trilete miospores with roughly rounded triangular equatorial outline. Proximally a shallow semi-circular depression occurs in each interradial position. These depressions are of equal size, and each contains a single oval to round body. Laesurae
prominent and may be open, reaching around three quarters of the way to the equator. Exine laevigate, and moderately thick.

**Discussion:** Due to the unique morphology of this genus, it would be better suited within a new infraturma, rather than Laevigati.

**Affinity:** Unknown.

**Trinidulus diaphidios** Felix and Paden 1964

*Plate 3, Figure 1-2*

**Holotype:** Felix and Paden (1964) pl. 1, fig.1.

**Type locality:** Shell Oil Company Blasdel No.1 well, Woodward County, Oklahoma, U.S.A.; Mississippian.

**Description:** Trilete miospores. Equatorial outline generally straight sided triangular, with broadly rounded to truncated apices. Interradials may be slightly convex in some specimens. On the proximal face, a large semi-circular depression occurs in each interradial position. The depressions open out towards the equatorial outline of the miospore. Within each depression, a single body sits. The shape of each body is irregular, ranging from semi-circular to straight sided triangular. The outer edge of each body may bear a subtle thickening at the margin. The three depressions alter the shape of the proximal face, giving a distinct three-lobed appearance (each lobe is slightly darkened where it meets the equatorial margin). Laesurae are long and distinct, and may be open and/or have a slight darkening in the region of the proximal pole. Laesurae range from half to just over three quarters of the radius of the miospore. Exine is laevigate, and moderately thick.

**Dimensions:** Body 35 (37) 41 (6 specimens; HF).
Discussion: From the plate and description in Felix and Paden (1964), the three bodies on the proximal face are only recorded as being oval or circular. The Bristol specimens vary from semi-circular to straight sided triangular, with no oval-circular morphologies being observed.

Occurrence: Harry Stoke B (Winterbourne Formation).


Infraturma APPENDICIFERI Potonié 1956

Genus ELATERITES Wilson 1943

Type species: *E. triferens* Wilson 1943

Description: Trilete miospores with a rounded triangular, rounded or oval equatorial outline. Three long elaters are spaced equidistantly around the equatorial outline; originating from an attached region at the distal pole. Elaters may either by coiled around the body, partially uncoiled or fully uncoiled. Elaters remain circinate over much of their distal length, even where the entire elater has uncoiled from around the miospore body. Miospore body laevigate. Exine of the elaters somewhat thinner than that of the miospore body.

Comparison: No other miospore bears elaters. Miospores which have lost their elaters would be indistinguishable from *Calamospora*.

Affinity: *Calamites* (*Calamocarpon insignis*) (Good and Taylor, 1974).
Elaterites triferens Wilson 1943

Plate 3, Figures 3

Holotype: Wilson (1943), pl.3, fig 1-3.

Type locality: What Cheer Clay Company pit, Des Moines Series, Iowa, U.S.A.; Asturian.

Description: Trilete miospores with a rounded triangular, rounded or oval equatorial outline. Miospore body 35-44 µm. Three long elaters are spaced equidistantly around the equatorial outline; emanating from a fused patch over the distal pole. Where the miospore body has been separated from the elaters, the elaters can be seen to form an equilateral ‘Y-shaped‘ structure. There is a tendency for all the elaters to coil the same way on a given specimen. Elaters around 20 µm wide over most of their length, abruptly tapering at the apices and terminating in a rounded tip. Elaters either coiled around the body, partially uncoiled or fully uncoiled. Elaters remain circinate over much of their distal length, even where the entire elater has uncoiled from around the miospore body. Laesurae less than half of miospore radius. Miospore body laevigate. Exine of the elaters somewhat thinner than that of the miospore body.

Dimensions: Body 33 (42) 45 (4 specimens; HF).

Discussion: These miospores are very rare in the Bristol material; most likely owing to the fragile nature of the diagnostic elaters. Slightly smaller than the 50-58 µm body dimensions given by Wilson (1934).

Occurrence: Harry Stoke B borehole, below Trench Coal to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Asturian (Wilson, 1943; Wilson, 1963; Turner, 1991).
Infraturma APICULATI (Bennie and Kidston) Potonié 1956
Subinfraturma GRANULATI Dybová and Jachowicz 1957a
Genus GRANULATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species: G. granulatus Ibrahim 1933.

Description: Trilete miospores with a consistently and distinctly triangular amb. The interradial regions may be slightly convex or concave, with rounded apices. Laesurae exceed half of the miospore radius, ranging up to two thirds or three quarters, depending on the species. The exine is covered in grana which are fairly uniform on each specimen, but are variable between species. The height of the ornament is generally only slight, and so the equator of the miospore is barely modified. Grana have rounded or flat apices on species where the ornament is big enough for their shape to be discernible. Exine is generally moderately thin.

Comparison: A triangular amb with regular granulate ornamentation is characteristic of this genus. Miospores with a circular amb and granulate ornament are referred to Cyclogranisporites.

Affinity: Ferns.

Granulatisporites adnataoides (Potonié and Kremp) Smith and Butterworth (1967)

Plate 3, Figure 4

1955 Leiotriletes adnataoides Potonié and Kremp, p. 38.

Holotype: Potonié and Kremp (1955), pl. 11, fig. 112.
Type locality: Baldur Seam, Ruhr Coalfield, Germany; Lower Bolsovian.

Description: Trilete miospores. Amb may be slightly concave to slightly convex. Laesurae are distinct, exceeding three quarters of the radius and may almost reach the
amb. Exine ornamented with minute 0.5 \( \mu \text{m} \) grana, which are closely spaced and barely project at the amb.

*Dimensions:* Body 28 (32) 39 (5 specimens; HF). Body 31 (34) 41 (3 specimens; Schulze and 2\% KOH).

*Comparison:* The long laesurae of this species differentiates it from *G. microgranifer*. Smith and Butterworth (1967) noted that concave and convex forms occur, and the interradial shape may vary even on a single specimen.

*Occurrence:* Harry Stoke B borehole to 65 The Dingle, Bickley Wood to above Trench Coal (Winterbourne Formation to Farrington Member).

*Known range:* Langsettian to upper Bolsovian.

**Granulatisporites granulatus** Ibrahim 1933

Plate 3, Figure 5

1933  *Granulatisporites granulatus* Ibrahim, p. 22, pi. 6, fig. 51.
1955  *Granulatisporites granulatus* (Ibrahim); Potonié and Kremp, p. 58.

*Holotype:* Ibrahim (1933), pl. 6, fig. 51.

*Type locality:* Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

**Description:** Trilete miospores with a triangular amb, with generally convex interradials and fairly narrowly rounded apices. Rare specimens with slightly concave interradials. Laesurae distinct, rarely open, and extend from three fifths to just over four fifths of the miospore radius. Ornament consists of grana, 0.5-1 \( \mu \text{m} \) in basal diameter. The grana apices may be rounded, or truncated. Bases of grana fairly closely spaced, but their bases do not touch. 45-55 grana project from the amb. Exine moderately thin.

*Dimensions:* Body 34 (36) 39 (3 specimens; HF). Body 30 (36) 41 (6 specimens; Schulze and 2\% KOH).
Comparison: Has the coarsest ornament of the genus. Smith and Butterworth (1967) also noted that this species can be concave or convex sided.

Occurrence: Harry Stoke B borehole to Westerleigh Hard Coal and shales associated with Shortwood Top Coal, Golden Valley to below Salridge Coal (Winterbourne Formation to Farrington Member).

Known range: Viséan to lower Bolsovian.

Granulatisporites microgranifer Ibrahim 1933
Plate 3, Figure 6

1933 Granulat-sporites microgranifer Ibrahim, p. 22.
1938 Azonotritles microgranifer (Ibrahim); Luber in Luber and Waltz
1955 Granulatisporites microgranifer Ibrahim et al., p. 5.

Holotype: Ibrahim 1933, pl. 5, fig. 52.
Type locality: Ruhr Coalfield, Germany; uppermost Duckmantian.

Description: Trilete miospores. Amb generally slightly concave, but some convex specimens occur, with narrowly to fairly broadly rounded angles. Laesurae distinct and may be open, around half to two thirds of the miospore radius in extent. Moderately thin exine is scabrate. The ornament is barely recognisable at the equator.

Dimensions: Body 30 (35) 38 (7 specimens; HF). Body 25 (33) 35 (3 specimens; Schulze and 2% KOH).

Comparison: G. adnatoides is a similar size with similarly sized grana, but is differentiated by its longer laesurae (>three quarters of the radius).

Occurrence: Harry Stoke B borehole to Westerleigh Hard Coal and Shortwood Hollybush Coal (Winterbourne Formation to Farrington Member).
Known range: Upper Langsettian to upper Bolsovian.

Genus CYCLOGRANISPORITES Potonié and Kremp 1954
Type species: C. leopoldi (Kremp 1952) Potonié and Kremp 1954.

Description: Trilete miospores with a circular amb. Laesurae may be a little shorter than half of the miospore radius, but may extend to four fifths in some specimens. Miospore covered with grana, the size of which is a major feature used to differentiate the species. Folds may be common, but these seem to occur more frequently in the larger specimens. Exine is moderately thin.

Comparison: As mentioned in Smith and Butterworth (1967), this genus has the same ornament as Granulatisporites but possesses a circular amb.

Affinity: Ferns and marattialean tree ferns. Also pteridosperms and noeggerathialeans

Cyclogranisporites aureus (Loose) Potonié and Kremp 1955
Plate 3, Figure 7

1934 Reticulati-sporites aureus Loose, p. 155.
1944 Punctati-sporites aureus (Loose); Schopf et al., p. 30.
1950 Plani-sporites aureus (Loose); Knox, p. 315.
1955 Cyclogranisporites aureus (Loose); Potonié and Kremp, p. 61.

Holotype: Potonié and Kremp (1955), pl. 13, fig. 184.
Type locality: Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

Description: Trilete miospores with a circular amb. The larger specimens of this species seem to be more prone to developing compression folds. Laesurae are distinct, ranging from three fifths to four fifths of the radius. The laesurae may be accompanied by lips,
which can vary from a mere line to 2-3 $\mu$m wide darkened regions. Ornament consists of grana, which range from 0.5-1 $\mu$m in diameter, and are often variable within a single specimen.

*Dimensions*: Body 51 (69) 79 (11 specimens; HF). Body 62 (61) 69 (6 specimens; Schulze and 2% KOH).

*Discussion*: Smith and Butterworth (1967) state the diameter of the grana of this species generally exceeds 1 $\mu$m, but the ornament was found to be highly variable even on a single specimen in this author’s samples. Given that these variable specimens often had lips, they were classified as *C. aureus*.

*Comparison*: *Convolutispora finis* has similar sized ornament, but with confluent bases which creates a rugulate ornament. *Cyclogranisporites multigranus* has smaller grana.

*Occurrence*: Harry Stoke B borehole to Westerleigh/Shortwood Hard Coal, above Trench Coal (Winterbourne Formation to Farrington Member).

*Known range*: Langsettian to Asturian.

**Cyclogranisporites multigranus** Smith and Butterworth 1967

Plate 3, Figure 8

*Holotype*: Smith and Butterworth (1967), pl. 4, fig. 10-13.

*Type locality*: Seafield No. 2 borehole, East Fife Coalfield, Scotland; Duckmantian.

Description: Trilete miospores with a circular amb. Laesurae distinct to faint, extending from less than half to two thirds of the miospore radius. Ornament of minute but dense grana, less than 0.5 $\mu$m height/diameter, which are often not discernible at the amb. Exine moderately thin, but appears slightly thicker than other members of the genus.

*Dimensions*: Body 49 (58) 67 (5 specimens; HF). Body 57 (1 specimen; Schulze and 2% KOH).

*Comparison*: The grana of *C. aureus* are bigger.
Occurrence: Harry Stoke B borehole to Shortwood Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known Range: Duckmantian to Asturian (Kosanke and Cecil, 1996).

Subinfraturma VERRUCATI Dybová and Jachowicz 1957
Genus CONVERRUCOSISPORITES Potonié and Kremp 1954
Type species: C. triquetrus (Ibrahim) Potonié and Kremp

Description: Trilete miospores with a triangular outline. Amb has typically almost straight interradials to slightly convex with narrowly rounded apices, but specimens with a slightly concave amb can be observed. Laesurae generally two thirds to three quarters of the miospore radius. Ornament consists of verrucae. Exine moderately thin to moderately thick.

Comparison: Ornament is similar to Verrucosisporites among circular miospores.

Affinity: Probably ferns.

Converrucosisporites armatus (Dybová and Jachowicz) Smith and Butterworth 1967

Plate 3, Figure 9

1957a Converrucitriletes armatus Dybová and Jachowicz, p. 128.

Holotype: Dybová and Jachowicz (1957a), pl. 31, fig. 1.

Type locality: Seam 12, Vaclav Colliery, Czechoslovakia; Namurian A.

Description: Trilete miospores. Amb typically slightly convex triangular, with narrowly rounded to pointed apices. Some specimens have straight interradials. Laesurae
indistinct generally, extending from two thirds up to four fifths of the way to the amb. Verrucae more prominent distally, where they are 3-5 µm wide and up to 2 µm tall. The ornament on any one specimen is variable. Apices are rounded, flattened or slightly pointed but it is often very subtle as the ornament is quite flat. 20-30 verrucae project at the amb. Exine moderately thick.

*Dimensions:* Body 34 (38) 55 (6 specimens; HF). Body 28-55 (2 specimens; Schulze and 2% KOH).

*Comparison:* *C. mosacoides* has finer ornament and more verrucae project at the equator. *C. sp.1* is large (30-45 µm) with more numerous equatorial projections.

*Occurrence:* Harry Stoke B borehole to Shortwood Top Coal, below Salridge Coal (Winterbourne Formation to Farrington Member).

*Known range:* Langsettian, and late Bolsovian-Asturian of Iowa (Ravn, 1986).

**Converrucosisporites mosacoides** (Imgrund) Potonié and Kremp 1955

Plate 3, Figure 10

1955 *Converrucosisporites mosacoides* (Imgrund); Potonié and Kremp, p. 64.

*Holotype:* Potonié and Kremp (1955), pl. 13, fig 192.
*Type locality:* Baldur Seam, Ruhr Coalfield, Germany; Lower Bolsovian.

Description: Trilete miospores with a triangular amb. Interradials are straight to subtly convex, with narrowly rounded angles. Laesurae indistinct, ranging from two thirds to four fifths of the radius. Ornament of verrucae which are around 2 µm wide, and less than 1.5 µm tall. As the height of the ornament is only slight, it is difficult to discern the shape of the apices. Around 30 verrucae project at the amb. Exine is moderately thick.
Comparison: *Converrucosisporites*. sp.1 is larger, and has more verrucae projecting from the amb in polar view. *C. armatus* (Dybová and Jachowicz) Smith and Butterworth 1967 is of a similar size, but has larger verrucae and correspondingly few equatorial projections. The Bristol specimens seem to have slightly more equatorial projections than the 20-25 noted by Coquel (1974), but are otherwise identical.

Occurrence: Harry Stoke B borehole to Shortwood Top Coal, Stonehill unnamed coal to Bickley Wood (Winterbourne Formation to Farrington Member).

Known range: Duckmantian to Bolsovian (Grebe, 1972).

*Converrucosisporites sp.1*
Plate 3, Figure 11

Description: Trilete miospores. Amb is triangular with straight interradials, and fairly broadly rounded apices. Laesurae distinct or indistinct, extending between two thirds and three quarters of the radius. Ornament of dense verrucae, 2 µm wide and 0.5-1 µm tall. Apices rounded to slightly pointed. 40-70 verrucae project at the margin. Exine is moderately thin.

Comparison: Bigger than *C. armatus* and *C. mosacoides*. Verrucae are smaller than those in *C. armatus* and there are over twice as many equatorial projections. While the verrucae of *C. mosacoides* are comparable, there are fewer equatorial projections than *Converrucosisporites* sp.1.

Occurrence: Harry Stoke B (Winterbourne Formation). Possibly to 65 The Dingle (Mangotsfield Member).
Genus VERRUCOSISPORITES (Ibrahim) Smith and Butterworth 1967

Type species: V. verrucosus (Ibrahim) Ibrahim 1933.

Description: Trilete miospores, with an amb ranging from circular to roundly triangular. In the coarser ornamented species, the equatorial outline is heavily modified by the ornament. Laesurae generally obscured by ornament, generally exceed half the miospore radius and may nearly reach the equatorial margin. Ornament dominated by verrucae of highly variable morphologies, spacing and sizes. Ornament height is equal to less than its width. Exine of variable thickness depending on species.

Comparison: Differs from Apiculatisporis by possessing distinctly verrucate ornament (where basal diameter is equal to or exceeds height). Ornament in Verrucosisporites consists of more or less discrete verrucae, which never form anastomosing ridges (cf. Camptotriletes and Convolutispora).

Affinity: Ferns, marattialean tree ferns, noeggerathialeans, pteridosperms

Verrucosisporites donarii Potonié and Kremp 1955

Plate 4, Figure 1

Holotype: Potonié and Kremp (1955), pl. 13, fig. 193.
Type locality: Donar Seam, Ruhr Coalfield, Germany; Lower Bolsovian.

Description: Trilete miospores. Amb originally circular, but the majority of specimens have prominent compression folds towards the equatorial margin. Laesurae often not visible, and the extremities may merge with the channels formed between the closely spaced ornament. When visible, laesurae range from half to two thirds of the miospore radius. Exine covered with verrucae, 2-3 µm in width and less than 1.5 µm in height. Verrucae are commonly polygonal and very closely spaced, formed a fairly uniform and
narrow negative reticulum in the intervening channels. In profile, the verrucae may either be rounded or parallel-sided with truncated apices. Around 55-65 verrucae project at the equator. Exine moderately thick, often with compression folds following the margin.

*Dimensions:* Body 47 (55) 80 (5 specimens; HF). Body 63 (1 specimen; Schulze and 2% KOH).

*Discussion:* Smith and Butterworth (1967) noted that this species is typically not folded due to the thickness of the exine.

*Comparison:* *V. microtuberosus* has smaller verrucae and is more distorted by folding. *V. microverrucosus* has larger verrucae which are more variable.

*Occurrence:* Harry Stoke B borehole to 65 The Dingle, Bickley Wood (Winterbourne Formation to Mangotsfield Member). Possibly below Salridge Coal (Downend Member).

*Known range:* Duckmantian to Asturian.
**Verrucosisporites microtuberosus** (Loose) Smith and Butterworth 1967

Plate 4, Figure 2

1934  *Tuberculatisporites microtuberosus* Loose, p. 147.
1944  *Punctatisporites microtuberosus* (Loose); Schopf *et al.*, p. 31.
1950  *Plani-sporites microtuberosus* (Loose); Knox, p. 316.
1955  *Micoreticulatisporites microtuberosus* (Loose); Potonié and Kremp, p. 100.
1957  *Planisporites microtuberosus* (Loose); Knox in Bharadwaj, p. 87.

**Holotype:** Potonié and Kremp (1955), pl. 15, fig. 273.

**Locality:** Ägir Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

**Description:** Trilete miospores, with an oval to circular amb (which may be modified by compression folding). Laesurae may or may not be apparent; when visible they range from half to three quarters of the miospore radius. Laesurae may rarely be slightly open for some, or all of their length. Exine ornamented with verrucae with rounded to slightly conical apices, less than 2 µm in width and around 1 µm tall. Verrucae of fairly uniform size and shape, closely spaced as to form a negative reticulum between their bases. In plan view verrucae are generally oval or roughly circular in shape. Over 70 verrucae project from the amb. Exine fairly thin for the genus, and is usually folded by at least one prominent fold.

**Dimensions:** Body 37 (55) 72 (5 specimens; HF). Body 40 (58) 75 (6 specimens; Schulze and 2% KOH).

**Comparison:** Verrucae slightly smaller and more rounded in shape than *V. donarii*. The amb of *V. donarii* is also circular, whereas *V. microtuberosus* is usually oval due to folding.

**Occurrence:** Harry Stoke B borehole to Westerleigh Hard Coal and Shortwood Great Coal, Golden Valley to below Salridge Coal (Winterbourne Formation to Farrington Member).
Known range: Langsettian to Asturian.

**Verrucosisporites microverrucosus** Ibrahim 1933

Plate 4, Figure 3

1933  *Verrucosi-sporites microverrucosus* Ibrahim, p. 25.
1944  *Punctati-sporites microverrucosus* (Ibrahim); Schopf *et al*., p. 31.
1950  *Verrucoso-sporites microverrucosus* (Ibrahim); Knox, p. 318

**Holotype:** Potonić and Kremp (1955), pl. 13, fig. 200.

**Type locality:** Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

**Description:** Trilete miospores with a circular to oval amb. Laesurae may be obscured by coarse ornament, but generally reach three quarters of the way to the equatorial margin. Exine features very variable verrucate ornamentation which are 3-6 \( \mu \text{m} \) wide at the base, and around 2 \( \mu \text{m} \) tall. Verrucae may be rounded, slightly pointed or parallel-sided with truncated apices in profile. In plan view, the verrucae are typically polygonal and irregular. Verrucae are closely spaced, and form an irregular negative reticulum between the ornament. 30-35 \( \mu \text{m} \) verrucae project from the amb. Exine is thick and usually unfolded.

**Dimensions:** Body 34 (45) 54 (3 specimens; HF). Body 50-55 (2 specimens; Schulze and 2\% KOH).

**Comparison:** The verrucae in this species are typically irregular in shape and spacing, and are comparatively large. Due to the thicker exine, this species is darker and folds are not as well developed as in *V. microtuberosus* and *V. donarii*.

**Occurrence:** Harry Stoke B borehole to 65 The Dingle, below Salridge Coal (Winterbourne Formation to Mangotsfield Member).

**Known range:** Langsettian to lower Bolsovian.
**Verrucosisporites sifati** (Ibrahim) Smith and Butterworth 1967

Plate 4, Figure 4

1955  *Microreticulatisporites sifati* (Ibrahim); Potonié and Kremp., p. 102.

**Holotype:** Potonié and Kremp (1955), pl. 15, fig. 282.
**Type locality:** Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

*Description:* Trilete miospore with a circular to oval amb. Laesurae usually visible, less or equal to half of the miospore radius. Low and broad verrucae ornament the exine, which have well rounded apices. Basal widths of verrucae are highly variable (2-6 µm) and have low relief (<1 µm). In plan view verrucae are very irregular in shape and spacing. In some areas clusters of verrucae form in close proximity, while in other areas the intervening spaces exceed the basal width of the verrucae. Verrucae may also be slightly elongate, and may even become confluent with other verrucae in localised patches. Exine moderately thick, compression folds may occur.

*Dimensions:* Body 83-85 (2 specimens; Schulze and 2% KOH).

*Comparison:* The verrucae in this species are typically irregular in shape and spacing, and are comparatively large. Due to the thicker exine, this species is darker and folds are not as well developed as in *V. microtuberosus* and *V. donarii*. No other members of the genus feature elongate and locally semi-confluent verrucae. This species is also generally larger than the other species observed.

*Occurrence:* Harry Stoke B borehole to Huckford Quarry (Winterbourne Formation to Mangotsfield Member).

*Known range:* Upper Langsettian to Asturian.
Genus CADIOSPORA (Kosanke) Venkatachala and Bharadwaj 1964

Type species: C. magna Kosanke 1950.

Description: Trilete miospores with a circular to rounded triangular amb. Laesurae two thirds to four fifths of miospore radius in length, bounded by prominent lips. Lips continuous for a little way past the radial limit of the laesurae, and typically bifurcate at their equatorial extremities and follow the edge of the contact area in the interradial region for several µm. Contact area of the proximal face is often clearly thinner than the rest of the miospore exine. Exine mostly laevigate, with locally developed coarse verrucate-type ornament on some specimens. Exine generally very thick.

Comparison: Cadiospora may look superficially similar to Punctatisporites, but the latter genus lacks the distinctive lips.

Discussion: Retusotriletes (Naumova) Strel has comparatively very narrow lips and a much thinner exine than Cadiospora.

Affinity: Lycopsid; unknown arborescent. Cadiospora has been found in-situ associated with gulate megaspores; Sublagenicula (Opluštil and Drábková, 2009). Opluštil and Drábková (2009) state that the cone is of probable Sigillarian affinity. Gulate megaspores are, however, more typical of Lepidodendron.

Cadiospora magna Kosanke 1950

Plate 4, Figure 5

1950 Cadiospora magna Kosanke, p. 50.
1954 Cadiospora sphaera Butterworth and Williams, p. 761.
1954 Gravisporites sphaera (Butterworth and Williams); Bharadwaj, p. 514.

Holotype: Kosanke (1950), pl. 16, fig. 1.
**Type locality:** La Salle Coal, McLeansboro Group, Illinois, U.S.A.; Asturian-Cantabrian.

Description: Trilete miospores with a circular to rounded triangular amb. Laesurae two thirds to four fifths of the miospore radius. Prominent lips, 3-4 µm wide, border the laesurae. The lips extend the full length of the laesurae, bifurcating at their radial extremities and following the limit of the contact area for several µm. In most specimens, the exine of the contact area is markedly thinner than on the rest of the miospore. Exine mostly laevigate or with localised patches of very fine grana. Some specimens have a few scattered verrucae, which may be up to 4 µm in diameter. Exine very thick, 4-6 µm.

**Dimensions:** Body 59 (73) 82 (4 specimens; HF). Body 62 (73) 80 (10 specimens; Schulze and 2% KOH).

**Discussion:** The verrucae clusters are generally very rare, and on some samples may be resin droplets or other debris adhering to the miospore surface (this was also noted by Smith and Butterworth, 1967).

**Comparison:** Cadiospora sp.1 has shorter, sinuous laesurae with much thinner lips.

**Occurrence:** Winterbourne Railway Cutting to Shortwood Top Coal and associated shales, above and below Trench Coal to Hursley Hill borehole (Mangotsfield Member to Publow Member). Possibly below and in Salridge Coal (Downend Member).

**Known range:** Asturian.

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**Cadiospora sp.1**  
Plate 4, Figure 6

Description: Trilete miospores with a circular amb. Laesurae half to two thirds of the miospore radius, generally sinuous. This sinuosity of the laesurae is often most well developed at the proximal pole, and decreases along the radial length of the laesurae. Prominent lips, 1-2 µm wide, border the laesurae. The lips extend the full length of the
laesurae, bifurcating at their radial extremities and following the limit of the contact area for several µm. The exine of the contact area is markedly thinner than on the rest of the miospore. Exine laevigate. Exine moderately thick.

*Dimensions:* Body 72-78 (2 specimens; Schulze and 2% KOH).

*Comparison:* Laesurae generally shorter and lips much thinner than in *C. magna*. *C. magna* also has a thicker exine and may possess grana/verrucae, and usually features straight or only slightly curved laesurae.

*Occurrence:* Shortwood Top Coal and associated shales (Farrington Member).

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Subinfraturma NODATI Dybová and Jachowicz 1957a

Genus LOPHOTRILETES (Naumova) Potonié and Kremp 1954

Type species: *L. gibbosus* (Ibrahim) Potonié and Kremp 1955.

*Description:* Trilete miospores with a distinctly triangular amb with rounded apices. Interradials may be concave or convex. Laesurae generally two thirds to three quarters of the miospore radius. Ornamented with cones of approximately equal basal width and height. Exine moderately thick, but variable between species.

*Comparison:* Similar forms with spinate ornament will be referred to *Acanthotriletes*.

*Affinity:* Ferns.
Lophotriletes commissuralis (Kosanke) Potonié and Kremp 1955

Plate 4, Figure 7

1905  Granulatisporites commissuralis (Kosanke); Potonié and Kremp, p. 20.
1955  Lophotriletes commissuralis (Kosanke) Potonié and Kremp, p. 73.

Holotype: Kosanke (1950), pl. 3, fig. 1.

Description: Trilete miospores with a triangular equatorial outline with rounded apices and convex, to straight interradials. Laesurae half to three quarters of the miospore radius. Conate ornament 1-1.5 µm wide, and about 1 µm tall. Coni may be pointed, rounded or commonly flattened with only slight relief. 35-50 coni project at the equator. Exine moderately thick.

Dimensions: Body 32 (35) 48 (15 specimens; HF).

Discussion: Includes forms similar to Lophotriletes granoornatus Artüz; these forms have straight interradials with slightly more widely spaced ornament.

Comparison: L. commissuralis has smaller ornament other members of the genus.

Occurrence: Harry Stoke B borehole to roof of Parkfield Hard Coal, Hursley Hill (Winterbourne Formation to Radstock Member). Possibly below Salridge Coal (Downend Member).

Known range: Upper Langsettian to Bolsovian.
**Lophotriletes gibbosus** (Ibrahim) Potonié and Kremp 1954

Plate 4, Figure 8

1933  *Verrucosi-sporites gibbosus* Ibrahim, p. 25.
1938  *Azonotriletes gibbosus* (Ibrahim); Luber in Luber and Waltz, p. 29.
1944  *Granulati-sporites gibbosus* (Ibrahim); Schopf, Wilson, and Bentall, p. 33.
1950  *Verrucoso-sporites gibbosus* (Ibrahim); Knox, p. 317.
1954  *Lophotriletes gibbosus* (Ibrahim); Potonié and Kremp, p. 129.

**Holotype:** Potonié and Kremp (1955), pl. 14, fig. 220.

**Type locality:** Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

*Description:* Trilete miospores with a triangular equatorial outline with rounded apices and concave interradials. Laesurae roughly two thirds of the miospore radius. Dense coni cover the exine, 1.5-2 μm tall and wide at the base. Ornament spaced at intervals roughly equal to the basal diameter of the ornament. Around 40-45 coni project at the equator.

*Dimensions:* Body 42 (1 specimen; HF). Body 44 (1 specimen; Schulze and 2% KOH).

*Comparison:* *L. mosaicus* has a thicker exine with straight interradial regions, and much denser ornament which forms a negative reticulum where bases of the coni abut. Consequently, *L. mosaicus* has slightly more equatorial projections.

*Occurrence:* Harry Stoke B borehole (Winterbourne Formation). Possibly at Huckford Quarry (Mangotsfield Member).

*Known range:* Duckmantian to lower Bolsovian.
**Lophotriletes microsaetosus** (Loose) Potonié and Kremp 1955

Plate 4, Figure 9

1934  *Setosisporites microsaetosus* (Loose) Loose, p. 148.
1944  *Granulatisporites microsaetosus* (Loose); Schopf *et al.*, p. 33.
1950  *Spinoso-sporites microsaetosus* (Loose); Knox, p. 314.
1955  *Lophotriletes microsaetosus* (Loose); Potonié and Kremp, p. 74.

**Holotype:** Potonié and Kremp (1955), pl. 14, fig. 229.

**Type locality:** Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

**Description:** Trilete miospores with a triangular equatorial outline with rounded apices. Interradial regions are most commonly concave, but rare forms with straight or slightly convex interradials have been observed. Laesurae usually easily discernible, and may be open or have a slight darkening in the region of the proximal pole. Laesurae three fifths to over four fifths of the miospore radius. Exine fairly densely covered with 2-3 µm tall coni, which gradually taper to form a pointed apices. Bases of coni generally slightly less than their height (1-1.5 µm). 35-50 coni project at the equator, their bases do not touch. Exine moderately thin.

**Dimensions:** Body 32 (37) 49 (7 specimens; HF).

**Comparison:** *L. commissuralis* has smaller coni. *L. mosaicus* has thicker exine, a more consistently straight-sided triangular amb and fewer equatorial projections.

**Occurrence:** Harry Stoke B borehole to 65 The Dingle, below Salridge Coal to above Trench Coal (Winterbourne Formation to Farrington Member). Possibly to Parkfield Great Coal (Farrington Member).

**Known range:** Upper Duckmantian to Bolsovian.
**Lophotriletes mosaicus** Potonié and Kremp 1955

Plate 4, Figure 10

1955  *Lophotriletes mosaicus* Potonié and Kremp, p. 75

*Holotype:* Potonié and Kremp (1955), pl. 14, fig. 227.

*Type locality:* Baldur Seam, Ruhr Coalfield, Germany; Lower Bolsovian.

**Description:** Trilete miospores with a triangular equatorial outline with rounded apices and straight interradials. Laesurae obscured by ornament, extremities merge with narrow channels between ornament. Dense coni cover the exine, 2-3 \( \mu \text{m} \) tall and wide at the base. Ornament is very closely spaced, with a narrow negative reticulum forming between the bases of the coni. Coni taper gradually over their entire length to form a point, sometimes becoming falcate. Around 25-35 coni project at the equator. Exine is much thicker than other members of the genus.

**Dimensions:** Body 31 (35) 44 (5 specimens; HF).

**Comparison:** *L. microsaetosus* has a thinner exine, concave sides and wider spaced and non-falcate ornament. *L. gibbosus* has a thinner exine, concaved interradials and more well-spaced coni.

**Occurrence:** Harry Stoke B borehole (Winterbourne Formation). Possibly in Frome Bank Gardens (Mangotsfield Member)

**Known range:** Namurian C-Bolsovian.
Genus WALTZISPORA Staplin 1960

Type species: W. lobophora (Waltz) Staplin 1960.

Description: Trilete miospores with a triangular amb. Interradials may be straight, but more commonly strongly concave. The angular junction between the radial and interradial margins is the main diagnostic feature of this genus. This junction may be accompanied by a lateral expansion of the apices in some species (although this is not always present). Laesurae generally three fifths to four fifths of the miospore radius. Exine may be laevigate, granulate or conate depending on the species. Exine moderately thick.

Comparison: Tetanisporites Ravn is differentiated by the presence of raised lip-like structures which accompany the laesurae.

Discussion: Sullivan (1964) transferred this genus to Apiculati, based on the ornament of the type species. In some species, the laterally expanded apices are very subtle or absent. Smith and Butterworth (1967) also noted this feature in W. polita, where an angular junction between the radial and interradial margins occurs instead.

Affinity: Unknown, but morphology suggests a fern affinity.

Waltzispora planiangulata Sullivan 1964

Plate 4, Figure 11

Holotype: Sullivan (1964), pl. 57, fig. 25-30.

Type locality: Drybrook Sandstone, Forest of Dean Coalfield, England; Viséan.

Description: Trilete miospores. Amb triangular with very strongly concave sides, so that the interradial margins become parallel with the laesurae. Apices pointed or rounded, with an angular interface occurring where the radial and interradial margins meet.
Laesurae variable, reaching from half to four fifths of the way to the radius. Exine ornamented with 0.5-1.5 μm tall coni, which often appear flattened. Exine moderately thin.

*Dimensions:* Body 34 (37) 40 (3 specimens; HF).

*Comparison:* The relatively coarse conate ornament of this species differentiates it from the other species. This species is similar to *Tetanisporites*, but lacks the lip-like thickenings adjacent to the laesurae.

*Occurrence:* Harry Stoke B borehole to Winterbourne Railway Cutting (Winterbourne Formation to Mangotsfield Member).

*Known range:* Viséan to Namurian A (Neves et al., 1972). Reworked.

**Waltzispora polita** (Hoffmeister *et al.*) Smith and Butterworth 1967

Plate 4, Figure 12


*Holotype:* Hoffmeister *et al.* (1955), pl. 36, fig. 1.
*Type locality:* Carter No. 3 borehole (TCO-82), Hardinsburg Formation, Kentucky, U.S.A.; Viséan-Namurian.

*Description:* Trilete miospores. Amb triangular with very strongly concave sides, so that the interradial margins become parallel with the laesurae. Apices pointed, with another angular interface occurring where the radial and interradial margins meet. Laesurae variable, reaching from half to four fifths of the radius. Exine laevigate, with a scabrate ornament being faintly discernible in small patches. Exine moderately thin.

*Dimensions:* Body 29 (32) 36 (4 specimens; HF). Body 2-38 (2 specimens; Schulze and 2% KOH).
Comparison: *W. planiangulata* has a similar equatorial shape and size, but is differentiated by the presence of distinct coni.

Occurrence: Harry Stoke B borehole to 65 The Dingle, Bickley Wood to below Trench Coal (Winterbourne Formation to Farrington Member). Possibly also in Shortwood Top Coal (Farrington Member).

Known range: Viséan to Namurian A. Reworked.

**Waltzispora cf. sagittata** Playford 1962

Plate 4, Figure 13

*Holotype:* Playford (1962), pl. 79, fig. 12.
*Type locality:* Birger Johnson, Culm succession, Spitsbergen; Mississippian.

Description: Trilete miospores. Amb triangular with straight interradial margins. Apices pointed, and laterally expanded to form prominent mushroom-like radial areas. *Laesurae* may be open, around three fifths of the miospore radius. Exine ornamented with tiny grana, around 0.5 µm in width and height.

*Dimensions:* Body 45 (1 specimen; HF). Body 48 (1 specimen; Schulze and 2% KOH).

Discussion: Sullivan (1964) states that the radial extremities “show slight, but definite tangential expansion”. The Bristol specimens have a very prominent lateral expansion. The specimens also differ from the type descriptions in having straight interradials and shorter laesurae.

Comparison: The prominent laterally expanded apices make this species distinctive.

Occurrence: Harry Stoke B borehole to 65 The Dingle (Winterbourne Formation to Mangotsfield Member).
Known range: Viséan (Neves and Ioannides, 1974) to Langsettian (Neves, 1968)

Genus APICULATASPORITES (Ibrahim) Smith and Butterworth 1957

Type species: A. spinulistratus (Loose) Ibrahim 1933.

Description: Trilete miospores with a circular equatorial margin. Laesurae three fifths to four fifths of the miospore radius. Exine densely covered by tiny grana-sized coni of approximately equal size. Exine moderately thin.

Comparison: Similar sized ornament to the triangular Planisporites. Apiculatisporis have larger ornament. Ornament is similar to the coni of Crassispora kosankei, but Apiculatasporites lacks an equatorial crassitude and has a thicker exine overall.

Affinity: Fern.

Apiculatasporites spinulistratus (Loose) Ibrahim 1933

Plate 5, Figure 1

1932 Apiculata-sporites spimilistratus (Loose), Ibrahim, p. 37.
1934 Apiculati-sporites globosus Loose, p. 152.
1944 Punctati-sporites spinulistratus (Loose); Schopf et al., p. 31.
1950 Spinoso-sporites spinulistratus (Loose); Knox, p. 314.
1955 Planisporites spinulistratus (Loose); Potonié and Kremp, p. 71.
1960 Apiculatasporites spinulistratus (Loose) Ibrahim; Potonié, p. 38.

Holotype: Potonié and Kremp (1955), pl. 14, fig. 214.
Type locality: Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.
**Description:** Trilete miospores with a circular equatorial outline. Laesurae fairly easily discernible and reaching up to four fifths of the way to the equator. Coni stand less than 2 µm tall, with 1-1.5 µm wide bases. Coni generally appear somewhat squat as the basal diameter often slightly exceeds the height. Coni fairly loosely packed with spacing exceeding the basal diameter of the ornament. Exine moderately thin, but not often folded.

**Discussion:** Body 37 (43) 48 (1 specimen; HF). Body 39 (54) 72 (3 specimens; Schulze and 2% KOH).

**Comparison:** Ornament and size is similar to *Crassispora kosankei*. *A. spinulistratus* has thicker exine, a definite trilete mark and no equatorial crassitude. Ornament is similar to *Planisporites cf. granifer*, but *Planisporites* is reserved for triangular miospores.

**Occurrence:** Harry Stoke B borehole to Shortwood Hard Coal, Bickley Wood to above Trench Coal (Winterbourne Formation to Farrington Member).

**Known range:** Langsettian to Asturian.

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**Genus APICULATISPORIS Potonié and Kremp 1956**

1933 *Apiculatisporites* Ibrahim, p. 23.
1956b *Apiculatisporis* Potonié and Kremp, p. 94.

Type species: *A. aculeatus* Ibrahim 1933.

**Description:** Trilete miospores with a rounded-triangular or circular amb. Laesurae may be obscured by ornament, but exceed half of the miospore radius where observed. Coni with rounded or slightly pointed apices densely cover the exine. Ornament is generally closely spaced. Ornament may be reduced on the proximal face.
Comparison: _Lophotriletes_ are distinctly triangular, but may have similar ornament. _Apiculatasporites_ and _Planisporites_ have smaller ornament, with the latter being triangular.

Affinity: Ferns.

**Apiculatisporis abditus** (Loose) Potonié and Kremp 1955

Plate 5, Figure 2

1934 _Verrucosi-sporites abditus_ Loose, p. 154.
1944 ? _Raistrickia abditus_ (Loose); Schopf *et al.*, p. 55.
1950 _Verrucososporites abditus_ (Loose); Knox, p. 317.

*Holotype:* Potonié and Kremp (1955), pl. 14, fig. 237.

*Type locality:* Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

**Description:** Trilete miospores with a rounded-triangular or circular amb. Laesurae often obscured by ornament, but exceed half of the miospore radius when they are apparent. Coni with rounded or slightly pointed apices densely cover the exine, with basal diameters and heights of 4-6 µm. Ornament is very closely spaced, with only narrow channels between the coni bases. Coni within a single specimen are highly variable in size and shape. Ornament may be reduced on the proximal face. 20-30 coni project at the equatorial margin. Exine is thick.

*Dimensions:* Body 35 (54) 57 (4 specimens; HF). Body 44-55 (2 specimens; Schulze and 2% KOH).

**Comparison:** This species has the coarsest ornament of the genus. _Raistrickia fulva_ can be distinguished by its apiculate and more squat ornament. _Raistrickia aculeata_ has more spinate and widely spaced ornament.

**Occurrence:** Harry Stoke B borehole to Shortwood Top Coal (Winterbourne Formation to Farrington Member).
Known range: Langsettian to Asturian.

**Apiculatisporis aculeatus** (Ibrahim) Smith and Butterworth 1967
Plate 5, Figure 3

Description: Trilete miospores, with a circular to sub-triangular amb. Laesurae occupy around half of the miospore radius. Exine covered with variably shaped coni, less than 2 µm in height. Ornament is moderately spaced, the intervening spaces between the ornament generally slightly exceeding the basal diameter of the coni. Around 35-40 coni project at the equator. Exine is moderately thick.

Dimensions: Body 40 (44) 52 (4 specimens; HF). Body 44-53 (2 specimens; Schulze and 2% KOH).

Discussion: Smith and Butterworth (1967) state there are around 25-35 of the 2.5 µm coni project at the equatorial margin. The coni in Bristol specimens have slightly smaller coni, which may account for the slightly higher number of equatorial projections recorded.

Comparison: The ornament of the species is both finer and more well-spaced than other members of the genus. Apiculataspores spinulistratus has smaller, grana-sized coni. Crassispora kosankei has smaller coni, and a prominent equatorial crassitude.

Occurrence: Harry Stoke B borehole to below Westerleigh Hard Coal, Bickley Wood to below Salridge Coal (Winterbourne Formation to Farrington Member).
**Known range:** Langsettian to Asturian.

**Apiculatisporis spinososaetosus** (Loose) Smith and Butterworth 1967

Plate 5, Figures 4-5

1932 *Sporonites spinososaetosus* Loose in Potonié et al., p. 452.
1933 *Apiculatisporites spinososaetosus* (Loose); Ibrahim, p. 24.
1944 *Raistrickia spinososaetosus* (Loose); Schopf et al., p. 56.

**Holotype:** Potonié and Kremp (1955), pl. 14, fig. 249.

**Type locality:** Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

**Description:** Trilete miospores with a rounded-triangular amb. Laesurae almost totally obscured by ornament, range from three fifths to almost the full distance to the equator. Ornament of bluntly conical or falcate coni, around 2-4 µm in height and basal width. Interspersed with the coni, squat baculae-like processes may be common on some specimens. Ornament size and shape very variable even within a single specimen. Ornament fairly closely spaced. Exine thick.

**Dimensions:** Body 39 (47) 50 (7 specimens; HF). Body 48-54 (2 specimens; Schulze and 2% KOH).

**Comparison:** Ornament consists of both coni and bacula, which differentiates *A. spinososaetosus* from other member of the genus.

**Occurrence:** Harry Stoke B borehole to 65 The Dingle, Bickley Wood (Winterbourne Formation to Mangotsfield Member). Possible in Huckford Quarry (Mangotsfield Member).

**Known range:** Langsettian to Bolsovian.
Genus PLANISPORITES (Knox) Potonié 1960

Type species: *P. granifer* (Ibrahim) Knox 1950.

Description: Trilete miospores with a generally convex triangular equatorial margin. Laesurae three fifths to three quarters of the miospore radius. Ornament consists of small broad-based coni with only slight relief. Apices may be pointed or truncated.

Comparison: Grana-sized coni are a diagnostic feature which sets this genus apart from *Apiculatisporis*, which typically have larger and more varied coni. *Apiculatisporis* also tend to be more rounded-triangular or circular in equatorial view. *Planisporites* is similar to *Apiculatasporites*, differing only in possessing a triangular amb in polar view. *Converrucosisporites* may look superficially similar, but is verrucate on close inspection of the ornament.

Affinity: Lycopsid; Sigillarian. Also reported from cycadales.

Planisporites cf. granifer (Ibrahim) Knox 1950

Plate 5, Figure 6

1933  *Granulati-sporites granifer* Ibrahim, p. 22.
1944  *Punctati-sporites granifer* (Ibrahim); Schopf et al., p. 31.
1950  *Planisporites granifer* (Ibrahim); Knox, p. 315.

Holotype: Potonié and Kremp (1955), pl. 13, fig. 207.
Type locality: Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

Description: Trilete, triangular miospores with rounded apices. Interradials are generally convex, but rare straight sided specimens can occur. Laesurae may be open, reaching from three fifths to three quarters of the spore radius. Broad-based (up to 4 µm) coni ornament the exine. Spaces between ornament is highly variable, but usually slightly exceeds to the basal width of the ornament. Coni relief is low, around 1 µm. Due to the
low height of the ornament, the pointed nature of the coni are usually only apparent at high magnifications. Coni barely modify the outline of the miospore. Exine moderately thin.

*Dimensions:* Body 46 (49) 52 (4 specimens; Schulze and 2% KOH).

*Discussion:* Specimens from Bristol appear to be slightly smaller than typical; a size range of 85-100 µm was reported by Potonié and Kremp (1955) when using schulze, but specimens as small as 60 µm were recorded by Smith and Butterworth (1967) which is comparable with the Bristol representation of the species.

*Occurrence:* Harry Stoke B borehole (Winterbourne Formation). Possibly in Winterbourne Railway Cutting (Mangotsfield Member).

*Known range:* Upper Langsettian to Bolsovian.

**Genus ACANTHOTRILETES (Naumova) Potonié and Kremp 1954**

Type species: *A. ciliatus* (Knox) Potonié and Kremp

*Description:* Trilete miospores. Amb triangular with rounded apices. Interradial margins are more or less straight, but may be slightly convex or concave depending on the species. Laesurae may or may not be apparent, and are commonly found open. Exine covered with spinae which gradual taper to a sharp point. Spinae are generally loosely packed, with intervening spaces being equal to or exceeding the basal diameter of the ornament. Exine is moderately thin.

*Comparison:* Distinguished from *Lophotriletes* by having spinae instead of coni. A triangular amb and spinate ornament separate this genus from *Apiculatisporis*.

*Affinity:* Ferns.
**Acanthotriletes microspinosus** (Ibrahim 1933) Potonié and Kremp 1955

Plate 5, Figure 7

1944  *Granulati-sporites microspinosus* (Ibrahim); Schopf *et al.*, p. 33.
1950  *Spinosa-sporites microspinosus* (Ibrahim); Knox, p. 314.
1955  *Acanthotriletes microspinosus* (Ibrahim); Potonié and Kremp, p. 84.
1964  *Acanthotriletes microspinosus* (Ibrahim); Laveine, p. 133.

**Holotype:** Ibrahim (1933), pl. 6, fig. 52.

**Type locality:** Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

**Description:** Trilete miospores. Triangular amb, which can either have straight or slightly convex interradial regions. Laesura are not always clear, ranging from two thirds to three quarters of the miospore radius. Laesurae usually only visible when they are partially open. Ornament consists of 3-4 µm tall spinae, with 1-1.5 µm wide bases. The long, hair-like spinae taper gradually to a sharp point. Spaces between spinae approximately equal to the basal widths of the ornament. 30-40 spinae project at the equatorial margin. Exine is moderately thin.

**Dimensions:** Body 32 (36) 45 (7 specimens; HF). Body 36-48 (2 specimens; Schulze and 2% KOH).

**Comparison:** Similar miospore size and number of projections as *Lophotriletes microsaetosus*, but the latter is conate and has slightly shorter processes. *A. triquetrus* is generally slightly larger and possesses more numerous and shorter spinae than *A. microspinosus*.

**Occurrence:** Harry Stoke B borehole (Winterbourne Formation). Possibly in 65 The Dingle and Dingle leaf bed (Mangotsfield Member).

**Known range:** Duckmantian to Bolsovian (Laveine, 1965; Corsin *et al.*, 1967).
**Acanthotriletes triquetrus** Smith and Butterworth 1967

Plate 5, Figure 8

_Holotype:_ Smith and Butterworth (1967), pl. 8, fig. 13-14.
_Type locality:_ Darkslade borehole, Cannock Chase Coalfield, England; Bolsovian.

**Description:** Triangular amb, with rounded apices and straight to slightly concave interradial regions. Laesurae normally distinct, but where the commissure is open, the exine may fold backwards giving the illusion of irregular lips. Laesurae generally exceed two thirds of the radius of the miospore. Exine covered with spinae, around 2 µm long and 1 µm wide, which taper to a point or appear truncated due to damage. These are spaced around 1-2 µm apart. Around 40-70 spinae project at the equatorial margin, depending on the size of the miospore. Exine thin.

**Dimensions:** Body 30 (36) 38 (5 specimens; HF). Body 26-45 (2 specimens; Schulze and 2% KOH).

**Discussion:** The length of the laesurae in the Bristol representation of this species generally exceed the lengths stated by Smith and Butterworth (1967). Both the laesurae length and concave interradial regions of this species are more typical of _Lophotriletes_, but the ornament is distinctly spinate and not conate. _Lophotriletes commissuralis_ is similar, but with conate ornament which is generally wider than its height.

**Comparison:** _A. microspinosa_ has longer spinae, and fewer equatorial projections.

**Occurrence:** Harry Stoke B to 65 The Dingle (Winterbourne Formation to Mangotsfield Member).

**Known range:** Upper Duckmantian to Bolsovian.
**Genus IBRAHIMISPORES Artüz 1957**

Type species: *I. microhorridus* Artüz 1957

*Description:* Trilete miospores with a generally circular or rounded-triangular amb. Laesurae almost always obscured by the ornament. Exine ornamented by closely spaced, wide-based spinae and coni which heavily modify the outline of the miospores. Spinae and coni are sharp tipped, ranging from straight to falcate (“rose thorns” in Artüz (1959)). Exine moderately thick.

*Comparison:* *Kraeuselisporites* has thinner and sparser spinae and is cingulizonate.

*Affinity:* Unknown.

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**Ibrahimispores brevispinosus** Neves 1961

Plate 5, Figure 10

*Holotype:* Neves (1961), pl. 31, fig. 2.

*Type locality:* Hipper Sick, Derbyshire, England; Yeadonian

*Description:* Trilete miospores. Amb broadly rounded-triangular in shape, heavily modified by ornament. Laesurae almost always totally obscured by ornament, around half to three fifths of the miospore radius. Ornament consists of broad-based spinae, 5-11 μm in length and 3-8 μm in basal width. Spinae are hollow and gently taper to a sharp point, bearing thickened tips which are visible to some degree on all specimens. Spinae are densely packed, with 35-60 equatorial projections. Exine is moderately thick.

*Dimensions:* Body 55 (61) 73 (7 specimens; HF).
**Description:** Generally smaller than the 70-100 µm range reported by Neves (1961). However, Neves (1961) macerated with Schulze and KOH, which may partially account for the size discrepancy.

**Occurrence:** Harry Stoke B borehole (Winterbourne Formation).

**Known range:** Namurian A to Langsettian (Neves, 1961). Reworked.

**Genus TETANISPORITES** Ravn 1979

Type species: *T. granulatus* Ravn 1979.

**Description:** Trilete miospores with a strongly concave triangular equatorial outline. Junction between interradial and radial margin is often angular, as in *Waltzispora*. The apices may also be slightly pointed. Laesurae longer than one half of the miospore radius. A raised, thickened ridge borders the laesurae. Exine ornamented with grana or coni. Exine moderately thick.

**Comparison:** The lip-like thickenings which accompany the laesurae differentiate this genus from *Waltzispora*, which may have a similar equatorial outline and ornament.

**Affinity:** No in situ records. Likely ferns due to similarity with *Lophotriletes* and other fern spores.

**Tetanisporites sp.1**

Plate 5, Figure 11

**Description:** Trilete miospore with a very pronounced concave triangular equatorial outline. Where the interradial and radial margins meet, the junction tends to be angular. The apices also tend to be slightly pointed. Laesurae around half of the miospore radius,
bordered with a thickened and elevated ridge in the interradial position. These ridges may be discontinuous, but generally occur along the length of the laesurae. Exine ornamented with 1 µm coni. Exine moderately thick.

*Dimensions*: Body 31 (1 specimen; Schulze and 2% KOH).

*Occurrence*: 65 The Dingle (Mangotsfield Member). Possibly in Huckford Quarry (Mangotsfield Member).

### Subinfraturma BACULATI Dybová and Jachowicz 1957a

**Genus RAISTRICKIA (Schopf et al.) Potonié and Kremp**

*Type species*: *R. grovensis* Schopf in Schopf *et al.* 1944.

*Description*: Trilete miospores with a rounded, oval or rounded-triangular equatorial outline. Laesurae length varies from half to the full radial length of the miospore, depending on the species. Exine densely covered by baculate ornament of a variety of sizes and morphologies. Baculae may be; apiculate, clavate, pointed, squat, truncated or a mixture of these morphologies. The distal surface is always fairly densely ornamented, but the proximal pole may bear greatly reduced ornament in some species. Exine is generally fairly thick.

*Comparison*: The baculate nature of the ornament distinguishes this genus from other Apiculati.

*Discussion*: Raistrickia have very variable ornament, even within species. Quite broad species groupings were chosen to avoid an otherwise excessive amount of splitting.

*Affinity*: Ferns (Tedelacean).
Raistrickia aculeata Kosanke 1950
Plate 6, Figure 1

**Holotype:** Kosanke (1950), pl. 10, fig. 9.

**Type locality:** McCleary's Bluff Coal, McLeansboro Group , Illinois, U.S.A.; Asturian-Cantabrian.

*Description:* Trilete miospores with a round to rounded-triangular amb. Laesurae usually at least partially obscured by ornament, ranging from three fifths to four fifths of the miospore radius. Exine densely covered with wide based, blunt spines. Spines around 7 µm tall, and 3 µm wide at the base. Spines may taper gradually along their whole length, or tapering may exponentially increase towards the base giving the spines a double-concave profile. Ornament gradually decreases in height across on the proximal face towards the proximal pole. Around 30 processes project from the equatorial outline. Exine moderately thick.

*Dimensions:* Body 50 (55) 64 (8 specimens; Schulze and 2% KOH).

*Discussion:* The spines on Raistrickia aculeata Kosanke 1950 are longer and more slender than in the Bristol representation of this species. The species has been assigned to Raistrickia aculeata Kosanke 1950 due to the slight differences in the type of ornament. Kosanke (1950) also didn’t record a reduction in the proximal ornamentation in his species, which may highlight another difference between the Bristol specimens and the holotype.

*Comparison:* Raistrickia aculeata looks very similar to Apiculatisporis abditus, but can be differentiated by its more elongate spinate ornament compared to the latter. R. microhorrida baculae have distinctly truncated apices.

*Occurrence:* 65 The Dingle to Coalpit Heath High Coal and siltstones above Shortwood Hard Coal (Mangotsfield Member to Farrington Member). Possibly above Trench Seam (Farrington Member).
Known range: Asturian.

Raistickia fulva Artüz 1957
Plate 6, Figure 2

Holotype: Artüz (1957), pl. 3, fig. 19
Type locality: Sulii Seam, Zonguldak Coalfield, Turkey; Langsettian.

Description: Trilete miospores with a rounded-triangular amb. Laesurae typically reach or nearly reach the equator. Ornament consists of squat baculae, 2-6 µm wide at the base and less than 4 µm tall. The baculae may have truncated or slightly pointed apices, but the vast majority bear distinctly apiculate tips. Density of ornament varies between specimens, and may either be fairly dense or moderately well-spaced. Around 20 baculae project at the equator. Exine is moderately thick.

Dimensions: Body 38 (45) 52 (5 specimens; HF). Body 47-57 (2 specimens; Schulze and 2% KOH).

Discussion: Ornament seems to be slightly finer than recorded by Smith and Butterworth (1967), and is more comparable to the “3-4 µm finger-shaped warts” mentioned by Artüz (1957) in the holotype.

Comparison: Slight similarity to Apiculatisporis spinososaetosus, but R. fulva has much coarser ornament with apiculate tips.

Occurrence: Harry Stoke B borehole to 65 The Dingle, Stonehill unnamed Coal (Winterbourne Formation to Mangotsfield Member). Possibly in Bickley Wood (Downend Member)

Known range: Langsettian to Bolsovian
Raistrickia microhorrida (Horst) Potonić and Kremp 1955

Plate 6, Figure 3

1943  Triletes (?) (Apiculati) microhorridus Horst
1955  Raistrickia microhorrida (Horst); Potonić and Kremp, p. 86.

Holotype: Horst (1943), fig. 3b.
Type locality: Ostrauer Seam, Mährisch-Ostrau, Czech Republic; Namurian A.

Description: Trilete miospores with a round to oval body. Laesurae generally not visible through the coarse ornament, but exceed half of the miospore radius. Ornament of baculae with truncated apices, 4-8 µm tall and 2-4 µm wide at the base. Ornament appears to be greatly reduced in height on the proximal face, where it appears more like broad-rounded coni. Some baculae may show a subtle apical expansion. The sides of the baculae are more or less parallel, with no tapering. Intervening spaces between the baculae generally approximate or slightly exceed their basal width. 20-25 baculae project at the equator. Exine moderately thin.

Dimensions: Body 32 (43) 58 (8 specimens; HF). Body 65 (1 specimen; Schulze and 2% KOH).

Discussion: Horst (1955) didn’t note the reduced ornament seen on the proximal face in his specimens. Likely forms a continuum with R. saetosa, as both species are almost always found in association in the Bristol samples.

Comparison: R. aculeata has tapering spine-like processes. Similar to the baculae of R. saetosa, but lacking the distinctive apical fraying, and usually less densely packed.

Occurrence: Harry Stoke B borehole to Shortwood Top Coal, below Salridge Coal (Winterbourne Formation to Farrington Member)

Known range: Namurian A (Horst, 1955) to Langsettian (Neves, 1958)
**Raistrickia pilosa** Kosanke 1950

Plate 6, Figure 4

**Holotype:** Kosanke (1950), pl.11, fig. 4.

**Type locality:** No7 Coal Bed, McLeansboro Group, Illinois, U.S.A; Asturian

*Description:* Trilete miospores with a rounded-triangular body. Laesurae reach over four fifths of the way to the equator. Laesurae may be obscured by the ornament. Exine with long baculae with rounded, slightly pointed or apiculate apices. Baculae are very variable in length, but are generally less than 8 µm in length and 2-5 µm in basal width.

**Dimensions:** Body 23 (1 specimen; HF). Body 36 (1 specimen; Schulze and 2% KOH)

*Discussion:* While the baculae are shorter than the 10-13 µm stated by Kosanke (1950), they are still around a quarter of the miospore diameter. The smaller size of the miospore body may be due to the different maceration techniques used.

*Occurrence:* Harry Stoke B borehole to Dingle leaf bed (Winterbourne Formation to Mangotsfield Member).

*Known range:* Bolsovian to Asturian (Kosanke, 1950; Peppers, 1993).

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**Raistrickia cf. pistillata** Hacquebard 1957

Plate 6, Figure 5

**Holotype:** Hacquebard (1957), pl.2, fig. 2.

**Type locality:** West Gore, Horton Group, Nova Scotia, Canada; Tournaisian.

*Description:* Trilete miospores with a generally circular outline. Laesurae not seen. Exine ornamented with clavate baculae, around 4 µm tall. Stems 1.5-3 µm wide swelling to a bulbous 3-4 µm wide apex. Stem portion of the ornament much shorter
than the height occupied by the bulbous portion of the clavate baculae. 20-25 clavate baculae protrude in equatorial view. Exine moderately thin.

*Dimensions:* Body 40 (1 specimen; HF). Body 52 (1 specimen; Schulze and 2% KOH).

*Discussion:* Specimens were generally much smaller than the 72-84 µm quoted by Hacquebard (1957), and feature slightly shorter processes. For this reason, the Bristol specimens have been assigned to *Raistrickia cf. pistillata*.

*Comparison:* The clavate nature of the baculae differentiate this species from other species of *Raistrickia*.

*Occurrence:* Harry Stoke B borehole to Huckford Quarry (Winterbourne Formation to Mangotsfield Member). Possibly in Bickley Wood (Downend Member).

*Known range:* Tournaisian. Reworked.

**Raistrickia saetosa** (Loose) Schopf *et al.* 1944

Plate 6, Figures 6-7

1933 *Setosi-sporites saetosus* (Loose); Ibrahim, p. 26.
1944 *Raistrickia saetosus* (Loose); Schopf *et al.*, p. 56.

*Holotype:* Potonié and Kremp (1955), pl. 15, fig. 264.

*Type locality:* Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

*Description:* Trilete miospores with a rounded, or occasionally oval amb. Laesurae often totally obscured by ornament, when visible they extend for just over half of the way to the equator. Exine covered with baculae, mostly between 5 and 12 µm tall with 2-6 µm wide bases. Baculae on a single specimen are fairly uniform. Baculae are parallel sided, but may flare slightly at the apices. Apices are most commonly apiculate but some
baculae may bear rounded, pointed or truncated apices. 25-35 baculae project at the equator. Exine moderately thick.

*Dimensions:* Body 44 (47) 56 (6 specimens; HF). Body 50-53 (2 specimens; Schulze and 2% KOH).

*Comparison:* *Raistrickia fulva* also has apiculate ornament, but the bacula are more squat. *R. fulva* also has a rounded-triangular amb.

*Occurrence:* Harry Stoke B borehole to Westerleigh/Shortwood Hard Coal and roof shales of Parkfield Hard Coal, Bickley Wood to Hursley Hill borehole (Winterbourne Formation to Publow Member).

*Known range:* Langsettian to Asturian.

**Raistrickia cf. superba** (Ibrahim) Schopf *et al.* 1944

Plate 6, Figure 8

1933  *Setosi-sporites superbus* Ibrahim, p. 27
1944  *Raistrickia superbus* (Ibrahim); Schopf *et al.*, p. 56.

*Holotype:* Potonić and Kremp (1955), pl. 15, fig. 262.

*Type locality:* Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

*Description:* Trilete miospores with a round to oval amb. Laesurae not often observed, generally exceed two thirds of the radius. Variably spaced baculae ornament the miospore, 3-10 µm in length and up to 3 µm wide at the base. Baculae vary from being in close contact to be widely spaced, even on the same specimen. Large areas of the exine may therefore be devoid of ornament. Baculae more or less of the same width over their entire length, some may bear slightly swollen apices. The apices are also variable; being rounded, truncated, pointed or slightly apiculate. Less than 30 baculae are visible at the equator. Exine usually thinner than other members of the genus.
Discussion: It may be likely that this species will include other species of Raistrickia that are either immature or have been severely damaged. Smith and Butterworth also recorded very similar *R. cf. superba*; possessing highly variable ornament like *R. superba* but having a relatively thin exine. A similar *R. cf. superba* was also reported by Bharadwaj (1957b).

Comparison: *Raistrickia saetosa* has more numerous and uniform ornament, which typically show a greater tendency to be roughly parallel sided with apiculate apices. *R. saetosa* has correspondingly more equatorial projections, and a typically thicker exine.

Occurrence: Harry Stoke B borehole to below Westerleigh Hard Coal and roof of Parkfield Hard Coal, Golden Valley to below Salridge Coal (Winterbourne Formation to Farrington Member).

Known range: Langsettian to Bolsovian.

**Genus SPACKMANITES Habib 1966**

Type species: *S. ellipticus* Habib 1966

Description: Trilete miospores with a round to oval outline. Laesurae almost always totally obscured by ornamentation. Ornament of this genus consists of very closely packed baculae, with almost no intervening space between them. The baculae are typically parallel sided rods, and terminate at rounded or truncated apices. The ornament often appears to be fused at the base, and at the apices (to a lesser extent). Exine is moderately thin underneath the ornament.

Comparison: *Spackmanites* has distinctly closely spaced and partially fused baculae. The ornament is packed tightly as in some species of *Verrucosisporites*, but the
ornament is distinctly baculate and not verrucate. The baculae of *Raistrickia* are more variable, more well-spaced and are not partially fused.

**Discussion:** Ravn (1986) emended the generic description to only include alete miospores. With careful focusing on some of the Bristol specimens, a partial trilete mark can indeed be seen. The author therefore retains the original trilete diagnosis of Habib (1966).

**Affinity:** Unknown.

**Spackmanites habibi** Ravn 1986

Plate 6, Figure 9

1954 *Verrucososporites facierugosus* (Loose); Butterworth and Williams, p. 754.
1966 *Spackmanites facierugosus* (Loose); Habib, p. 638.
1979 *Spackmanites facierugosus* (Loose) Habib 1966, Ravn, p.32.
1979 *Verrucosisporites facierugosus* (Loose) Butterworth and Williams; Ettensohn and Peppers.
1986 *Spackmanites habibi* Ravn, p. 117.

**Holotype:** Ravn (1986), pl. 35, fig. 10.

**Type locality:** Blackoak Coal, Des Moines Group, Iowa, U.S.A.; Duckmantian.

**Description:** Trilete miospores with a round outline. Laesurae only partially seen with careful focusing. Exine covered with closely spaced rod-shaped baculae, which appear to be partially fused at their bases. Baculae are generally fairly squat, around 4-6 µm tall with 2-4 µm bases. The apices of the baculae are truncated or slightly rounded, some baculae may show subtle bifurcation. Exine below the ornament is moderately thin when visible.

**Dimensions:** Total 32 (39) 46 (5 specimens; HF). Total 37 (43) 46 (3 specimens; Schulze and 2% KOH).
Comparison: Ornament is similar in morphology to *Raistrickia microhorrida*, but it finer and much closer spaced.

Discussion: Harry Stoke B borehole to roof of Parkfield Hard Coal (Winterbourne Formation to Farrington Member).

Known range: Duckmantian (Habib, 1966) to Asturian (Peppers, 1970; Ravn, 1986).

**Infraturma MURORNATI Potonié and Kremp 1954**

**Genus SINUSPORES** (Artüz) McLean 2004

Type species: *S. sinuatus* (Artüz) Ravn 1986

Description: Trilete miospores. Amb circular or oval. Laesurae generally exceeds half of the radius of the miospore, but may reach four fifths in some species. Exine with broad sinusoidal/curved areas muri on the distal surface. Exine very thick.

Discussion: Artüz (1957) describe the equatorial structure as a cingulum (Gürtelzone). McLean *et al.* (2004) emended the genus and described this same feature as a “curvaturae ridge”, and describing the ornament as consisting of “low, broad, “sinuous muri and sometimes with low, broad verrucae”. Despite the presence of ornament, McLean *et al.* (2004) still placed the genus in Laevigati. The present author relocates the genus to Murornati, based on the murinate exine sculpture.

Affinity: Unknown.
**Sinuspores sinuatus** (Artüz) Ravn 1986

Plate 6, Figure 10

1957  **Sinuspores sinuatus** Artüz, p. 254.
1958  **Punctatisporites densoarcuatus** Neves, p. 6.
1958  **Punctatisporites coronatus** Butterworth and Williams, p. 360.
1986  **Sinuspores sinuatus** (Artüz) Ravn, p. 80.

**Holotype:** Artüz (1957), pl. 7, fig. 48.

**Type locality:** Sulu or Büyük Seam, Zonguldak Coalfield, Turkey; Langsettian.

**Description:** Trilete miospores. Amb circular or oval. Laesurae generally exceeds half of the radius of the miospore, but may reach four fifths in some species. Exine with broad sinusoidal/curved areas muri, 7-8 µm in width, on the distal surface. Exine very thick; 7 µm.

**Dimensions:** Body 90 (1 specimen; Schulze and 2% KOH).

**Comparison:** Very similar to **Punctatisporites obesus**, specifically **Punctatisporites cf. obesus**. The only differing feature is the sinusoidal muri, which differentiates **Sinuspores sinuatus**.

**Occurrence:** Dingle leaf bed to Huckford Quarry (Mangotsfield Member).

**Known range:** Langsettian to Duckmantian. Reworked.

**Genus CAMPTOTRILETES** (Naumova) Potonié and Kremp 1954

Type species: **C. corrugatus** (Ibrahim) Potonié and Kremp 1954.

**Description:** Trilete miospores with a triangular equatorial outline. Laesurae from half to two thirds of the miospore radius in length. Exine ornamented by an irregular network of rugulae, which may coalesce to form a poorly-defined reticulum in localised areas.
This ornament is restricted to the distal hemisphere of the miospores. Exine is moderately thick.

*Comparison:* Ornament is most similar to *Convolutispora*, but is typically irregular and not well developed.

*Affinity:* Ferns.

*Camptotriletes triangularis* Peppers 1970

Plate 6, Figure 11


*Type locality:* Between Colchester (No. 2) and Cardiff Coals, Carbondale Formation, Illinois; U.S.A.; Asturian.

*Description:* Trilete miospores with a triangular amb. Interradials are most commonly convex or straight, and apices are rounded. Rare specimens show slightly concave interradials with truncated apices. Trilete rays extend from half to two thirds of the radius of the miospore. The distal surface is covered with a low and variable network of rugulae, which anastomose and coalesce to form a poorly defined and patchy reticulum. The ornament is 2-3 µm wide, and less than 1 µm high with rounded apices.

*Dimensions:* Total 41 (42) 43 (4 specimens; HF). Total 36 (39) 43 (3 specimens; Schulze and 2% KOH).

*Discussion:* This species is commonly found in the Asturian of the Interior Basin of the United States of America, however, Ravn (1986) extends the range of this species to include the Duckmantian-Bolsovian Kilbourn and Floris formations of Iowa.

*Comparison:* Ornament differs from *Camptotriletes* sp. 1.
Occurrence: Harry Stoke B borehole to Parkfield Great Coal, Bickley Wood to below Salridge Coal (Winterbourne Formation to Farrington Member).

Known range: Duckmantian-Asturian (Ravn, 1986).

Camptotritetes sp.1
Plate 6, Figure 12

Description: Trilete miospores with a triangular amb. Interradials are most commonly convex or straight, and apices are rounded. Trilete rays extend from half to two thirds of the radius of the miospore. The distal surface is covered with a low and variable network of rugulae, which anastomose and coalesce to form a poorly defined and patchy reticulum. The ornament is 3 μm wide, and less than 3-5 μm high, with pointed apices.

Dimensions: Total 54 (1 specimen; HF).

Comparison: Ornament differs from Camptotritetes triangularis.

Occurrence: Huckford Quarry (Mangotsfield Member).

Genus CONVOLUTISPORA Hoffmeister et al. 1955
Type species: C. florida Hoffmeister et al. 1955.

Description: Trilete miospores with a round to oval amb. Laesurae usually more visible on the finer-ornamented species, ranges from half to over three quarters of the miospore radius. Ornament consists of convoluted rugulae which are closely packed, and often anastomose around and overlap each other. The size and disposition of the convolute rugulae vary between species. Exine generally fairly thin.
Comparison: Ornament consists of rugulae, anastomosing verrucae, muri and isolated verrucae.

Discussion: *Convolutispora* are a common feature of Viséan to Namurian assemblages, and have a patchy record in the Westphalian. Well-preserved *Convolutispora* are relatively common in both coals and clastics in the Bolsovian-aged Winterbourne Formation of Bristol, suggesting these are not reworked taxa.

Affinity: Fern.

*Convolutispora ampla* Hoffmeister *et al.*, 1955

Plate 7, Figure 1

*Holotype*: Hoffmeister *et al*. (1955), pl. 38, fig. 12.

*Type locality*: Hardinsburg Formation, Chester Series, Kentucky, U.S.A; Viséan-Namurian

Description: Trilete miospore with a circular to slightly oval outline. Laesurae range from half to two thirds of the miospore radius. Ornament consists of sinuous and irregular 2-3 μm wide rugulae which tend to fork before terminating. Rounded to polygonal verrucae may be interspersed with the rugulae, which are of a similar size. In plan view the ornament therefore consists of a tessellated pattern of elongated, forking elements and the more discrete verrucae. Ornament is around 1 μm tall with broadly rounded apices. Lumina are narrow and elongate, usually of uniform width. Exine thick.

*Dimensions*: Total 45 (67) 82 (6 specimens; HF).

Discussion: Rugulae may bifurcate, which is not mentioned in the original description.

Comparison: *C. finis* has finer, shorter and more regular and more closely packed ornament, and is generally smaller.
**Occurrence:** Harry Stoke B borehole to Huckford Quarry, below Salridge Coal (Winterbourne Formation to Mangotsfield Member). Possibly in Bickley Wood and siltstones above Shortwood Hard Coal (Downend Member to Farrington Member).

**Known range:** Viséan to Namurian.

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**Convolutispora finis** Love 1960

Plate 7, Figure 1

*Holotype:* Love, (1960) pl. 1, fig. 7.

*Type locality:* Pumpherson Shell Bed, Lower Oil-Shale Group, Scotland; Viséan.

**Description:** Trilete miospores with a round to slightly rounded-triangular outline. Laesurae range from half to two thirds of the miospore radius. Ornament consists of 1 µm wide convolute rugulae, which anastomose and branch along the length. Rugulae are of low relief, usually slightly less than their width. The rugulae, as well as the intervening spaces are fairly uniform in size. Lumina are narrower than the rugulae. Exine is moderately thin.

**Dimensions:** Total 42 (58) 69 (3 specimens; HF). Total 42 (46) 49 (5 specimens; Schulze and 2% KOH).

**Comparison:** *C. ampla* has coarser, taller and less regular and less closely packed ornament, and is generally larger. May look superficially like *Cyclogranisporites aureus*, which has similar sized granulate ornament. Careful focusing allows the confluent bases of the ornament to be seen, producing a rugulate ornament.

**Occurrence:** Harry Stoke B borehole to Coalpit Heath High Coal, Bickley Wood (Winterbourne Formation to Farrington Member).

**Known range:** Viséan (Love, 1960).
**Convolutispora florida** Hoffmeister *et al.* 1955

Plate 7, Figure 3

*Holotype:* Hoffmeister *et al.* 1955, pl. 38, fig. 6.
*Type locality:* Carter No. 3 borehole (TCO-82), Hardinsburg Formation, Kentucky, U.S.A; Viséan-Namurian.

**Description:** Trilete miospore with a circular to subcircular amb. Laesurae nearly always obscured by ornament. Densely packed, coarse convolute rugulae ornament the exine. Rugulae 2-7 µm wide and up to 4µ tall with well-rounded apices. Rugulae anastomose and overlap in a very irregular pattern. 10-20 rugulae project at the equator.

*Dimensions:* Total 30 (35) 38 (10 specimens; HF). Total 35-41 (2 specimens; Schulze and 2% KOH).

*Comparison:* This species is smaller than other members if the genus, and possesses relatively coarse ornament for its size.

*Occurrence:* Harry Stoke B borehole to siltstones above Shortwood Hard Coal (Winterbourne Formation to Farrington Member).

*Known range:* Viséan to Asturian (Love, 1960; Peppers, 1993; Peppers, 1996).

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**Convolutispora usitata** Playford 1962

Plate 7, Figure 4

*Holotype:* Playford (1962) pl. 9, fig. 9-10.
*Type locality:* Triungen Spitsbergen; Mississippian.

**Description:** Trilete miospores with a generally oval amb, although rare specimens with a triangular amb occur. Laesurae usually obscured by ornament, range from half to two thirds of the miospore radius. Exine ornamented by convoluted rugulae, 2-4 µm wide.
Rugulae do not tend to branch, but can be seen to bend through ninety degrees as they deflect around and even overlap other rugulae. Rugulae are broad and low with well-rounded apices, seldom exceed 1 µm in height. Lumina are very narrow, greatly subordinate to the rugulae. 20-40 rugulae project from the equator. Exine thick.

*Dimensions:* Total 43 (58) 90 (11 specimens; HF). Total 46 (59) 70 (4 specimens; Schulze and 2% KOH).

*Discussion:* The Bristol miospores are smaller than those Playford (1962) based his description, and are of a similar size range to other British miospores described by Smith and Butterworth (1967). The latter authors noted that the difference in size may be due to differing maceration methods. *Convolutispora mellita* Hoffmeister *et al.* 1955 is also similar to the species described above, and is known to range into the Bolsovian on Wales (Sullivan, 1962) and Desmoinesian (=Asturian) of Iowa (Ravn, 1986).

*Comparison:* The ornament of *C. usitata* is coarser and more regularly and coarsely convolute than *C. finis* and *C. ampla*. The comparative scarcity of forking of the coarse rugulae, and their tendency for near right-angled bends make the ornament of *C. usitata* distinctive.

*Occurrence:* Harry Stoke B borehole to Huckford Quarry, Golden Valley to Bickley Wood (Winterbourne Formation to Mangotsfield Member). Possibly in shales associated with Shortwood Hard Coal and below Salridge Coal (Downend-Mangotsfield Member boundary Farrington Member).

*Known range:* Viséan for *Convolutispora usitata*. Similar coarsely convolute *C. mellita* also found in Bolsovian/Asturian.
**Convolutispora varicosa** Butterworth and Williams 1958

Plate 7, Figure 5

*Holotype:* Butterworth and Williams (1958), pl. 2, figs. 22-23.

*Type locality:* Queenslie Bridge borehole, Central Coalfield, Scotland; Namurian A.

*Description:* Trilete miospores with a circular to oval amb. Laesurae range from half to two thirds of the miospore radius. Exine ornamented by low, irregular, convoluted rugulae, 3-5 µm wide and <3 µm tall which branch and anastomose. Rugulae vary in development and spacing on any specimen, but are typically spaced >4 µm apart. Ornament consist of polygonal verrucae in areas where rugulae are poorly developed, and regions on the exine may be devoid of ornament. Exine thick.

*Dimensions:* Total 44 (62) 75 (5 specimens; HF). Body 62-88 (2 specimens; Schulze and 2% KOH).

*Discussion:* The Bristol specimens are typically smaller than *C. varicosa.*

*Comparison:* The variable spacing of the ornament, as well as the discontinuous nature of the broad and low rugulae differentiates this genus from other members of the genus.

*Occurrence:* Harry Stoke B borehole to 65 The Dingle, below Salridge Coal (Winterbourne Formation to Mangotsfield Member)

*Known range:* *Convolutispora varicosa* ranges from the Namurian to Bolsovian.

**Convolutispora sp.1**

Plate 7, Figure 6

*Description:* Trilete miospores with a rounded-triangular amb. Laesurae between half and two thirds of the miospore radius. Ornament of very irregular, boudin-like rugulae
which widen and narrow along their lengths. Rugulae are around 3 µm wide and 2 µm tall, with broadly rounded apices. Lumina fairly regular in width,

*Dimensions:* Total 44 (54) 60 (3 specimens; HF).

*Comparison:* The varying widths of the boudin-like rugulae serve to distinguish this species from the fairly uniform and parallel sided rugulae of C. usitata.

*Occurrence:* Harry Stoke B borehole to Dingle leaf bed (Winterbourne Formation to Mangotsfield Member)

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**Genus MICRORETICULATISPORITES (Knox) Potonié and Kremp 1954**

Type species: *M. lacunosus* (Ibrahim) Knox 1950.

*Description:* Trilete miospores with a triangular to circular amb. Laesurae typically exceed two thirds of the miospore radius. Miospore covered with a reticulate ornament made up of fairly fine muri, with regular and narrow lumina. Lumina tend to be elongate, forming narrow troughs and small polygonal pits either side of the muri. Exine generally fairly thick.

*Comparison:* *Convolutispora* have a more convolute rugulate ornament, which never forms a well-defined reticulum. The ornament of *Dictyotritetes* is typically much coarser, with larger lumina.

*Affinity:* Tree fern.
**Microreticulatisporites nobilis** (Wicher) Knox 1950

Plate 7, Figure 7

1934  *Sporites nobilis* Wicher, pl. 15, fig. 279.
1944  *Punctati-sporotes nobilis* (Wicher); Schopf et al., p. 31.
1950  *Microreticulatisporites nobilis* (Wicher); Knox, p. 321.

*Holotype:* Potonié and Kremp (1955), pl. 15, fig. 279.
*Type locality:* Seam R, Wehofen Colliery, Ruhr Coalfield, Germany; Bolsovian.

**Description:** Trilete miospores with a triangular amb, with straight to slightly convex interradials. Apices are moderately pointed, to narrowly rounded. Laesurae usually fairly easily discernable, reaching from three quarters to the full radius of the miospore. Ornament is reticulate, made up of 2-3 μm wide muri which enclose 1-2 μm wide polygonal lumina. Muri are about 1 μm tall, with well-rounded apices. 30-40 muri project at the equatorial margin. Exine fairly thick.

*Dimensions:* Total 35 (39) 42 (9 specimens; HF). Total 37-45 (2 specimens; Schulze and 2% KOH).

**Comparison:** *M. sulcatus* has coarser ornament, with correspondingly few muri projections at the equator. It seems that these species grade into each other.

**Occurrence:** Harry Stoke B borehole to Shortwood Hard Coal and roof of Parkfield Hard Coal, Bickley Wood to below Trench Coal (Winterbourne Formation to Farrington Member).

**Known range:** Duckmantian to Asturian (Butterworth, 1964)
Microreticulatisporites punctatus Knox 1950

Plate 7, Figure 8


Type locality: Milton Main Seam, Righead borehole, West Fife Coalfield, Scotland; Namurian A.

Description: Trilete miospores with an oval to rounded amb. Laesurae half to two thirds of the radius. Reticulate ornament made up of 2 µm wide muri, with 1-4 µm wide polygonal lumina. Exine moderately thick.

Dimensions: Total 35 (41) 50 (3 specimens; HF). Total 49-55 (2 specimens; Schulze and 2% KOH).

Discussion: Lumina appear slightly larger than in Knox (1950) and Smith and Butterworth (1967).

Comparison: The circular amb of this species differentiates it from M. nobilis and M. concavus.

Occurrence: Harry Stoke B borehole to Huckford Quarry (Winterbourne Formation to Mangotsfield Member).

Known range: Namurian. Reworked.
**Microreticulatisporites sulcatus** (Wilson and Kosanke) Smith and Butterworth 1967

Plate 7, Figure 9

1944 *Punctati-sporites sulcatus*; Wilson and Kosanke.


**Cotype:** Wilson and Kosanke (1944).

**Type locality:** Angus Coal Co. Colliery, Iowa, U.S.A.; Asturian

**Description:** Trilete mioospores with a triangular amb, with straight to slightly convex interradials. Apices are moderately pointed, to narrowly rounded. Laesurae usually fairly easily discernible, reaching from three quarters to the full radius of the mioospore. Ornament is reticulate, made up of 4-7 µm wide muri which enclose 1-2 µm wide polygonal lumina. Muri are about 1 µm tall, with well-rounded apices. 18-25 muri project at the equatorial margin. Exine fairly thick.

**Dimensions:** Total 44-45 (2 specimens; Schulze and 2% KOH).

**Comparison:** Coarser ornament, with correspondingly few muri projections at the equatorial margin than *M. nobilis*.

**Occurrence:** Huckford Quarry to roof Parkfield Hard Coal, below Trench Coal (Mangotsfield Member to Farrington Member).

**Known range:** Bolsovian to Asturian.

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**Genus DICTYOTRILETES (Naumova) Smith and Butterworth 1967**

Type species: *D. bireticulatus* (Ibrahim) Potonié and Kremp 1954.
Description: Trilete miospores with a generally round to oval amb. Laesurae generally obscured by the ornament of the exine. Prominent reticulate ornament covers the distal surface, or both hemispheres in some species. Reticulate ornament consists of a well-developed mesh-like network of muri which enclose comparatively large polygonal lumina. Exine of variable thickness.

Comparison: The mesh-like network of muri are distinctly different than the muri of Microreticulatisporites. Reticulatisporites has a similar style of muri, but has a prominent tripartite cingulum. Cordylosporites features prominent crestal modifications of the muri at their junctions.

Affinity: Ferns. D. muricatus (as Reticulatisporites muricatus) has been recovered from cones of possible sphenophylls affinity (Bek and Libertín, 2010)

Dictyotriletes bireticulatus (Ibrahim) Smith and Butterworth 1967

Plate 7, Figure 10

1932  Sporonites bireticulatus Ibrahim in Potonié et al., p. 447.
1933  Reticulati-sporites bireticulatus Ibrahim, p. 35.
1934  Reticulata-sporites bireticulatus Ibrahim; Loose.
1950  Reticulatisporites mediareticulatus Ibrahim; Knox, p. 323.
1952  Reticulatisporites mediareticulatus Ibrahim; Balme, p. 176.
1952  Reticulati-sporites cf. mediareticulatus Ibrahim; Balme and Butterworth.
1954  Reticulati-sporites cf. mediareticulatus Ibrahim; Butterworth and Millott.
1956  Reticulatisporites mediareticulatus Ibrahim; Butterworth and Millott.
1967  Dictyotriletes bireticulatus (Ibrahim) Smith and Butterworth, p. 194.

Holotype: Potonié and Kremp (1955), pl. 16, fig. 296.
Type locality: Ágir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

Description: Trilete miospores with a triangular amb, with straight to convex interradials and rounded apices. Laesurae may be highlighted by prominent folds, and
extend for over three quarters of spore radius. Reticulate ornament restricted to the distal hemisphere. 1-1.5 μm wide muri enclose 3-10 μm polygonal lumina. The lumina on any one specimen are fairly regular in size and shape, 15-20 lumina are delimitated by the mesh-work. Exine moderately thin.

**Dimensions:** Total 33 (39) 45 (8 specimens; HF). Total 31 (37) 40 (4 specimens; Schulze and 2% KOH).

**Discussion:** Present in Westerleigh Hard Coal, and generally doesn’t have the same appearance as other reworked taxa.

**Comparison:** The triangular amb and fine, regular reticulum makes this species fairly distinct from other *Dictyotriletes*.

**Occurrence:** Harry Stoke B borehole to Westerleigh Hard Coal and roof of Parkfield Hard Coal, Bickley Wood (Winterbourne Formation to Farrington Member).

**Known range:** Langsettian to lower Bolsovian.

*Dictyotriletes muricatus* (Kosanke) Smith and Butterworth 1967

Plate 7, Figure 11

1950 *Reticulati-sporites muricatus* Kosanke, p. 27.

**Holotype:** Kosanke (1950), pl. 4, fig, 7.

**Type locality:** La Salle Coal, Upper Mcleansboro Group, Illinois; USA; Asturian-Cantabrian.

**Description:** Trilete miospores with a circular to oval outline. Laesurae usually fairly easily discernible despite the coarse ornament, about half to two thirds of the miospore radius. Prominent reticulate ornament, which appears to only be developed distally. Muri 2-4 μm wide and project up to 15 μm at the equator. Lumina enclosed by the muri
are large and polygonal, and difficult to measure due to the way the tall muri collapse over the body upon compression. Exine moderately thin.

*Dimensions:* Total 51 (65) 70 (4 specimens; HF). Total 66 (80) 87 (4 specimens; Schulze and 2% KOH).

*Comparison:* *Reticulatisporites reticulatus* looks superficially similar, but is cingulate and features a distinctive tripartite equatorial structure.

*Occurrence:* Harry Stoke B borehole to 65 The Dingle (Winterbourne Formation to Mangotsfield Member).

*Known range:* Langsettian to lower Bolsovian.

**Genus Reticulitriletes (Mädler) Ravn 1986**

1964a *Reticulitriteles* Mädler, p. 76.

Type species: *R. globosus* Mädler 1964.

*Description:* Trilete miospores with a generally round to oval amb. Laesurae generally obscured by the ornament of the exine. Prominent reticulate ornament covers the both hemispheres in some species. Reticulate ornament consists of a well-developed mesh-like network of muri which enclose comparatively large polygonal lumina. Exine of variable thickness.

*Comparison:* The mesh-like network of muri are distinctly different than the muri of *Microreticulatisporites*. *Reticulatisporites* has a similar style of muri, but has a prominent tripartite cingulum. *Cordylosporites* features prominent crestal modifications of the muri at their junctions. *Dictyotritiles* features a reticulate distal hemisphere only.
**Affinity:** Almost certainly ferns, like the morphological similar *Dictyotriletes.*

**Reticulitriletes clatriformis** (Artüz) Ravn 1986

Plate 7, Figure 12

1957 *Reticulatisporites clatriformis* Artüz, p.248.

**Holotype:** Artüz (1957), pl. 4, fig. 25.
**Type locality:** Büyük Seam, Zonguldak Coalfield, Turkey; Langsettian.

**Description:** Trilete miospores with a round or oval equatorial outline. Laesurae nearly always totally obscured by ornament. Exine covered by prominent reticulation. 2 µm wide muri enclose the fairly regular polygonal 4-7 µm lumina. Muri may be of variable height, ranging from 1-4 µm, which may be a feature of different compression orientations or differing maturity of the miospores. 15-30 muri project in equatorial view.

**Dimensions:** Body 37 (41) 55 (4 specimens; HF). Total 36-55 (2 specimens; Schulze and 2% KOH).

**Comparison:** The generally round shape of the amb and reticulation appearing on both hemispheres differentiate this from *D. bireticulatus.*

**Occurrence:** Harry Stoke B borehole to shales associated with Shortwood Top Coal, (Winterbourne Formation to Farrington Member).

**Known range:** Langsettian to Bolsovian.
**Reticulitriletes falsus** (Potonié and Kremp) Ravn 1986

Plate 8, Figure 1

1965  *Dictyosporites falsus* (Potonié and Kremp) Laveine, p. 133.

**Holotype:** Potonié and Kremp (1955), pl. 16, fig. 303.

**Type locality:** Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

*Description:* Trilete miospores with an oval equatorial outline. Laesurae half to three quarters of the miospore radius. 2-3 µm broad muri form a reticulate ornament, with very irregularly shaped 2 µm wide lumina. The lumina may be polygonal, elongate or slit like (with all these morphologies occurring on a single specimen). Muri are low, projecting less than 2 µm at the equator. Around 15 muri project at the amb. Exine moderately thin for the genus.

*Dimensions:* Total 38 (40) 44 (3 specimens; HF). Total 38 (44) 52 (7 specimens; Schulze and 2% KOH).

*Comparison:* The highly irregular nature of the lumina are diagnostic of this species.

*Occurrence:* Harry Stoke B borehole to 65 The Dingle, Bickley Wood to below Salridge Coal (Winterbourne Formation to Mangotsfield Member).

*Known range:* Langsettian to lower Bolsovian.

**Genus CORDYLOSPORITES** Playford and Satterthwait 1985

Type species: *C. sepositus* Playford and Satterthwait 1985.

*Description:* Trilete miospores with a generally round to oval amb. Laesurae generally obscured by the ornament of the exine. Prominent reticulate ornament covers the distal
surface; may be absent or greatly reduced proximally. Reticulate ornament consists of a well-developed mesh-like network of muri which enclose comparatively large polygonal lumina. Muri feature baculae-like crestal modifications, formed at the junction between two or more muri. Exine of variable thickness.

Comparison: Crestal modification of muri differentiates this genus from *Dictyotriletes*.

Affinity: Almost certainly ferns, like the morphological similar *Dictyotriletes*.

**Cordylosporites papillatus** (Naumova) Playford and Satterthwait 1985

Plate 8, Figure 2

1938 *Aptea papillata* Naumova, p.27.
1963 *Dictyotriletes papillatus* (Naumova) Byvscheva, p. 599.
1971 *Reticulatisporites papillatus* (Naumova) Playford, p. 31-32.
1977 *Dictyotriletes peltatus* (Playford) Clayton *et al.* pl. 13, fig.3.
1985 *Cordylosporites papillatus* (Naumova) Playford and Satterthwait, p. 145.

**Holotype:** Naumova (1938), pl. 3, figs. 2.

**Type locality:** Unable to acquire a copy of the original text to check this information.

**Description:** Trilete miospores with a round to slightly oval body. Laesurae nearly always totally obscured by ornamentation, but are typically around three quarters of the miospore radius. Coarsely reticulate exine, with 3-4 µm wide muri enclosing irregular polygonal lumina around 5-10 µm in diameter. Muri junctions feature crestal modifications; 4-9 µm clavate process projects at right angles to the miospore surface. This clavae consist of a 3 µm stem which swells to form a bulbous 4-5 µm wide mass at the apex. 10-25 of these clavate project at the equator. Exine moderately thick.

**Dimensions:** Total 45 (60) 71 (7 specimens; HF). Total 58 (72) 90 (3 specimens; Schulze and 2% KOH).
Comparison: The clavate processes at the junctions of the muri differentiate this species from member of Dictyotriletes.

Occurrence: Harry Stoke B borehole to Winterbourne Railway Cutting (Winterbourne Formation to Mangotsfield Member).

Known range: Namurian A (Clayton et al., 1977). Reworked.

**Infraturma PSEUDOCINGULATI Neves 1961**

**Genus SECARISPORITES Neves 1961**

Type species: S. lobatus Neves 1961

Description: Trilete miospores with a circular, oval or rounded-triangular equatorial outline. Laesurae reach to the equatorial margin. Exine ornamented with a dense network of anastomosing rugulae and verrucae, which coalesce to form a highly irregular reticulum on the distal face of the miospore. At the equator, these rugulae expand into a series of broad lobate projections. Several rugulae may unite and fuse into a single, large lobe. The lobes vary in size and continuity on any single specimen. Exine is moderately thick.

Comparison: Distal ornament is similar to Convolutispora. The ornament at the edges of Secarisporites overlaps the amb and fuses into lobate pads, which separates it from Convolutispora.

Affinity: Unknown.
Secarisporites remotus Neves 1961
Plate 8, Figures 3-4

Holotype: Neves (1961), pl.32, fig. 8-9.
Type locality: Pot Clay Coal, Derbyshire Coalfield, England; Namurian (Yeadonian).

Description: Trilete miospores with a rounded-triangular to circular equatorial outline. Laesurae are often at least partially obscured by the ornament, but generally reach the equatorial margin. Distally the exine is ornamented with a complex and dense network of rugulae and isolated verrucae. The rugulae anastomose freely, and branch and coalesce to form a prominent but irregular distal reticulum. At the equatorial margin, one or more rugulae may fuse onto one of several large lobate projections. These projections vary from 5 to 20 µm in breadth and 2-5 µm in height. Between 5 and 10 lobate pads project at the equatorial margin. Exine is moderately thick.

Dimensions: Total 30 (36) 41 (6 specimens; HF). Total 40 (43) 46 (3 specimens; Schulze and 2% KOH).

Comparison: Convolutispora florida has a broadly comparable ornament, but lacks the large lobate projections at the equator.

Occurrence: Harry Stoke B borehole to Huckford Quarry (Winterbourne Formation to Mangotsfield Member).

Subturma ZONOTRILETES Waltz 1935
Infraturma AURICULATI (Schopf) Dettmann 1963
Genus AHRENSISPORITES Potonié and Kremp 1954

Type species: *A. guerickei* (Horst) Potonié and Kremp 1954.

**Description:** Trilete microspores with a triangular equatorial outline, with straight to slightly convex interradials. Apices may be rounded, or truncated. Prominent auriculae occur at the apices, which often project and laterally expand beyond the equator. These auriculae are connected via a kyrtome, which are along the interradial regions of the distal surface of the microspore. Laeisurae may extend slightly into the auriculae. Exine laevigate or granulate.

**Comparison:** The apical thickenings are less well developed in *Triquitrites*, and are not connected via a kyrotome. *Tripartites* auriculae also do not feature a kyrotome connection.

**Affinity:** Gleichenacean fern, based on similarity with *Triquitrites* and *Tripartites*

*Ahrensisporites guerickei* (Horst) Potonié and Kremp 1954

Plate 8, Figure 5

<table>
<thead>
<tr>
<th>Year</th>
<th>Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>1943</td>
<td><em>Triletes guerickei</em> Horst</td>
</tr>
<tr>
<td>1954</td>
<td><em>Ahrensisporites guerickei</em> (Horst); Potonié and Kremp, p. 155.</td>
</tr>
</tbody>
</table>

**Holotype:** Horst (1955), pl. 23, fig. 63.

**Type locality:** Seam VI, Karsten Central Colliery, Beuthen, Upper Silesia; Langsettian.

**Description:** Trilete microspores with a triangular equatorial outline. Interradials may be straight to slightly convex, and apices may be rounded or truncated. Prominent auriculae occur at the apices, which project beyond the equatorial outline of the microspore and often expand laterally along their radial lengths. Auriculae 10-16 µm wide, and 6-8 µm
in radial length. These auriculae are connected by a prominent and unbroken kyrtome in the interradial region of the distal surface, and arcs towards the distal pole. The kyrotome is generally 3-5 µm wide in polar view, and generally of a fairly constant width with only slight undulation. Laesurae exceed half of the miospore radius, and may reach the inner margin of the auriculae. Exine typically laevigate, but may feature scattered grana.

*Dimensions:* Total 32 (38) 52 (8 specimens; HF). Total 39-44 (2 specimens; Schulze and 2% KOH).

*Comparison:* *Triquitrites sinani* has a kyrotome-like structure, with ridges extending from the valvae on the distal side of the equator. This kyrotome-like structure does not join up at the distal pole, or may only join up some of the ridges. The discontinuous nature of this structure is different from the true kyrotome-bearing *Ahrensisporites* miospores.

*Occurrence:* Coombe Brook to Huckford Quarry, Bickley Wood (Winterbourne Formation to Mangotsfield Member).

*Known range:* Namurian to Duckmantian (Smith and Butterworth, 1967). Reworked.

**Genus TRIPARTITES (Schemel) Potonié and Kremp 1954**

Type species: *T. vetustus* (Horst) Schemel 1950.

*Description:* Trilete miospores with a triangular outline, with concave interradials. Prominent auriculae are situated at the apices, which project beyond the equatorial outline. The auriculae are fan shaped; laterally expanding as they project from the equator, giving the miospore a tri-lobed appearance. Auriculae may be connected in the interradial regions of the equator by a flange. Laesurae may reach the inner margin of the auriculae. Exine laevigate.
Comparison: *Triquitrites* features less well developed (valvate) radial thickenings which lack the radial plications and typically do not project considerably beyond the miospore equator. *Ahrensisporites* features a prominent kyrotome connecting the auriculae.

Affinity: Gleichenacean tree fern with structurally similar *Triquitrites*.

**Tripartites trilinguis** (Horst) Smith and Butterworth 1967

Plate 8, Figure 6

1943  *Triletes (Zonales) trilinguis* Horst.
1957  *Tripartites cristatus* Dybova and Jachowicz, p. 141.
1957  *Tripartites rugosus* Dybova and Jachowicz, p. 139.
1957  *Tripartites trifoliatus* Dybova and Jachowicz, p. 140.
1958  *TripartitesIanthina* Butterworth and Williams, p. 373

**Holotype:** Horst (1955), pl. 23, fig. 56.
**Type locality** Flora Seam, Michael Colliery, Moravska-Ostrava; Namurian A.

**Description:** Trilete miospores with a strongly concave triangular equatorial outline, and rounded apices. Auriculae project beyond amb, expanding laterally along their radial length to give them a fan-shape. The strongly concave interradials and fan-shaped auricular give the miospores a distinctive tri-lobed equatorial outline. Laesurae exceed half of the radial length, and may almost reach the inner margin of the auriculae. Exine laevigate.

**Dimensions:** Total 42 (1 specimens; HF).

**Comparison:** *T. vetustus* is very similar, but typically has plicated auriculae which are less laterally expanded so that the equatorial outline doesn’t become tri-lobed. *Westphalensisporites* is cingulate, but may look similar to *T. trilinguis* specimens that have a relatively broad or undulating equatorial flange.
Occurrence: Mangotsfield coals of Church Lane Colliery to Huckford Quarry (Downend-Mangotsfield Member boundary to Mangotsfield Member).

Known range: Upper Viséan to Namurian. Reworked.

Tripartites vetustus Schemel 1950

Plate 8, Figure 7

Holotype: Schemel (1950), pl. 40, fig. 11.

Type locality Coal ~550 ft. above uppermost Madison Formation, Utah, U.S.A.; Mississippian.

Description: Trilete miospores with a concave triangular equatorial outline, and rounded apices. Auriculae project beyond amb and are strongly radially plicated, giving them a sharply undulating equatorial outline. Laesurae exceed half of the radial length, and may almost reach the inner margin of the auriculae. Exine laevigate.

Dimensions: Total 36–49 (2 specimens; HF). Total 35 (1 specimens; Schulze and 2% KOH).

Comparison: The auriculae of T. trilinguis are fan shaped which; combined with the strongly concave interradials, gives this species a distinctly tri-lobed equatorial outline.

Occurrence: Grove Cottage to Huckford Quarry (Mangotsfield Member).

Known range: Upper Viséan to Namurian. Reworked.
Genus TRIQUITRITES (Wilson and Coe) Potonié and Kremp 1954

Type species: T. arculatus Wilson and Coe 1940.

*Description:* Trilete miospores with a triangular outline, apices may be rounded or truncated. Exine at the apices is thickened, so as to form discrete valvae. Valvae typically do not project beyond the equatorial outline, or only project slightly. Valvae shape varies from smooth to lobed or crenulated. The valvae may be joined by a narrow equatorial flange in rare cases. Laesurae exceed half of the miospore body radius, and often reach close to or into the inner margin of the valvae. Exine laevigate on most species, with some species developing verrucae or rugulae on the distal surface.

*Comparison:* Ahrensisporis has a kyrotome. The auriculae of Tripartites are larger, crinkled more fan-shaped.

*Affinity:* Fern (Gleichenacean) (Yao and Taylor, 1988).

**Triquitrites cf. additus** Wilson and Hoffmeister 1956

Plate 8, Figure 8

*Holotype:* Wilson and Hoffmeister (1956), pl. 3, fig. 6.

*Type locality:* Croweburg Coal, Des Moines Series, Oklahoma, U.S.A.; Asturian

*Description:* Trilete miospores with a triangular outline and rounded apices. Interradials may be straight, rounded or concave. Apices thickened to produce valvae, which project beyond the equatorial outline of the miospore body. Valvae are poly-lobed, commonly with three to five lobes, which feature subtle radial plications which coincide with the lobes. Valvae may extend into the interradial regions, producing a continuous equatorial flange which connects the valvae. Valvae range in width from 18-24 µm, and 6-8 µm in radial length. Laesurae exceed three fifths of the miospore radius, often reaching the
inner margin of the valvae. Exine laevigate, with scattered low-relief verrucae on the distal surface of some specimens.

Dimensions: Total 35 (37) 43 (5 specimens; Schulze and 2% KOH).

Discussion: T. cf. additus features plicated valvae and a variable equatorial cingulum which is not present on the type species. Wilson and Hoffmeister (1956) also describe T. additus as having “tubular or lobed projections, 9 to 10 microns long and 2.5 to 9 microns wide” on the valvae, which are much smaller than the subtly rounded lobes on the Bristol specimens.

Comparison: Verrucate specimens may look superficially similar to Triquitrites sculptilis, but the verrucae are much more infrequent and are not fused at the base. The valvae of T. sculptilis do not project beyond the miospore body in such a pronounced way.

Occurrence: Harry Stoke B borehole to Shortwood Top Coal, below Salridge Coal (Winterbourne Formation to Farrington Member).

Known range: Asturian (Wilson and Hoffmeister, 1956).

**Triquitrites bransonii** Wilson and Hoffmeister 1956

Plate 8, Figure 9

*Holotype:* Wilson and Hoffmeister (1956), pl. 3, fig. 1.

*Type locality:* Croweburg Coal, Des Moines Series, Oklahoma, U.S.A.; Asturian

Description: Trilete miospores with a triangular outline and truncated or narrowly rounded apices. Interradials typically straight or slightly convex, with rare specimens featuring slightly concave interradials. Apices thickened to produce valvae which vary in development, ranging from a slight darkening of the apices to dense pads which
project beyond the equatorial outline of the miospore. Where the valvae project beyond
the miospore body, the valvae are generally smooth and may be rounded, truncated or
lobed. Valvae range in width from 10 to 20 µm, and 3-8 µm in radial length. Laesurae
exceed half of the miospore radius, often reaching the inner margin of the valvae, and
may be open. Exine laevigate.

*Dimensions:* Total 31 (35) 41 (5 specimens; HF). Total 30 (32) 34 (3 specimens; Schulze and 2% KOH).

*Comparison:* *Triquitrites tribullatus* is bigger (>40 µm), with a much higher tendency
towards bilobed valvae.

*Occurrence:* Harry Stoke B borehole to Westerleigh Hard Coal, Bickley Wood to above
Trench Coal (Winterbourne Formation to Farrington Member). Possibly in Golden
Valley (Winterbourne Formation).

*Known range:* Upper Bolsovian to Asturian.

*Triquitrites sculptilis* (Balme) Smith and Butterworth 1967

Plate 8, Figure 10

1952  *Triquitrites sculptilis* Balme, p. 181.
1957b  *Triquitrites coesfelcieits* Bharadwaj, p. 123.
1958  *Triquitrites buccuientus* Guennel, p. 73.

*Lectotype:* Balme (1952), pl. 12, fig 10-11.
*Type locality* Seam at 670 ft. 10 in., Manton Colliery No. 4 Shaft, Yorkshire Coalfield,
England; Bolsovian.

*Description:* Trilete miospores with a triangular outline and truncated or narrowly
rounded apices. Interradials almost always straight to slightly concave, but modification
of the equatorial outline by the exine ornament gives most specimens an irregular
outline. Apices thickened to produce often indistinct valvae which seldom modify the
outline of the apices. Valvae may extend to form a narrow interradial flange-like connection around the miospore equator. Laesurae exceed three fifths of the miospore radius and often reach the inner margin of the valvae. Exine laevigate proximally. The distal surface of the miospore is ornamented by low relief verrucae, which coalesce to form an irregular network.

*Dimensions:* Total 28 (32) 40 (9 specimens; HF). Total 33 (1 specimen; Schulze and 2% KOH).

*Discussion:* Extreme forms may feature a poorly formed reticulum, approaching that of *Triquitrites cf. sculptilis.*

*Comparison:* *Triquitrites sculptilis* features a distinctive ornament and comparatively ill-defined valvae compared with the other species. *T. cf. sculptilis* has a more prominent sculpture typically forming a well-defined, though discontinuous, reticulum.

*Occurrence:* Harry Stoke B borehole to roof of Parkfield Hard Coal, Golden Valley to below Salridge Coal (Winterbourne Formation to Farrington Member).

*Known range:* Upper Duckmantian to lower Asturian.

*Triquitrites cf. sculptilis* (Balme) Smith and Butterworth 1967

Plate 8, Figure 11

*Description:* Trilete miospores with a triangular outline and truncated or narrowly rounded apices. Interradials almost always straight to slightly concave, but modification of the equatorial outline by the exine ornament gives most specimens an irregular outline. Apices thickened to produce often indistinct valvae which seldom modify the outline of the apices. Valvae may extend to form a narrow interradial flange-like connection around the miospore equator. Laesurae exceed three fifths of the miospore radius and often reach the inner margin of the valvae. Exine appears laevigate
proximally. The distal surface of the miospore is ornamented by a poorly developed reticulum.

*Dimensions:* Total 32 (33) 37 (5 specimens; HF).

*Comparison:* *Triquitrites sculptilis* is characterised by low relief coalescing verrucae, which even on the most ornamented specimens never approaches the prominent ornament of *T. cf. sculptilis*. The high variability and prominence of the distal reticulum differentiates this species from other members of the genus.

*Occurrence:* Harry Stoke B borehole to Dingle leaf bed (Winterbourne Formation to Mangotsfield Member). Possibly in Huckford Quarry (Mangotsfield Member).

*Triquitrites sinani* Artüz 1957

Plate 8, Figure 12

*Holotype:* Artüz (1957), pl. 4, fig. 27.

*Type locality:* Sulu or Büyük Seam, Zonguldak Coalfield, Turkey; Langsettian.

*Description:* Trilete miospores with a triangular outline and rounded apices. Interradials may be straight, rounded or concave. Apices thickened to produce valvae, which project beyond the equatorial outline of the miospore body. Valvae smooth in outline with a crescentic shape, and slightly laterally expanding along their length. Some specimens exhibit subtly bi-lobed valvae. Valvae often extend into the interradial regions, producing a narrow flange-like extension which connects the valvae around the equatorial outline. Valvae range in width from 10 to 19 μm, and 5 to 12 μm in radial length. On the distal surface two ridges extend from each valvæ and reach poleward along the interradial region, flanking the laesurae. In some specimens some of the ridges may join with the ridges from one of the other valvae to produce a pseudo-kyrotome. In most cases however, the ridges terminate short of the distal pole. Laesurae often reach the inner margin of the valvae. Exine laevigate.
Comparison: *Ahrensisporites guerickei* possesses a true kyrotome which is continuous along all three interradial regions of the distal face.

Occurrence: Harry Stoke B borehole to Huckford Quarry, Bickley Wood (Winterbourne Formation to Mangotsfield Member).

Known range: Langsettian to Duckmantian. Reworked.

*Triquitrites subspinous* Peppers 1970

Plate 8, Figure 13-14

Holotype: Peppers (1970), pl. 11, fig. 8.

Type locality: Summum (No. 4) Coal, Carbondale Formation, Illinois, U.S.A.; Asturian.

Description: Trilete miospores with a triangular outline with straight interradials. Equatorial outline of the interradials undulate due to modification by ornament. Apices thickened to produce valvae which typically have an irregular, crenulated outline. Valvae may slightly project beyond the equatorial outline of the apices. Laesurae exceed half of the miospore radius and often reach the inner margin of the valvae. Exine laevigate proximally. The distal surface of the miospore is ornamented by coni and spinae, which are connected by indistinct and discontinuous network of rugulae.

Dimensions: Total 41 (46) 54 (10 specimens; Schulze and 2% KOH).

Discussion: *Triquitrites sculptilis* is smaller, and is ornamented by coalescing verrucae (cf. the spinate ridges of *T. subspinous*).

Occurrence: 65 The Dingle to Shortwood Hard Coal (Mangotsfield Member to Farrington Member).
**Known range:** Asturian (Peppers, 1970).

**Triquitrites tribullatus** Ibrahim (Schopf *et al.*, 1944)

Plate 9, Figure 1

1932 *Sporonites tribullatus* Ibrahim in Potonié *et al.*, p. 448; pi. 15, fig. 13.
1933 *Laevigatisporites tribullatus* Ibrahim, p. 20, pi. 2, fig. 13.
1934 *Valvisisporites tribullatus* (Ibrahim); Loose, p. 152, pi. 7, fig. 21.
1938 *Azonotriletes tribullatus* (Ibrahim); Luber in Luber and Waltz, pi. 7, fig. 8.
1944 *Triquitrites tribullatus* (Ibrahim); Schopf, Wilson, and Bentall, p. 47.

**Lectotype:** Potonié and Kremp (1955), pl. 17, fig. 319.

**Type locality** Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

**Description:** Trilete miospores with a triangular outline and truncated or narrowly rounded apices. Interradials typically straight or slightly convex, with rare specimens featuring slightly concave interradials. Apices thickened to produce valvae which vary in development, ranging from a slight darkening of the apices to dense pads which project beyond the equatorial outline of the miospore. Where the valve project beyond the miospore body, the valvae are generally smooth and may be rounded, truncated or bi-lobed. Valvae range in width from 9 to 15 µm, and 6-8 µm in radial length. Laesurae exceed half of the miospore radius, often reaching the inner margin of the valvae, and may be open. Exine laevigate.

**Dimensions:** Total 44 (1 specimen; HF). Total 40-43 (1 specimens; Schulze and 2% KOH).

**Comparison:** *Triquitrites bransonii* is smaller (<35 µm).

**Occurrence:** Harry Stoke B borehole to Shortwood Hard Coal and roof of Parkfield Hard Coal, Bickley Wood to Hursley Hill (Winterbourne Formation to Publow Member).
Known range: Namurian A to Bolsovian.

**Genus MOOREISPORITES Neves 1958**

Type species: *M. fustis* Neves 1958

*Description:* Trilete miospores with a triangular outline, apices generally rounded. Apices feature baculae which project beyond the equatorial outline. These baculae are often fused at their bases to produce valvae-like thickenings at the miospore apices. The apices of the baculae may be rounded, truncate, pointed, apiculate; each specimen often features more than one of these termination styles. Laesurae exceed half of the miospore body radius, and often reach close to or into the inner margin of the valvae-like thickened baculae bases. Exine laevigate or granulate, with scattered baculae or coni on some specimens.

*Comparison:* *Triquitrites* has true valvae, without the prominent baculae of *Mooreisporites*.

*Affinity:* Likely ferns.

**Mooreisporites fustis** Neves 1958

Plate 9, Figure 2

*Holotype:* Neves (1956), pl. 1, fig. 1

*Type locality:* *G. subcrenatum* marine chales, Quarnford, North Staffordshire Coalfields, England; Namurian C.

*Description:* Trilete miospores with a triangular equatorial outline and truncated or rounded apices. Interradials concave. Apical baculae variable, ranging from 15 to 21 µm in radial length and 3 to 6 µm in width. Three to six baculae project from each apex.
Apices of baculae typically apiculate. Bases of baculae are often fused, to produce valvae-like thickenings of the miospore apices. Cluster of baculae also occur at the distal pole. Laesurae half to three quarters of the miospore radius, and may be open. Exine laevigate.

*Dimensions:* Body 55 (1 specimens; Schulze and 2% KOH).

*Discussion:* Only one specimen was found, which was in a sample with contained other *Mooreisporites* species.

*Comparison:* Apical baculae are more prominent than on other species of *Mooreisporites*. Other species also lack the baculae on the distal pole.

*Occurrence:* Dingle leaf bed (Mangotsfield Member).

*Known range:* Namurian to Duckmantian. Reworked.

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**Mooreisporites inusitatus** (Kosanke) Neves 1958

Plate 9, Figure 3

1958 *Mooreisporites inusitatus* (Kosanke); Neves, p. 8.

*Holotype:* Kosanke (1950), pl. 8, fig. 7

*Type locality:* No. 2 Coal, Carbondale Group, Illinois, U.S.A.; Asturian

*Description:* Trilete miospores with a triangular equatorial outline and truncated or rounded apices. Interradials almost always concave, straight sided specimens being very rare. Apical baculae variable, ranging from 3 to 10 µm in radial length and 3 to 6 µm in width. Three to five baculae project from each apex. Apices of baculae typically rounded or truncate, with rare and subtle bifurcation. Bases of baculae are often fused,
to produce valvae-like thickenings of the miospore apices. Laesurae half to three quarters of the miospore radius, and may be open. Exine laevigate.

*Dimensions*: Body 60 (70) 82 (7 specimens; HF).

*Comparison*: Bristol specimens are nearly always feature concave interradials, whereas Kosanke (1950) described the species as having straight sides. Many specimens show baculae which approach those of *M. lucidus* in morphology.

*Occurrence*: Frome Bank Gardens to Coalpit Heath High Coal and roof of Parkfield Hard Coal, Bickley Wood to Hurlsey Hill (Downend Member to Radstock Member).

*Known range*: (?uppermost Bolsovian to) Asturian (Peppers, 1996).

**Mooreisporites lucidus** (Artüz) Felix and Burbridge 1967

Plate 9, Figure 4

1957 *Tripartites lucidus* Artüz, p. 249.

*Holotype*: Artüz (1957), pl. 4, fig. 29.
*Type locality*: Büyük Seam, Zonguldak Coalfield, Turkey; Langsettian.

*Description*: Trilete miospores with a triangular equatorial outline and truncated or rounded apices. Interradials straight to slightly concave. Apical baculae are typically tapered and sinuous, commonly with apiculate terminations. The bases of the baculae are fused to form a prominent valvae-like thickening at each apex of the miospore, which are 15-28 μm in width. The baculae, including their fused lower portion, are 3-11 μm in radial length. Where the baculae emerge from the valve-like base they are 2-3 μm in width. Laesurae around half of the miospore radius, and may be open. Exine laevigate.
Discussion: This species first occurs at a similar stratigraphical level to *Mooreisporites inusitatus*, and gradational forms between both species we also examined in the Bristol material. The specimens of *Mooreisporites lucidus* are therefore interpreted as not being reworked from older strata.

Comparison: Irregular, almost frayed nature of the bacula separates this species from the other species. The apical thickenings are also more pronounced that in other species.

Occurrence: Frome Bank Gardens to Shortwood Top Coal (Mangotsfield Member to Farrington Member).

Known range: Langsettian.

*Infraturma TRICRASSATI* Dettmann 1963

**Genus DIATOMOZONOTRILETES** (Naumova) Playford 1963

*Type species:* *D. saetosa* (Hacquebard and Barss) Hughes and Playford 1961

Description: Trilete miospores with a triangular miospore body; interradials straight, or more usually, strongly concave. Equatorial outline modified by an equatorial corona of discrete saetae which taper along their length towards the apex, and are typically truncated or rounded at their apices. Saetae may be fused at their bases, but are typically widely separated at their apices to form clearly distinct structures. Corona of saetae is typically broadest at the centre of the interradial outline; gradually reducing in width towards the apices, where is may be greatly reduced or absent. Laesurae long, extending almost to the equatorial margin.

Comparison: In *Reinschospora* saetae are finer and fused along their entire length, thereby forming a more prominent and well-developed corona than *Diatomozonotriletes*.
**Affinity:** Unknown.

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**Diatomozonotriletes saetosus** (Hacquebard and Barss) Hughes and Playford 1961

Plate 9, Figure 5

**Description:** Trilete miospores with a triangular miospore body. Interradials strongly concave, apices rounded to slightly truncated. Equatorial outline modified by an equatorial corona of discrete saetae which taper along their length towards the apex, and are typically truncated or rounded at their apices. Saetae 2-3 µm broad at the base, and up to 9 µm long in the centre of the interradials where they are best developed. There are 12-13 saetae in each interradial area. Saetae gradually decrease in length towards the apices, where they are either absent or reduced to a barely discernable, apiculate ridge which arcs around the apices. Laesurae extend two thirds to three quarters of the way to the apical equatorial margin. Exine laevigate, but may also bear patches of grana in some areas.

**Dimensions:** Total 56 (1 specimen; HF).

**Occurrence:** Questionable identification in Grove Cottage (Downend Member).

**Known range:** Viséan. Reworked.

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1938  **Zonotriletes speciosus** Loose; Waltz in Luber and Waltz, p. 14.
1956  **Diatomozonotriletes speciosus** (Loose); Ischchenko, p.99.
1957  **Reinschospora saetosus** Hacquebard and Barss, p. 41.
1961  **Reinschospora bellitas** (Hacquebard and Barss) in Hughes and Playford, p. 40.

**Holotype:** Hacquebard and Barss (1957), pl. 6, fig. 3..

**Type locality:** 4ft. coal, South Nahanni River, Northwest Territories, Canada; Upper Mississippian.

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Genus REINSCHOSPORA Schopf et al. 1944

Type species: R. speciosa (Loose) Schopf et al., 1944.

Description: Trilete miospores with a triangular miospore body; interradials straight to strongly concave with rounded apices. Equatorial outline modified by an equatorial corona of saetae, to give a triangular or roughly circular shape in polar view. The corona is broadest at the centre of the interradial outline and narrowest, or absent, at the apices. Laesura exceed half of the miospore radius, and may reach the apices. Exine laevigate to granulate.

Comparison: Diatomozonotriletes corona of saetae are coarser and more strongly developed.

Affinity: Ferns.

Reinschospora speciosa (Loose) Schopf et al., 1944

Plate 9, Figure 6

1934 Alati-sporites speciosus Loose, p. 151.
1938 Zonotriletes speciosus (Loose); Waltz in Luber and Waltz.
1944 Reinschospora bellitas Bentall in Schopf, et al., p. 52.

Holotype: Potonié and Kremp (1956), pl. 19, fig. 419.
Type locality: Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

Description: Trilete, triangular miospores with a strongly concave body with rounded apices. Equatorial outline modified by an equatorial corona of saetae, so that the miospores have a rounded to rounded-triangular shape in polar view. The corona is composed of saetae, less than or equal to 1 \( \mu \)m in diameter, which are closely adpressed but only weakly attached and prone to separation along their radial length. The corona is broadest at the centre of the interradial margin, where they reach lengths of up to 19 \( \mu \)m. The corona progressively decreases in width towards the apices, where is may be

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reduced to 2-4 µm or absent. Corona overlaps with miospore body on the proximal surface. Laesurae range from half to nearly the full length of the miospore body radius. Exine laevigate to granulate.

*Dimensions:* Total 61-76 (2 specimens; HF). Total 66 (1 specimen; Schulze and 2% KOH).

*Comparison:* *Reinschospora triangularis* has consistently straight interradials and typically more discrete and smaller saetae.

*Occurrence:* Harry Stoke B borehole to Westerleigh Hard Coal and siltstones above Shortwood Hard Coal (Winterbourne Formation to Farrington Member).

*Known range:* Langsettian to Asturian.

*Reinschospora triangularis* Kosanke 1950  
Plate 9, Figure 7

*Holotype:* Kosanke (1950), pl. 9, fig. 6-7.  
*Type locality:* Carlinville Coal, McLeansboro Group, Illinois, U.S.A.; Asturian-Cantabrian.

*Description:* Trilete miospores with a straight-sided triangular body with rounded to pointed apices. Equatorial outline is modified by a corona of saetae, which are typically adpressed only at the base. Saetae are slightly tapered, and may be clavate. Corona is broadest in the centre of the interradial outline, reaching a maximum of 10-12 µm, and decreases in width progressively towards the apices where it is greatly reduced or absent. The corona may overlap the miospore body on the proximal surface. Laesurae reach nearly to the equatorial outline of the miospore, and may be accompanied by folds which simulate the appearance of lips. Exine laevigate to granulate.

*Dimensions:* Total 44 (52) 56 (3 specimens; HF).
Comparison: *Reinschospora speciosa* has a more well-defined corona of closely adpressed saetae, which typically do not taper along their lengths. The body of *R. speciosa* is also strongly concave and typically has thicker exine than *R. triangularis*.

Occurrence: Harry Stoke B borehole to Dingle leaf bed, Bickley Wood (Winterbourne Formation to Mangotsfield Member).

Known range: Duckmantian. Reworked.

*Infraturma CINGULATI* (Potonié and Klaus) Dettmann 1963

*Genus KNOXISPORITES* (Potonié and Kremp) Neves and Playford 1961

Type species: *K. hageni* Potonié and Kremp 1954

Description: Trilete miospores with a circular, oval, triangular or polygonal equatorial outline. A distinct cingulum is present at the equator, occupying a quarter to a third of the miospore radius, which is conformable with the outline of the miospore body. A prominent ring-shaped or polygonal thickening encircles the distal pole of most species, being situated roughly half way between the equator and the distal pole. This thickening may be attached to the interradial areas of the equator by radial rugulae, usually either one or two per interradial. Laesurae three fifths to four fifths of the miospore radius, usually reaching the inner margin of the cingulum.

Affinity: Ferns
**Knoxisporites pristinus** Sullivan 1968

Plate 9, Figure 8

*Holotype:* Sullivan (1968), pl. 27, fig. 4.

*Type locality:* Cementstone Group, Ayrshire, Scotland; Tournaisian.

*Description:* Trilete miospores with an originally circular to oval equatorial outline, heavily modified by folding. Cingulum is present at the equator, 6-10 µm wide which corresponds to a third of the original miospore radius. 6-8 µm wide rugulae/muri extend from the distal surface of the cingulum, and coalesce towards the pole. These rugulae/muri are often poorly defined. In most specimens 4 or 5 muri are visible emerging from the cingulum, but due to compression it is not possible to ascertain exactly how many. Laesurae extend to the inner margin of the cingulum. Exine laevigate.

*Dimensions:* Total 52 (54) 70 (3 specimens; HF).

*Comparison:* Differentiated from other members of the genus on the basis of the prominent folding, and its thick but often ill-defined muri/rugulae. Almost all specimens of *Knoxisporites* show a proximal-distal orientation and little or no folding.

*Occurrence:* Harry Stoke B borehole to Grove Cottage, Bickley Wood (Winterbourne Formation to Downend Member).

*Known range:* Tournaisian (Sullivan, 1968). Reworked.

**Knoxisporites rotatus** Hoffmeister *et al.*, 1955

Plate 9, Figure 9

*Holotype:* Hoffmeister *et al.*, (1955), pl. 37, fig. 13.

*Type locality:* Hardinsberg Formation, Chester Series, Kentucky; Upper Mississippian.
Description: Trilete miospores with a circular to oval equatorial outline. A 3-7 μm wide distinct cingulum is present at the equator, occupying a quarter to a third of the miospore radius, which is conformable with the outline of the miospore body. A prominent 2-8 μm ring-shaped thickening encircles the distal pole, being situated roughly half way between the equator and the distal pole. The inner diameter of this distal ring is 8-32 μm. One rugula radiates from the distal ring, at the centre of the interradial region. These rugulae may or may not extend into the cingulum. Laesurae three fifths to four fifths of the miospore radius, usually reaching the inner margin of the cingulum. Exine laevigate.

Dimensions: Total 33 (41) 54 (5 specimens; HF). Total 33 (1 specimen; Schulze and 2% KOH).

Comparison: K. stephanephorus has a button-shaped distal thickening at the pole and less strongly developed extensions connecting the distal ring to the cingulum.

Occurrence: Harry Stoke B borehole, below Trench Coal (Winterbourne Formation to Farrington Member).

Known range: Tournaisian (Sullivan, 1964) to Namurian A (Butterworth and Williams, 1958). Reworked.

Knoxisporites stephanephorus Love 1960

Plate 9, Figure 10

Holotype: Love (1960), pl. 2, fig. 1.

Type locality: Pumpherston Shell Bed, Lower Oil-Shale Group, Scotland, England; Viséan.

Description: Trilete miospores with a circular, oval or triangular equatorial outline. A 3-7 μm wide distinct cingulum is present at the equator, occupying a quarter to a third of the miospore radius, which is conformable with the outline of the miospore body. A
prominent 3-8 µm wide ring-shaped thickening encircles the distal pole, being situated roughly half way between the equator and the distal pole. The inner diameter of this distal ring is 12-27 µm. At the centre of this ring, at the distal pole, is a 5-10 µm circular to rhombohedral papillae. One rugula radiates from the distal ring, at the centre of the interradial region. These rugulae may or may not extend into the cingulum. Laesurae three fifths to four fifths of the miospore radius, usually reaching the inner margin of the cingulum. Laesurae may be accompanied by narrow lip-like thickenings which may diverge and fuse to the cingulum. Exine laevigate to granulate.

*Dimensions*: Total 35 (41) 49 (14 specimens; HF). Total 37-49 (2 specimens; Schulze and 2% KOH).

*Comparison*: Differentiated from *K. rotatus* by the presence of a circular to rhombohedral distal thickening at the pole. Both Love (1960) and Felix and Burbridge (1967) also recognised more prominent lips in *K. stephanophorus*.

*Occurrence*: Harry Stoke B borehole to roof of Parkfield Hard Coal, Bickley Wood to above Trench Coal (Winterbourne Formation to Farrington Member).

*Known range*: Viséan to Asturian.
**Knoxisporites cf. triangularis** Higgs *et al.*, 1988

Plate 9, Figure 11

1938  *Zonotrilites literatus* Waltz, Luber and Waltz, p. 18.
1941  *Stenozonotriletes literatus* (Waltz) Naumova, p. 87-88.
1963  *Archaeozonotriletes literatus* (Waltz) Naumova var. triangularis Kedo, p.76.
1963  *Knoxisporites literatus* (Waltz) Playford, p.634.

**Holotype:** Kedo (1963), pl. 18, fig. 191.

**Type locality:** Yelsk Borehole 23, Pripyat Basin, Republic of Belarus; Tournaisian.

**Description:** Trilete miospores with a hexagonal oval equatorial outline, and a convexly triangular inner body. A 7-8 µm wide distinct cingulum is present at the equator, occupying a third of the miospore radius. A 3 µm wide thick triangular-shaped ring encircles the distal pole, its apices aligned to the interradial regions. A rugula extends radially from each apex of this triangle, which is fused to the interradial region of the cingulum. Laesurae extend almost to the equatorial outline of the cingulum, and are accompanied by narrow fold simulating lips. Exine laevigate.

**Dimensions:** Total 39 (1 specimen; HF).

**Discussion:** *Knoxisporites triangularis* features a triangular-shaped distal ring, where the apices are directly fused to the cingulum. In the Bristol specimens, the triangular-shaped ring is much smaller and is connected to the cingulum not by the apices, but by rugulae.

**Comparison:** The convexly triangular miospore body, and discordant hexagonal equatorial outline distinguish this species from other members of the genus. The triangular-shaped distal ring is also a unique feature of this species.

**Occurrence:** Harry Stoke B (Winterbourne Formation).
Known range: Tournaisian (Higgs et al., 1988). Reworked.

**Knoxisporites triraditus** Hoffmeister et al. 1955

Plate 9, Figure 12

*Holotype:* Hoffmeister et al. (1955), pl. 37, fig. 1-12.

*Type locality:* Hardinsburg Formation, Chester Series, Kentucky; Upper Mississippian.

**Description:** Trilete miospores with a circular or oval equatorial outline. A 5-6 µm wide distinct cingulum is present at the equator, occupying a quarter to a third of the miospore radius, which is conformable with the outline of the miospore body. Distally, one distal bands extends poleward from the centre of the interradial region of the cingulum. These bands are 5 µm wide and fuse at the distal pole. Laesurae three fifths to four fifths of the miospore radius, usually reaching the inner margin of the cingulum. Exine laevigate to granulate.

**Dimensions:** Total 48 (1 specimen; HF). Total 40-56 (2 specimens; Schulze and 2% KOH).

**Comparison:** Differentiated from other members of the genus by a lack of a distal ring-shaped thickening, and the presence of three bands that extend out from the distal pole and fuse to the interradial regions of the cingulum.

**Occurrence:** Winterbourne Railway Cutting to Dingle leaf bed, below Trench Coal (Downend Member to Mangotsfield Member).

**Known range:** Viséan to Namurian. Reworked.
**Knoxisporites sp.1**
Plate 10, Figure 1

*Description*: Trilete miospores with a polygonal equatorial outline. A 3-4 µm wide cingulum is present at the equator, occupying two fifths to a quarter of the miospore radius, which is conformable with the outline of the miospore body. Two 2-3 µm wide rugulae extend distally from the cingulum, and fuse to form a ring-shaped thickening. The rugulae, as well as the ring, are sinuous. Laesurae extend to the inner margin of the cingulum. Exine laevigate.

*Dimensions*: Total 38 (1 specimen; Schulze and 2% KOH).

*Discussion*: *Knoxisporites* sp.1 may be a heavily distorted form of *K. rotatus*.

*Occurrence*: Harry Stoke B (Winterbourne Formation).

**Genus SAVITRISPORITES Bharadwaj 1955**

Type species: *S. triangularis* Bharadwaj 1955

Description: Trilete triangular miospores with a triangular equatorial outline; interradials may be concave or convex, depending on the species. A distinct cingulum of generally equal width encircles the equatorial outline of the miospore. Junction between the miospore body and the cingulum is very clear, unless obscured by ornamentation. Cingulum occupies a fifth to two fifths of the miospore radius. Laesurae typically extend to, or just short of, the inner margin of the cingulum. Distal surface of miospore body is ornamented with a dense and varied assortment of verrucae, coni, rugulae or muri; depending on the species. Proximal surface unornamented, apart from lip-like ridges which border the laesurae in the interradial regions of the contact areas.
**Discussion:** Many authors (Smith and Butterworth, 1967; Sullivan 1964; Coquel, 1974; Loboziak, 1971; and others) consider *Savitrisporites* to be co-generic with *Callisporites*. *Callisporites* differs in having an ornamented proximal face, whereas *Savitrisporites* sensu stricto has an unornamented proximal face with only prominent lips bounding the laesurae. Careful focussing and inspection of the Bristol specimens, most clearly seen in *Savitrisporites camptotus*, does suggest an unornamented proximal face; hence this author retains these species in the genus *Savitrisporites*. Sullivan (1964) also noted that upon careful examination of *Callisporites* reveals that the ornament is restricted to the distal surface.

**Affinity:** Fern (Teddacean).

**Savitrisporites cingulatus** (Alpern) Laveine 1965

Plate 10, Figure 2

1958  *Dictyostriletes cingulatus* Alpern, p. 77.
1959  *Dictyostriletes cingulatus* Alpern, p. 145.
1965  *Callisporites cingulatus* (Alpern); Laveine, p. 133.

*Holotype:* Alpern (1959) pl. 5, fig. 110.
*Type locality:* Odette Vein, Folschviller, Lorraine, France; Asturian.

**Description:** Trilete triangular miospores with a triangular equatorial outline; with concave interradials. Equatorial cingulum one fifth to two thirds of spore radius. Junction between miospore body and the cingulum is clearly defined. Laesurae extend to, or just short of, the inner margin of the cingulum. Distal surface of miospore body covered by a reticulum of 2 µm wide muri enclosing 2-3 µm wide rounded, phaseolate or oval lumina. Reticulum may be incomplete in localised patches on some specimens; being represented only by coalescing rugulae. 3-4 µm wide lip-like ridges border the laesurae in the interradial regions of the contact areas on the proximal surface of the spore body, extending just to the inner margin of the cingulum. Exine moderately thin.
Comparison: *S. majus* is bigger with a coarser and consistently well-developed reticulum.

Occurrence: Harry Stoke B borehole to Huckford Quarry, Bickley Wood to below Trench Coal (Winterbourne Formation to Mangotsfield Member).

Known range: Upper Bolsovian to Asturian.

**Savitrisporites majus** Bharadwaj 1957

Plate 10, Figures 3-4

1957a *Savitrisporites majus* Bharadwaj, p. 97.
1958 *Dictyotritles camptotus* Alpern, p. 77.
1964 *Savitrisporite camptotus* (Alpern); Venkatachala and Bharadwaj, p. 179.

Holotype: Bharadwaj (1957a) pl.24, fig.11.

Type locality: Schwalbah Seam, Göttelborn Mine, Saarland, Germany; Stephanian B.

Description: Trilete triangular miospores with a triangular equatorial outline; with slightly convex interradials. Equatorial cingulum one fifth to two thirds of spore radius. Junction between miospore body and the cingulum is clearly defined, and may be demarked by a narrow furrow. Laesurae extend to, or just short of, the inner margin of the cingulum. Distal surface of miospore body reticulate; with generally rounded or sub-rounded 2-5 µm wide lumina, which are regular in their shape, spacing and size on any single specimen. These lumina are separated by 3-4 µm wide, regular muri which do not extend beyond the limits of the miospore body. 4 µm wide lip-like ridges border the laesurae in the interradial regions of the contact areas on the proximal surface of the spore body, extending just to the inner margin of the cingulum. Exine thick.

Dimensions: Total 49 (52) 53 (3 specimens; HF). Total 45 (49) 52 (3 specimens; Schulze and 2% KOH).
Comparison: *S. cingulatus* is smaller with concave margins and a thinner exine, with a finer reticulum which may locally be reduced to coalescing rugulae on some specimens.

Occurrence: Winterbourne Railway Cutting to below Westerleigh Hard Coal (Mangotsfield Member to Farrington Member).

Known range: Asturian to Stephanian (Clayton *et al.*, 1977).

*Savitrisporites nux* (Butterworth and Williams) Smith and Butterworth

1967

Plate 10, Figure 5

1958  *Callisporites nux* Butterworth and Williams, p. 377.
1964  *Savitrisporites nux* (Butterworth and Williams); Sullivan, p. 373.

Lectotype: Smith and Butterworth (1967), pl.15.

Type locality: Upper Hirst Seam, West Fife Coalfield, Scotland; Namurian A.

Description: Trilete triangular miospores with a triangular equatorial outline; interradials may be straight or slightly concave or convex. Equatorial cingulum generally one fifth to two thirds of the miospore radius. Junction between miospore body and the cingulum is clearly defined, but often partially obscured by the ornament. Laesurae extend to, or just short of, the inner margin of the cingulum. Distal surface of miospore body covered with 2-4 µm broad verrucae and coni, which partially coalesce at the base to form an irregular network of poorly defined rugulae. Ornament height equal to, or slightly less, than its basal diameter. 3-4 µm wide lip-like ridges border the laesurae in the interradial regions of the contact areas on the proximal surface of the spore body, extending just to the inner margin of the cingulum. Exine thick.

Dimensions: Total 37 (43) 49 (11 specimens; HF).
Comparison: *S. cingulatus* is smaller with concave margins, and a thinner exine.

Occurrence: Harry Stoke B borehole to siltstones above Shortwood Hard Coal, Bickley Wood (Downend Formation to Farrington Member).

Known range: Viséan to Bolsovian (Clayton et al., 1977).

cf. *Savitrisporites nux* (Butterworth and Williams) Smith and Butterworth 1967

Plate 10, Figure 6-7

Description: Trilete triangular miospores with a triangular to rounded-triangular equatorial outline; interradials may be straight or slightly concave or convex. Equatorial cingulum generally very narrow or not apparent, but specimens commonly in oblique compression. Laesurae extend to, or just short of, the inner margin of the cingulum. Distal surface of miospore body ornamented by 3-4 μm rugulae, which originate near the apex of the radial region, and extend and diverge parallel to the equatorial outline of the interradials. These rugulae cross cut the diverging rugulae, originating from the adjacent apex, to form a sort of reticulum which encloses irregular rounded to polygonal lumina, about 2 μm in diameter. Proximal surface of the miospore body features lip-like thickening which extend parallel to the laesurae in the contact areas. There are often two of these parallel ridges in each interradial area.

Dimensions: Total 35 (43) 49 (7 specimens; HF).

Discussion: Almost identical to *S. majus* (as *S. camptotus*) in Plate 2, Fig 12 in Coquel et al. (1976) and Plate 21, Fig 13 in Clayton et al. (1977). However, the Bristol specimens do not feature the clear reticulate distal pole which is a key feature of *S. majus*. It seems that this species appears superficially similar to the proximal ornament of *S. majus*. The range of this species also does not match that of *S. majus* in the Bristol Coalfield; it has a much longer stratigraphical range which is more akin to *S. nux*. 

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Comparison: Differs from *S. nux* in the nature of the distal ornament, and being most commonly preserved in oblique compression. *S. majus* is generally bigger and has a coarser and more constantly well-formed reticulum. Retained as cf. *Savitrisporites* as it is not clear if these specimens are indeed cingulate.

Occurrence: Harry Stoke B borehole to Westerleigh Hard Coal (Winterbourne Formation to Farrington Member).

**Genus RETICULATISPORITES (Ibrahim) Neves 1964**

Type species: *R. reticulatus* Ibrahim 1932.

Description: Trilete miospores with a circular, convex triangular or polygonal equatorial outline. Miospores have a distinctive tripartite equatorial cingulum; consisting of an outer and inner concentric zone of thickening, which is separated by a relatively narrower thinner zone. Inner thickened zone often broader than the outer zone, and typically overlaps the miospore body. Cingulum occupies a third of the total miospore radius. Distal surface features a network of broad, well-developed muri which enclose large and relatively equi-dimensional polygonal lumina. Muri extend to the edge of the cingulum, fusing with the outer thickened zone and forming node-like projections. Laesurae extend over around half of the miospore radius, and typically don’t reach the inner margin of the cingulum. Proximal surface is laevigate.

Comparison: Differs from *Knoxisporites* in possessing a tripartite structured cingulum in polar view.

Affinity: Fern (Teddacean).
Reticulatisporites reticulatus (Ibrahim) Ibrahim 1933

Plate 10, Figure 9

1933 Reticulati-sporites reticulatus Ibrahim, p. 33.
1938 Azonotriletes reticulatus (Ibrahim); Luber in Luber and Waltz.

Holotype: Smith and Butterworth (1967), pl. 14, fig. 16. After Ibrahim.
Type locality: Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

Description: Trilete miospores with a roughly round to rounded triangular equatorial outline, which is modified to polygonal by the coarse ornament. Equatorial cingulum with a tripartite structure; with a middle thinned zone (1-3 µm wide) bounded by an inner (2-7 µm wide) and outer zone (1.5-2 µm wide) of concentric thickening. Total cingulum 7-12 µm wide, occupying roughly a third of the total miospore radius. Inner thickened zone of cingulum overlaps the miospore body. Distal surface features a prominent network of muri, which are 2-4 µm in width. Muri on any one specimen are fairly uniform in diameter. Muri may branch as they extend outwards from the miospore body, and fuse with the outer thickened zone of the tripartite cingulum; muri fuse with the cingulum at the equatorial outline. Muri separate 2-4 µm wide and tall polygonal lumina; around 7-13 muri project onto the cingulum on the distal side of the miospore. Node-like swellings are common at the junction between the muri and the outer thickened zone of the cingulum. Lumina of fairly constant sizes on a single specimen. Laesurae approximately half of the miospore radius, and do not reach the margin of the miospore body. Proximal surface of miospore is laevigate.

Dimensions: Total 50 (62) 68 (4 specimens; HF). Total 64 (75) 80 (4 specimens; Schulze and 2% KOH).

Occurrence: Harry Stoke B borehole to 65 The Dingle, Bickley Wood (Winterbourne Formation to Mangotsfield Member).

Known range: Namurian C to Bolsovian (Clayton et al., 1977).
Subturma ZONOLAMINATRITRILETES Smith and Butterworth 1967

Infraturma CRASSITI (Bharadwaj and Venkatachala) Smith and Butterworth 1967

Genus CRASSISPORA (Bharadwaj) Sullivan 1964

Type species: C. kosankei (syn. C. ovalis) (Potonié and Kremp) Bharadwaj 1957

Description: Trilete miospores with an oval, circular or slightly rounded-triangular equatorial margin. Crassitudinous thickening occurs at the equatorial margin of the miospore. Laesurae are not always visible, generally reaching four fifths to the full length of the miospore radius. The proximal surface of the exine generally appears laevigate, while coni and spinae occur distally. Exine is thin.

Comparison: Ornament is similar to Apiculatasporites and Planisporites, but both of these genera lack an equatorial crassitude.

Affinity: Lycopsid; Sigillarian.

Crassispora kosankei (Potonié and Kremp) Smith and Butterworth 1967

Plate 10, Figures 10-11

1957 Planisporites ovalis Bharadwaj, p. 86.
1957b Crassispora ovalis Bharadwaj, p. 126.
1957b Crassispora kosankei (Potonié and Kremp) Bharadwaj, p. 127.
1957a Apiculatasporites apiculatus (Ibrahim); Dybová and Jachowicz (non sensu Ibrahim), p. 87.
1964 Crassispora plicata Peppers, p. 17.
1967 Crassispora kosankei (Potonié and Kremp) Smith and Butterworth, p. 234.

Holotype: Potonié and Kremp (1955), pl. 13, fig. 208.

Type locality: Seam R1, Ruhr Coalfield, Germany; Duckmantian.
**Description:** Trilete miospores with circular to oval equatorial outline. Most specimens show a tendency towards a slightly rounded-triangular shape. A prominent crassitude is present at the equator of the miospore, which is usually 3-8 µm wide. Laesurae are most often not seen, or represented by a triangular-shaped tear at the proximal pole. When visible the laesurae exceed four fifths of the miospore radius, often reaching the equator. Distally the exine features 1-1.5 µm tall coni, interspersed with rare spinae. Exine is thin.

**Dimensions:** Total 40 (55) 56 (11 specimens; HF). Total 48 (57) 62 (3 specimens; Schulze and 2% KOH).

**Comparison:** Similar to *Planisporites*, but possesses a definite equatorial crassitude. *Crassispora plicata* Peppers is identical, but features prominent 3 µm apical papillae (1 in each interradial area) which is seen occasionally in the Bristol representatives of *Crassispora*.

**Occurrence:** Harry Stoke B borehole to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

**Known range:** Namurian to Asturian.

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**Genus OSWALDISPORA Neville 1980**

Type species: *O. xenika* Neville 1989.

**Description:** Trilete miospores with a rounded-triangular body, with convex interradials. Intexine separated from exoexine, forming a central area which is coarsely ornamented. Ornament is reduced or absent proximally. Exoexine forms a thick and prominent equatorial cingulum, which is reduced or absent at the radials to give the spore a tri-lobed equatorial outline. Laesurae extend to the inner margin of the cingulum.
Comparison: Tri-lobed nature of the cingulum differentiates this genus form other cingulate genera.

Affinity: Unknown.

_Oswaldispora xenika_ Neville 1989
Plate 10, Figure 12

1960  _Spore Type 3_ Love, p. 123.
1973  _?Rotaspora xenika_ Neville in Neves et al., p.38.
1989  _Oswaldispora xenika_ Neville, p. 104.

_Holotype:_ Neville (1989), pl. 1, fig. 5.
_Type locality:_ Anstruther Borehole, East Fife, Scotland; Viséan.

_Description:_ Trilete miospores with a rounded-triangular body, with convex interradials. Intexine separated from exoexine, forming a central area which is ornamented with 2-4 μm broad coalescing verrucae and irregular rugulae. Ornament is reduced or absent proximally. Exoexine forms a thick and prominent equatorial cingulum, which is reduced or absent at the radials to give the spore a tri-lobed equatorial outline. Cingulum occupies a third of the miospore radius, and is laevigate. Laesurae extend to the inner margin of the cingulum.

_Dimensions:_ Total 43-45 (2 specimens; HF).

_Discussion:_ Neville (1989) states that the laesurae are half to three quarters of the spore body radius, which is shorter than observed in the Bristol representatives.

_Occurrence:_ Harry Stoke B (Winterbourne Formation).

_Known range:_ Viséan. Reworked.
Infraturma CINGULICAVATI Smith and Butterworth 1967

Genus DENSOSPORITES (Berry) Butterworth et al. 1964

Type species: D. covensis Berry 1937.

Description: Trilete miospores with a generally oval, rounded or rounded-triangular equatorial outline. Intexine separated from exoexine, forming a thin central body which may be laevigate or faintly granulate. Exoexine forms a thick and prominent equatorial cingulum. Cingulum is slightly less than half of the total miospore radius. Cingulum may taper slightly towards the equatorial margin. Laesurae may be indistinct or distinct, and extend into the cingulum. Cingulum may be laevigate or with ornament of varying types and sizes, depending on the species.

Comparison: Cingulizonates has a distinctly bizonate cingulum, with a raised inner section and thin flange-like outer zone. Cristatisporites has variably saetose ornament and a ring of processes surrounding the central exoexine.

Affinity: Lycopsid; some herbaceous records (Porostrobus (Bek and Opluštil, 1998), but generally interpreted as being sub-arborescent (Sporangiostrobus, from Omphalophloios (Opluštil et al., 2010)). The ‘Densospore Group’ includes; Densosporites, Cristatisporites, Cingulizonates and Radizonates. This group will be considered as having a sub-arborescent lycopsid affinity in palaeoecological sections of this study.
**Densosporites anulatus** Loose (Smith and Butterworth 1967)

Plate 10, Figure 13

1932  *Sporonites anulatus* Loose in Potonié et al., p. 451.
1944  *Densosporites annulatus* (Loose); Schopf et al., p. 40.
1956  *Anulatisporites anulatus* (Loose); Potonié and Kremp, p. 112.
1950  *Densosporites reynoldsburgensis* Kosanke, p. 33.

**Holotype:** Potonié and Kremp (1956), pl. 17, fig. 365.

**Type locality:** Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

**Description:** Trilete miospores with a rounded-triangular equatorial outline. Intexine forms a fairly thin central body, generally laevigate but may have faint granulation. Exoexine separated to form a thick cingulum which is laevigate. Cingulum is most commonly of uniform thickness, but some specimens show a slight thinning or fraying at the equator. Cingulum two fifths to half of the total miospore radius. Laesurae generally not discernible, but can be seen to extend slightly into the cingulum when visible.

**Dimensions:** Total 31 (36) 48 (13 specimens; HF).

**Discussion:** Although both the original description and the emendation in Smith and Butterworth (1967) do not note that the central body may have a faint granulation, this feature was also seen in the preparations of Coquel (1974).

**Comparison:** Other species of *Densosporites* have coni.

**Occurrence:** Harry Stoke B borehole to Westerleigh Hard Coal and roof of Parkfield Hard Coal, Golden Valley to below Trench Coal (Winterbourne Formation to Farrington Member).

**Known range:** Viséan to lower Bolsovian.
**Densosporites sphaerotriangularis** Kosanke 1950

*Holotype:* Kosanke (1950), pl. 6, fig.7.

*Type locality:* Bald Hill Coal, Tradewater Group, Illinois, U.S.A.; Middle Pennsylvanian.

*Description:* Trilete miospores with a rounded-triangular equatorial outline. Intexine forms a thin inner body, which may be faintly granulate. The grana may partially coalesce to form a micro-rugulate pattern in some specimens. Exoexine expanded to form a dark cingulum, which may be slightly thinned or frayed at the equatorial margin. Cingulum two fifths to half of the total miospore radius. Laesurae may or may not be easily discernible, and extended a little of the way into the cingulum. Scattered 0.1-1 μm coni ornament the cingulum, which are typically only visible under oil immersion. The coni may be so widely spaced that they are not immediately noticeable.

*Dimensions:* Total 37 (41) 46 (4 specimens; HF). Total 36 (41) 50 (8 specimens; Schulze and 2% KOH).

*Comparison:* *D. sphaerotriangularis* is not ornamented enough to be easily confused with *Cristatisporites*.

*Occurrence:* Harry Stoke B borehole to Westerleigh Hard Coal and shales associated with Shortwood Hard Coal, Bickley Wood to Hursley Hill borehole (Winterbourne Formation to Publow Member).

*Known range:* Langsettian to Asturian.

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**Densosporites spinifer** Hoffmeister *et al.* 1955

*Holotype:* Hoffmeister *et al.*, (1955), pl. 36, fig.16-17.

*Type locality:* Bald Hill Coal, Tradewater Group, Illinois, U.S.A.; Middle Pennsylvanian.
Description: Trilete miospores with a rounded-triangular equatorial outline. Central body formed by intexine is thin. Exoexine separated to form a dark cingulum which appears slightly thinner at the equatorial outline. Cingulum two fifths to half of the miospore radius. Cingulum and body are ornamented by 2 µm tall spinae. The spinae on the cingulum are very variable in shape and disposition, but the interstitial spaces generally exceed the basal diameter of the ornament by several times. Spinae are comparatively rarer on the body than the cingulum.

Dimensions: Total 35 (41) 40 (3 specimens; HF). Total 35 (48) 60 (5 specimens; Schulze and 2% KOH).

Comparison: D. sphaerotriangularis has smaller, more widely spaced coni that don’t modify the equatorial outline of the miospore in such a way that is typical of most examples of D. spinifer. The ornament of this species may approach that of Cristatisporites, but is never fused at the base to form cristae, and features a distinct cingulum.

Occurrence: Coombe Brook to Westerleigh Hard Coal and roof of Parkfield Hard Coal, Bickley Wood (Winterbourne Formation to Farrington Member).

Known range: Viséan to Namurian.

Densosporites sp. 1
Plate 11, Figure 2

Description: Trilete miospores with a rounded-triangular equatorial outline. Central body formed by intexine is thin. Exoexine separated to form a dark cingulum. Cingulum three fifths to half of the miospore radius. Cingulum and body are ornamented by 2-3 µm broad verrucae with pointed apices.

Dimensions: Total 49 (1 specimen; HF). Total 48 (1 specimen; Schulze and 2% KOH).
Comparison: This species may grade into *D. spinifer*.

Occurrence: Winterbourne Railway Cutting to Westerleigh Hard Coal (Mangotsfield Member to Farrington Member).

**Genus WESTPHALENSISPORITES Alpern 1958**
Type species: *W. irregularis* Alpern 1958

Description: Trilete miospores with a strongly concave triangular equatorial outline. A broad and thick cingulum is developed at the equator, which is characteristically irregular. The irregular nature of the cingulum gives the miospore a very irregular concave triangular outline in polar view. Laesurae may reach to the inner margin of the cingulum, but rarely into the cingulum. Exine is laevigate on both the miospore body and the cingulum.

Affinity: Ferns.

**Westphalensisporites irregularis** Alpern 1958

Plate 11, Figure 3

1958 *Westphalensisporites irregularis* Alpern., p. 78.  

*Holotype:* Alpern (1958), pl. 1, fig 15.  
*Type locality:* Bois Doré borehole, Saar Lorraine, France; Asturian

Description: Trilete miospores with a strongly concave triangular equatorial outline. Equatorial outline modified by a prominent cingulum, which has a highly irregular undulating equatorial outline. Cingulum is fairly broad, roughly two thirds to two fifths
of the miospore radius. Laesurae extend to or just short of the inner margin of the cingulum. Exine laevigate.

*Dimesions:* Total 31 (32) 35 (5 specimens; HF). Total 37 (1 specimen; Schulze and 2% KOH).

*Occurrence:* Harry Stoke B borehole to Huckford Quarry, Bickley Wood to below Trench Coal (Winterbourne Formation to Farrington Member).

*Known range:* Langsettian to Asturian (Loboziak, 1971; Coquel, 1974; Coquel, 1976; Ravn, 1986).

**Genus LYCOSPORA (Schopf et al.) Potonié and Kremp 1954**

Type species: *L. micropapillata* (Wilson and Coe) Schopf *et al.*, 1944.

*Description:* Trilete miospores with a rounded-triangular equatorial outline. Intexine and exoexine are separated forming and inner body surrounded by a bizonate cingulum, with a darker inner cingulum and a thinner outer zona. The bizonate cingulum is fairly narrow, generally between a third and half of the miospore radius. Cingulum and zona generally of similar widths in polar view. Laesurae extend at least into the cingulum, and usually into the zona. Exine is ornamented by grana generally, or more rarely by coarser ornament such as verrucae and rugulae. Ornament is often coarser and more prominent on the inner body, with ornament being greatly reduced in size or absent on the bizonate cingulum.

*Comparison:* Species in this genus are typically smaller and have a relatively narrow cingulum compared to other genera of Cingulicavati. *Cirratriradites* are morphologically similar, but are larger with prominent distal foveae.

*Discussion:* Cingulum (including outer zona) width in proportion to total miospore diameter is an important criterion for differentiating members of the genus. This is
measured by subtracting the miospore body diameter from the total miospore diameter along its long axis. Bek (2012) proposed that *Lycospora* be divided into six morphological groups; five groups of cingulizone miospores (*L. granulata*, *L. brevijuga*, *L. pellucida*, *L. uber* and *L. subtriquetra* Groups) and one group of cingulate miospores (*L. micropapillata* Group).

**Affinity:** Lycopsid; Lepidodendrid. Some authors propose that forms with a broader bizonate cingulum (i.e. *Lycospora pellucida*) were derived from *Lepidophloios*, a genus typical of waterlogged peat mires, whereas those with a narrower bizonate cingulum (i.e. *Lycospora brevijuga*) were derived from ‘*Lepidodendron*’, which was better adapted to clastic swamps (DiMichele and Phillips, 1994). The present author will not differentiate between these two lycopsid genera. These lycopsid genera are considered as closely related evolutionary, developmentally and reproductively (Bateman *et al.*, 1992; DiMichele and Phillips, 1994). Given the closely related nature of these two lycopsid genera, as well as the difference in cingulum only being ~2 µm between these two species, the present author will interpret *Lycospora* as being derived from Lepidodendracean lycopsids, which may refer to both ‘*Lepidodendron*’ and *Lepidophloios*, in this case.

*Lycospora brevijuga* Kosanke 1950
Plate 11, Figure 4

**Holotype:** Kosanke (1950), pl. 10, fig. 5.
**Type locality:** No. 2 (Colchester) Coal, Carbondale Group, Illinois, U.S.A; Asturian.

**Description:** Trilete miospores with a round or oval amb equatorial outline, with a hint of a rounded-triangular shape. A bizonate cingulum is formed by the separated exoexine, with a thickened inner cingulum and a thin outer zona. The inner and outer zones are of comparable width. In total the bizonate cingulum is 3-4 µm wide, making up a quarter of the miospore radius. Laesurae extend into inner zone of cingulum, or
more rarely into the zona. Dense grana ornament the inner body and cingulum, and appear slightly reduced on the zona.

*Dimensions:* Total 31 (33) 36 (6 specimens; HF). Total 30 (33) 39 (3 specimens; Schulze and 2% KOH).

*Discussion:* The Bristol specimens are very similar to *Lycospora pusilla*, as figured (Pl. 20, fig. 10-11) by Smith and Butterworth (1967) which appears as clearly cingulizonate. *L. pusilla* is interpreted as a cingulate miospore (Ibrahim, 1933; Somers *et al.*, 1972), in contrast to the cingulizonate nature of other member of the genus. This is discussed in detail in Bek (2012), who included all cingulate species of *Lycospora* to the *L. micropapillata* Group. However, the Bristol specimens feature a clear bizonate equatorial structure which slightly exceeds the 3 µm thickness for this species (Somers *et al.*, 1972). The Bristol representation of this species cannot therefore be adequately accommodated by *L. pusilla* or any other species of the *L. micropapillata* Group as proposed by Bek (2012). *L. brevijuga* Kosanke is the closest comparable species reviewed by Bek (2012), included in his *L. brevijuga* Group. However, Kosanke (1950) notes that *L. brevijuga* is considered to be a variation of *L. pusilla*; a conclusion which the present author agrees with. Although *L. pellucida* has seniority, given that the holotype and most descriptions state this species is cingulate with a 3 µm cingulum, *L. brevijuga* will be used for the Bristol specimens.

*Comparison:* Has a more well-rounded amb and a narrower cingulum/zona than *L. pellucida*.

*Occurrence:* Harry Stoke B borehole to Westerleigh/Shortwood Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

*Known range:* Langsettian (Smith, 1962) to Asturian.
**Lycospora noctuina** Butterworth and Williams 1958

Plate 11, Figure 5

**Holotype:** Butterworth and Williams (1958) pl. 20, fig. 5.

**Type locality:** Darnley No. 3 borehole, Central Coalfield, Scotland; Namurian A.

*Description:* Trilete miospores with a rounded-triangular to convex triangular equatorial outline. A bizonate cingulum, with an inner thickened cingulum and thin outer zona, is formed by the exoexine. The inner and outer zones are of comparable width. The total cingulum occupies two fifths to half of the miospore radius, and is 7-10 µm in width. Laesurae extend into inner zone of cingulum on into the outer zona. Miospore body is ornamented with grana, verrucae and rugulae. The verrucae and rugulae may be up to 4 µm in width, between which the numerous grana are scattered. Grana may occur on the cingulum, but the zona is almost always laevigate.

*Dimensions:* Total 35 (37) 49 (6 specimens; HF).

*Comparison:* The verrucae and rugulae on the inner body of this species differentiate it from other members of the genus. This species is a member of the *L. uber* Group of Bek (2012).

*Occurrence:* Harry Stoke B borehole to Westerleigh Hard Coal, Bickley Wood to Hursley Hill borehole (Winterbourne Formation to Publow Member).

*Known range:* Viséan to Asturian (Peppers, 1993).
**Lycospora pellucida (Wicher) Schopf et al., 1944**

Plate 11, Figure 6

1934  *Sporites pellucidus* Wicher, p. 186.
1944  *Lycospora pellucida* (Wicher); Schopf, Wilson, and Bentall, p. 54.

**Holotype:** Potonié and Kremp (1955), pl. 17, fig. 341.

**Type locality:** Wehofen Colliery, Ruhr Coalfield, Germany; Bolsovian.

*Description:* Trilete miospores with a rounded-triangular equatorial outline. Exoexine is expanded to form a bizonate cingulum consisting of a thick inner cingulum and thin outer zona. Cingulum and zona of roughly equal widths. In total, the bizonate cingulum makes up two fifths to half of the miospore radius (5-8 µm). Laesurae extend into inner zone of cingulum, and may be accompanied by folding along their length. Exine ornamented by grana, which appear to be slightly denser on the inner body and cingulum.

*Dimensions:* Total 33 (34) 38 (10 specimens; HF). Total 36-38 (2 specimens; Schulze and 2% KOH).

*Comparison:* *L. brevijuga* has a narrower bizonate cingulum and is generally more rounded than this species. This species is a member of the *L. pellucida* Group of Bek (2012).

*Occurrence:* Harry Stoke B borehole to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Golden Valley to above Hursley Hill borehole (Winterbourne Formation to Publow Member).

*Known range:* Viséan to Asturian.
Genus CRISTATISPORITES (Potonié and Kremp) Butterworth et al. 1964

Type species: C. indignabundus (Loose) Potonié and Kremp 1954.

Description: Trilete miospores with a rounded-triangular equatorial margin. Intexine and exoexine separated to form an inner body, with a broad equatorial cingulum. The base of the zona seems crassitudinous, but the width of this crassitude is obscured by the dense ornament. The cingulum occupies around two fifths to three fifths of the miospore radius, but the exact extent is difficult to measure due to the nature of the ornamentation. Distally the miospore is covered with dense spinae and coni, which may be fused basal to produce discontinuous crests. The ornament appears denser on the inner body and the crassitudinous base of the cingulum. The ornament continues onto the cingulum but is reduced in density and size. The equatorial outline of the miospore is highly modified by the ornament. The proximal surface is laevigate, or sparsely ornamented by greatly reduced spinae and coni.

Comparison: Prominent distal sculpture separates Cristatisporites from other Cingulicavati.

Discussion: Due to the dense and variable ornament in the genus it is unclear how persistent the crassitude is, and it may indeed be part of the “ring of saetae” mentioned in Butterworth et al. (1964). However, a large portion of the Bristol specimens do appear to have a crassitude at the base of the zone rather than a ring of saetae or spines. Upon compression, the distal ornament of the central body becomes radially arranged and may give the appearance of a ring of ornament surrounding the central body. Close inspection usually reveals the “ring” is in fact this radially arranged ornament lying on top of a crassitude. Due to the density of the distal ornament, it is almost often impossible to discern the nature of the proximal surface in polar compressed specimens. For this reason, species descriptions will only refer to the nature and disposition of the visible distal ornament.

**Cristatisporites indignabundus** (Loose) Staplin and Jansonius 1964

Plate 11, Figures 7-8

<table>
<thead>
<tr>
<th>Year</th>
<th>Reference</th>
</tr>
</thead>
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<tr>
<td>1944</td>
<td><em>Densosporites indignabundus</em> (Loose); Schopf <em>et al.</em>, p. 40.</td>
</tr>
<tr>
<td>1954</td>
<td><em>Cristatisporites indignabundus</em> (Loose); Potonié and Kremp, p. 142.</td>
</tr>
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</table>

**Holotype:** Potonié and Kremp (1955), pl. 16, fig. 294.

**Type locality:** Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

**Description:** Trilete miospores with a rounded-triangular equatorial margin. Cingulum formed by exoexine occupies two fifths to just over half of the miospore radius. Cingulum appears to have a crassitudinous base, but this may be a feature of the distal ornamentation. Laesurae only usually visible when accompanied by folds, where they can be seen to extend into the crassitudinous area of the cingulum. Distally, the inner body formed by the intexine is densely ornamented by 2-3 µm tall coni and subordinate spinae. The distal ornament becomes reduced in size and more widely spaced on the cingulum, projecting only 1-2 µm at the equatorial margin. In some specimens the distal ornament on the cingulum is so reduced it does not project at the equator.

**Dimensions:** Total 36 (45) 55 (8 specimens; HF).

**Discussion:** Likely an extreme end member of *C. solaris*, as the two species are typically found in close stratigraphical association in the Bristol samples.
Comparison: *Cristatisporites solaris* has longer ornament, which tends to be dominated by spinae rather than coni. The ornament *C. solaris* is more uniform over the entire distal surface and modifies the equatorial outline of the miospore to a greater degree.

Occurrence: Harry Stoke B borehole to Winterbourne Railway Cutting, Bickley (Winterbourne Formation to Mangotsfield Member). Possibly in Dingle leaf bed (Mangotsfield Member).

Known range: Duckmantian to Bolsovian.

*Cristatisporites solaris* (Balme) Smith and Butterworth 1967
Plate 11, Figure 9

1952  *Densosporites solaris* Balme.

Lectotype: Smith and Butterworth (1967), pl. 20, fig. 24.
Type locality: Houghton Thin Seam, Yorkshire Coalfield, England; Lower Bolsovian.

Description: Trilete miospores with a rounded-triangular equatorial margin. Exoexine separated to form a cingulum which occupies two thirds to three fifths of the miospore radius. Cingulum appears to have a crassitudinous base, but is unclear and often associated with the dense distal ornament. Laesurae usually only visible when accompanied by folds, when visible they extend into the crassitudinous portion of the cingulum. The distal face of miospore is ornamented with numerous 2-4 µm spinae and subordinate coni which are densely packed and may be partially fused, forming cristae. The ornament is slightly reduced in density on the cingulum when compared with the inner body. The spinae and coni project strongly at the equator, where 25-35 projections are visible.

Dimensions: Total 34 (37) 39 (8 specimens; HF).
Comparison: *Cristatisporites indignabundus* is typically characterised by smaller and more well-spaced ornament, which is much denser on the body than the zona. The ornament of *C. indignabundus* also rarely forms cristae, due to is more well-spaced disposition.

*Occurrence*: Harry Stoke B borehole to Dingle leaf bed (Winterbourne Formation to Mangotsfield Member).

*Known range*: Upper Duckmantian to Bolsovian.

**Genus CIRRATRIRADITES Wilson and Coe 1940**

*Type species*: *C. saturni* (Ibrahim) Schopf et al., 1944.

*Description*: Trilete miospores with a triangular equatorial outline. Shape in generally convex triangular, with pointed apices. Exoexine is expanded to form a broad zona around the equator of the miospore, which is usually minutely striated. These striations are most clearly seen at the equatorial margin, where they give the zona a serrate outline at high levels of magnification. The base of the zona may bear a prominent crassitude which overlaps the miospore body, and/or radial thickenings may be present within the zona. The zona is typically broadest at the apices. On the distal pole the miospore body may have a number of foveae, which bear distinctive thickened margins. Laesurae extend to the margin of the miospore body, and are often accompanied by prominent folds which extend to the margin of the zona. Exine of the miospore body is relatively much thicker than that of the zona.

*Comparison*: Other members of Cingulicavati (*Lycospora, Densosporites, Cingulizonates and Cristatisporites*) have a cuneiform cingulum, this overlaps the miospore body at both poles.

*Affinity*: Lycopsida; *Selaginella* (Bek et al., 2009b).
**Cirratriradites annulatus** Kosanke 1950

Plate 11, Figure 10

*Holotype:* Kosanke (1950), pl. 7, fig. 4.

*Type locality:* No. 6 Coal, Carbondale Group, Illinois, U.S.A; Asturian.

*Description:* Trilete miospores with a convex triangular to rounded-triangular outline. Interradials convex with rounded or pointed apices. Zona formed by equatorial expansion of exoexine which may have a prominent crassitudinous base. The zona makes up less than one quarter of the miospore radius; either being of equal width around the equator, or being slightly expanded at the apices. Zona minutely striated which gives the miospore a serrate equatorial outline, typically only visible under high magnification. Outer region of zona may bear irregular concentric bands of thickening. Distally 4-5 foveae are present on the inner body defined by the intexine. The margins of these foveae are bordered by a 1-2 µm thickened rim. These foveae are generally rounded-polygonal, due to deformation produced by adjacent foveae abutting against one another. Exine of the inner body is to granulate.

*Dimensions:* Total 46 (1 specimen; HF). Total 62 (66) 80 (6 specimens; Schulze and 2% KOH).

*Comparison:* *C. saturni* has fewer (1-3) distal foveae, and a typically broader zona.

*Occurrence:* Winterbourne Railway Cutting to 65 The Dingle, below Trench Coal to Hursley Hill borehole (Mangotsfield Member to Publow Member).

*Known range:* Asturian.
Cirratriradites annuliformis Kosanke 1950
Plate 11, Figure 11

Holotype: Kosanke (1950), pl. 7, fig. 6.
Type locality: No. 6 Coal, Carbondale Group, Illinois, U.S.A; Asturian.

Description: Trilete miospores with a convex triangular outline. Interradials strongly convex with pointed apices. Zona formed by equatorial expansion of exoexine which may have a prominent crassitudinous base when it overlaps with the miospore body. The zona is broad, making up between on two fifths to three fifths of the miospore radius. The zone is typically of a constant width in the interradial region, and slightly expanded at the apices. Distally 1-2 foveae are present on the inner body defined by the intexine. One large, circular distal foveae seems to be the dominant morphology. The foveae may not be present, or may be only subtle as they lack a thickened rim which is typical of other species. Exine of the inner body is punctate.

Dimensions: Total 31 (35) 41 (5 specimens; HF). Total 54 (64) 76 (3 specimens; Schulze and 2% KOH).

Comparison: Cirratriradites saturni has a typically broader, striated zona. C. annulatus and C. saturni both have distinct foveae, due to prominent encircling thickened rims.

Occurrence: Westerleigh Hard Coal, below Salridge Coal (Downend Member to Farrington Member). Possibly in Huckford Quarry (Mangotsfield Member).

Known range: Asturian.
**Cirратriradites saturni** (Ibrahim) Schopf et al., 1944
Plate 11, Figure 12

1938  *Zonotriletes saturni* (Ibrahim); Luber in Luber and Waltz.
1944  *Cirratriradites saturni* (Ibrahim); Schopf, Wilson, and Bentall, p. 44.

*Holotype:* Ibrahim (1932), pl. 15, fig. 14.
*Type locality:* Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

**Description:** Trilete miospores with a convex triangular outline. Interradials strongly convex with pointed apices. Zona formed by equatorial expansion of exoexine which may have a prominent crassitudinous base when it overlaps with the miospore body. The zona is broad, making up between on quarter and a third of the miospore radius. The zona is typically of a constant width in the interradial region, and slightly expanded at the apices. Zona minutely striated which gives the miospore a serrate equatorial outline, typically only visible under high magnification. Outer region of zona may bear concentric bands of thickening. Distally 1-3 foveae are present on the inner body defined by the intexine. One large, circular distal foveae seems to be the dominant morphology. The margins of these foveae are bordered by a 1-2 µm thickened rim. When more than one foveae occur, they are generally rounded-polygonal due to deformation produced by adjacent foveae abutting against one another. Exine of the inner body is granulate, but may be punctate in some specimens.

*Dimensions:* Total 62 (71) 85 (11 specimens; HF). Total 72-79 (2 specimens; Schulze and 2% KOH).

*Comparison:* May have 1-3 distal foveae, as noted by Smith and Butterworth (1967). The broad zona and relatively few distal foveae differentiate *C. saturni* from other species.
Occurrence: Harry Stoke B to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Namurian to Bolsovian.

Genus CINGULIZONATES (Dybová and Jachowicz) Butterworth et al. 1964
Type species: C. bialatus (Waltz) Smith and Butterworth, 1967.

Description: Trilete miospores with a rounded-triangular equatorial outline. Exoexine separated to form a bizonate equatorial structure; a thick cingulum at the base with a thin zona surrounding it. Inner cingulum is distinctly raised and much thicker than the outer zona. Laesurae distinct, extending to the margin of the inner body defined by the intexine. Exine ornamented in some way, with either grana or small verrucae.

Comparison: Presence of the prominent crassitude at the base of the zona distinguishes this genus from other Cingulicavati.

Affinity: Lycopsida. Almost certainly from Sporangiostrobus-type sub-arborescent forms that also bear the similar Densosporites and Cristatisporites. See discussion in genus Densosporites.
**Cingulizonates loricatus** (Loose) Butterworth and Smith (in Butterworth *et al.*, 1964)

Plate 11, Figure 13

1944  *Densosporites loricatus* (Loose); Schopf, Wilson, and Bentall, p. 40.
1964  *Cingulizonates loricatus* (Loose) Butterworth and Smith; Butterworth *et al.*, p. 1053.

*Holotype:* Potonié and Kremp (1956), pl. 18, fig. 400.

*Type locality:* Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

*Description:* Trilete miospores with a rounded-triangular equatorial outline. Separation of the exoexine from the intexine produces a bizonate cingulum/zona which makes up two fifths to half of the miospore radius. The cingulum is relatively much thicker than both the inner body and the outer zona, and is clearly raised in relation to both. Outer zona is generally less than the width of the cingulum; the junction between which is often crenulate. Laesurae extend to the edge of the inner body, or just into the cingulum in some specimens. Intexine bears grana of varying sizes, which may persist on the cingulum.

*Dimensions:* Total 33 (36) 42 (13 specimens; HF).

*Comparison:* *C. bialatus* contains tubercles that project into the zona.

*Occurrence:* Harry Stoke B borehole to Westerleigh Hard Coal, Golden Valley to below Trench Coal (Winterbourne Formation to Farrington Member). Possibly in Hursley Hill borehole (Publow Member).

*Known range:* Langsettian to Bolsovian.
Genus *RADIIZONATES* Staplin and Jansonius 1964

Type species: *R. aligerens* (Knox) Staplin and Jasonius 1964.

*Description:* Trilete miospores with a rounded-triangular equatorial outline, which may approach circular in some specimens. Exoexine expanded equatorially to form a bizonate structure, consisting of an inner cingulum and a much thinner zona around the margin. The width of the cingulum in relation to the zona varies between species. The total bizonate cingulum occupies two fifths to half of the miospore radius. Prominent radial striae originate from the cingulum, and extend through the zona to the equatorial margin. Laesurae typically extend into the cingulum. Intexine and cingulum may be laevigate, granulate or rugulate.

*Comparison:* *Cingulizonates* lacks strong radial ribbing on the outer zona, and generally has a better defined inner body. *Cirratriradites* are zonate with a slightly crassitudinous base in some specimens, and have prominent distal foveae.

*Affinity:* Lycopsid; sub-arborescent; *Sporangiostrobus* (Courvoisier and Phillips, 1975). See discussion in genus *Densosporites*.

*Radiizonates aligerens* (Knox) Staplin and Jasonius 1964

Plate 12, Figure 1

1950 *Cirratriradites aligerens* Knox, p. 329.
1964 *Radiizonates aligerens* (Knox); Staplin and Jansonius, p. 106.

*Neotype:* Smith and Butterworth (1967), pl. 19, fig. 9-10 (Chosen by Staplin).

*Type locality:* Glass Seam, Lothians Coalfield, Scotland; Langsettian.

*Description:* Trilete miospores with a rounded-triangular to circular equatorial outline. Bizonate cingulum formed by exoexine. Inner cingulum is relatively narrow, up to 4-5 μm wide. The outer zona is relatively thin, but much broader than the inner cingulum (7-
18 µm). In total the bizonate cingulum occupies two fifths to half of the miospore radius. Numerous prominent striae originate from the cingulum, and extend through the zona to the margin of the miospore. The thinner striae tend to taper towards the equator, whereas the thicker striae are a more consistent width along their entire length. Laesurae fairly prominent, extending to the margin of the inner body and slightly into the narrow cingulum. Inner body ornamented with grana, and rarer small verrucae.

*Dimensions:* Total 43 (49) 63 (7 specimens; HF). Total 45 (54) 68 (3 specimens; Schulze and 2% KOH).

*Occurrence:* Harry Stoke B borehole to roof of Parkfield Hard Coal, below Trench Coal to Hursley Hill borehole (Winterbourne Formation to Publow Member).

*Known range:* Langsettian. Reworked.

**Radiizonates striatus** (Knox) Staplin and Jasonius 1964

Plate 12, Figure 2

1957 *Densosporites marginata* Artüz, p. 252.
1958 *Densosporites striatus* (Knox); Butterworth and Williams, p. 380.
1964 *Radiizonates striatus* (Knox); Staplin and Jansonius, p. 106.

*Neotype:* Butterworth and Williams (1954), pl. 18, fig. 1.

*Type locality:* Ruabon Yard Seam, Llay Colliery, North Wales Coalfield, Wales; Upper Langsettian.

*Description:* Trilete miospores with a rounded-triangular to circular equatorial outline. Bizonate cingulum formed by exoexine; inner cingulum relatively much wider than the outer zona. In total the bizonate cingulum occupies two fifths to half of the miospore radius. Inner cingulum is strongly modified by radial striae, with protrude into the zona. Due to the radial striae, the cingulum/zona interface is undulating and irregular. Laesurae usually prominent, extending to the margin of the inner body and slightly into
the narrow cingulum. Inner body ornamented with grana, and rarer small verrucae. Some of the more coarsely ornamented specimens show coalescence of the ornament to form a network of rugulae, but this is rare.

*Dimensions*: Total 37 (38) 44 (5 specimens; HF). Total 38-42 (2 specimens; Schulze and 2% KOH).

*Discussion*: Almost certainly an extreme form of *Cingulizonates loricatus*, which this species it typically found in association with.

*Occurrence*: Harry Stoke B borehole to roof of Parkfield Hard Coal, Bickley Wood to above Trench Coal (Winterbourne Formation to Farrington Member).

*Known range*: Langsettian to Bolsovian (Grebe, 1972).

**Suprasubtumra PSEUDOSACCITRILETES Richardson 1965**

**Infraturma MONOPSEUDOSACCITI Smith and Butterworth 1967**

**Genus ENDOSPORITES Wilson and Coe 1940**

*Type species*: *E. ornatus* Wilson and Coe 1940

*Description*: Trilete pseudosaccate miospores with a round to rounded-triangular equatorial outline. Exoexine separated from the intexine to form a relatively large pseudosaccus; the pseudosaccus is attached to the proximal surface of the inner body defined by the intexine. The pseudosaccus usually possesses a limbus. A small pore is often visible in the pseudosaccus at the apices/radial margins, but is usually only apparent after close inspection. The inner body may be round to rounded-triangular, but may not be conformable to the equatorial outline of the pseudosaccus. Laesurae extend to the margin of the inner body, and are commonly accompanied by prominent folds that may persist to the equator of the pseudosaccus. Pseudosaccus surface is granulate. Inner body is slightly thicker, and therefore marginally darker than the pseudosaccus.
Comparison: *Florinites* saccus is distally attached and has an infrareticulate ornament.

Discussion: Swelling is common when macerated in Schulze solution (Smith and Butterworth, 1967), so sizes will vary between coals and clastics.

Affinity: Lycopsid; sub-arborescent forms such as *Chaloneria* (Pigg and Rothwell, 1983).

**Endosporites globiformis** (Ibrahim) Schopf *et al.*, 1944

Plate 12, Figure 3

1933 *Zonales-sporites globiformis* Ibrahim, p. 28.
1938 *Zonotriletes globiformis* (Ibrahim); Luber in Luber and Waltz.
1944 *Endosporites globiformis* (Ibrahim); Schopf, Wilson, and Bentall, p. 45.

Holotype: Potonié and Kremp (1956), pl. 20, fig. 459.

Type locality: Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

Description: Trilete pseudosaccate miospores with a round to rounded-triangular equatorial outline. Exoexine separated from the intine to form a pseudosaccus which usually possesses a prominent limbus. A small pore is often visible in the pseudosaccus at the apices/radial margins, but is usually only apparent after close inspection. The inner body may be round to rounded-triangular, but may not be conformable to the equatorial outline of the pseudosaccus. The inner body occupies less than half of the total miospore radius. Laesurae extend to the margin of the inner body, and are commonly accompanied by prominent folds that may persist to the equator of the pseudosaccus. Pseudosaccus surface is granulate. Inner body is slightly thicker, and therefore marginally darker than the pseudosaccus.

Dimensions: Total 76 (97) 110 (14 specimens; HF). Total 77 (84) 111 (6 specimens; Schulze and 2% KOH).
Comparison: When the body to pseudosaccus ratio exceeds 50%, species will be assigned to *E. zonalis*.

Occurrence: Harry Stoke B borehole to roof of Parkfield Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

**Known range:** Upper Langsettian to Asturian.

*Endosporites zonalis* (Loose) Knox 1950

Plate 12, Figure 4

1944 *Cirratriradites zonalis* (Loose); Schopf, Wilson, and Bentall, p. 44.
1950 *Endosporites zonalis* (Loose); Knox, p. 332.

**Holotype:** Potonié and Kremp (1956), pl. 20, fig. 455.

**Type locality:** Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

Description: Trilete pseudosaccate miospores with a round to rounded-triangular equatorial outline. Exoexine separated from the intexine to form a pseudosaccus which usually possesses a prominent limbus. A small pore is often visible in the pseudosaccus at the apices/radial margins, but is usually only apparent after close inspection. The inner body may be round to rounded-triangular, but may not be conformable to the equatorial outline of the pseudosaccus. The inner body occupies over half of the total miospore radius. Laesurae extend to the margin of the inner body, and are commonly accompanied by prominent folds that may persist to the equator of the pseudosaccus. Pseudosaccus surface is granulate. Inner body is slightly thicker, and therefore marginally darker than the pseudosaccus.

**Dimensions:** Total 60 (79) 107 (12 specimens; HF). Total 92 (1 specimen; Schulze and 2% KOH).
Comparison: When the body to pseudosaccus ratio is less than 50%, species will be assigned to *E. globiformis*.

Occurrence: Harry Stoke B borehole to siltstones above Shortwood Hard Coal, Bickley Wood to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Upper Langsettian to Asturian.

**Genus HYMENOSPORA Neves 1961**

Type species: *H. palliolata* Neves 1961

Description: Trilete miospores with a circular to subcircular equatorial outline. Pseudosaccus developed equatorially by separation on the intexine and exoexine. Pseudosaccus proximally attached, but this is difficult to see in practice. Laesurae may vary between three quarters to nearly the full radius of the central body. Pseudosaccus densely plicated, with the densest folding occurring in the region of the poles. Pseudosaccus relatively thick, body also relatively thick.

Comparison: The prominent pseudosaccus folds differentiate this genus from similar pseudosaccate forms such as *Endosporites*.

Discussion: Peppers (1970) also noted that the folding (“rugulae”) tend to be densest at the poles, and that the folds may attain a verrucose shape.

Affinity: Unknown.
Hymenospora multirugosa Peppers 1970
Plate 12, Figure 5

Holotype: Peppers (1970), pl. 13, fig.8.
Type locality: Danville (No. 7) Coal, Carbondale Formation, Illinois, U.S.A.; Asturian.

Description: Trilete miospores with a circular to subcircular equatorial outline. Pseudosaccus developed equatorially by separation of the intexine and exoexine. Pseudosaccus proximally attached, but this is difficult to see in practice. Laesurae may vary between three quarters to nearly the full radius of the central body, often accompanied by narrow lip-like thickenings. Pseudosaccus densely plicated with radially orientated folds, with folds being concentrated at the poles (most prominent distally). Folds often extend to the edge of the inner body, giving it an irregular outline. Folds may almost attain a verrucate-like morphology in some areas. Pseudosaccus is fairly thick, occupying around a third of the spore radius. Central body is moderately thick and dark.

Dimensions: Total 35-49 (2 specimens; HF). Total 41 (47) 50 (4 specimens; Schulze and 2% KOH).

Discussion: The Bristol representation of this species seems to be smaller than the holotype, and the 32.5-41.8 µm size range seen by Ravn (1979).

Comparison: This species is superficially very similar to Discernisporites sp.1 , and often occurs in the same samples. However, the saccus in Discernisporites sp.1 is minutely granulate and without the prominent plications seen in Hymenospora.

Occurrence: Coombe Brook to Dingle leaf bed, below Salridge Coal (Winterbourne Formation to Mangotsfield Member).

Known range: Namurian to Asturian (Peppers, 1970; Butterworth, 1984; Ravn, 1986)
Genus RUGOSPORA (Neves and Owens) Turnau 1978
Type species: R. corporata Neves and Owens 1966

Description: Trilete miospores with an oval, round or rounded triangular equatorial outline. Exoexine is slightly separated from the intexine, only being attached in the region of the trilete mark on the proximal pole. The greatest separation of the intexine and exoexine occurs near the distal pole. The separated exoexine is thin and densely wrinkled, often forming an almost microrugulate pattern. Laesurae two fifths to half of the miospore radius in length, but generally obscured by the wrinkling of the exoexine. Exine thin and laevigate.

Comparison: A superficially similar genus is Corrugitriletes Turner and Spinner, which is acamerate (to ?camerate) with “outer layer characterised by conspicuous muroid thickenings arranged radially at the equator”. Corrugitriletes appears to be used by 3 authors for UK-based Namurian-aged studies (Turner and Spinner, 1993; McLean, 1995) whereas use of Rugospora is more stratigraphically, and geographically, widespread.

Affinity: Unknown.

Rugospora minuta Neves and Ioannides 1974
Plate 12, Figure 6

Holotype: Neves and Ioannides (1974), pl. 8, fig.7.
Type locality: 781.2 m Splimersford Borehole, East Lothian, Scotland; Viséan.

Description: Trilete miospores with an oval amb. Exoexine is slightly separated from the intexine, may be attached at the proximal pole (unclear). The exoexine on the distal pole may be separated from the intexine by up to 3 µm. The separated exoexine is thin and densely wrinkled. Wrinkles around 1 µm in height and width. Laesurae three
fifths to three quarters of the miospore radius in length, but generally at least partially obscured by the exoexine folds. Exine thin and laevigate.

*Dimensions:* Total 37 (1 specimen; Schulze and 2% KOH).

*Discussion:* May be superficially similar to the *Corrigutrilletes radiatus* Turner and Spinner 1992.

*Comparison:* *Rugospora* sp.1 is bigger, with longer laesurae and clear proximal attachment of exoexine.

*Occurrence:* Harry Stoke B borehole to Winterbourne Railway Cutting (Winterbourne Formation to Mangotsfield Member).

*Known range:* Viséan (Neves and Ioannides, 1974). Reworked.

**Rugospora polyptycha** Neves and Ioannides 1974

Plate 12, Figure 7

*Holotype:* Neves and Ioannides (1974), pl. 8, fig.2.

*Type locality:* 781.2 m Splimersford Borehole, East Lothian, Scotland; Viséan.

*Description:* Trilete miospores with rounded-triangular equatorial outline. Exoexine separated; intexine forms an indistinct inner body which makes up three fifths to four fifths of the miospore radius. Exoexine densely wrinkled in the region of the inner body, wrinkles persist to or just beyond the margin of the inner body. Exoexine beyond the margin of the inner body is without wrinkling, forming a 8-14 µm wide laevigate equatorial zone surrounding the densely wrinkled inner body. Wrinkles up to 2 µm in diameter, giving an almost rugulate appearance to the miospore. Laesurae extend to the margin of the inner body, usually accompanied by folds which persist to the equatorial margin of the miospore.
Dimensions: Total 65 (66) 66 (3 specimens; HF).

Discussion: *Discernisporites irregularis* Neves 1958 is morphologically similar, however, the ornament less pronounced and consists mainly of verrucae rather than elongated elements. The ornament also tends to be restricted to the regions of exoexine overlying the body in *D. irregularis*.

Occurrence: Harry Stoke B borehole (Winterbourne Formation).

Known range: Viséan (Neves and Ioannides, 1974). Reworked.

**Rugospora sp.1**

Plate 12, Figure 8

Description: Trilete miospores with an oval to circular amb. Exoexine is slightly separated from the intexine, only being attached in the region of the trilete mark on the proximal pole. The exoexine on the distal pole may be to be separated from the intexine by up to 6 \( \mu \text{m} \). The separated exoexine is thin and densely wrinkled. Wrinkles around 1 \( \mu \text{m} \) in height and width. Laesurae two fifths to half of the miospore radius in length. Exine thin and laevigate.

Dimensions: Total 51 (1 specimen; Schulze and 2% KOH).

Comparison: Larger size, shorter laesurae and fusion of the intexine and exoexine at the proximal pole differentiate this species from *Rugospora minuta*.

Occurrence: Harry Stoke B borehole (Winterbourne Formation). Likely reworked with other members of genus.
**Genus PROPRISPORITES Neves 1958**

Type species: *P. rugosus* Neves 1958

*Description:* Trilete miospores, with a generally rounded or oval amb. Laesurae about three quarters of the miospore radius. Exoexine is thin and folded to form straight to gently sinuous ridges on the surface of the miospore. Exine is laevigate.

*Affinity:* Unknown.

*Proprisporites laevigatus* Neves 1961

Plate 12, Figure 9

*Holotype:* Neves (1961), pl. 33 fig. 9.

*Type locality:* Marine shales, Congleton Edge Quarry, Staffordshire, England; Namurian A/B.

*Description:* Trilete miospores with an oval amb. Laesurae around three quarters of the miospores radius in length. Exoexine is folded, to form straight and slightly sinuous ridges which are well-spaced and generally fairly conformable with one another. The exoexine is still in close contact with the intexine in between the ridges. Ridges 2-3 µm wide and up to 4 µm tall. As well as the elongate ridge-like folds, shorter verrucae-like folds also occur. Exine is laevigate.

*Dimensions:* Total 58 (1 specimen; HF).

*Occurrence:* Coombe Brook (Winterbourne Formation). Possibly in Winterbourne Railway Cutting (Mangotsfield Member).

Genus DISCERNISPORITES (Neves) Neves and Owens 1966

Type species: D. irregularis Neves 1958.

*Description:* Trilete pseudosaccate miospores with rounded-triangular equatorial outline. Exoexine separated from the intexine to form a pseudosaccus. The inner body rounded-triangular, and is conformable to the equatorial outline of the pseudosaccus. Inner body occupies well over half of the total miospore radius. Laesurae reach to the edge of the inner body, often accompanied by folding which may approach or reach the equatorial margin of the pseudosaccus. Pseudosaccus surface is granulate. Inner body is thin and almost indistinguishable from the thick pseudosaccus.

*Comparison:* The thickness of the pseudosaccus and relatively indistinct body differentiates the genus from *Endosporites*. *Discernisporites* also never possess a limbus, whereas *Endosporites* nearly always possess this feature.

*Affinity:* Unknown.

Discernisporites micromanifestus (Hacquebard) Sabry and Neves 1971

Plate 12, Figures 10-11

1957 *Endosporites micromanifestus* Hacquebard, p. 317.
1958 *Discernisporites concentrus* Neves, p. 5.
1960 *Auroraspora micromanifestus* (Hacquebard); Richardson, p. 51.
1971 *Discernisporites micromanifestus* Hacquebard; Sabry and Neves, p. 1445.

*Lectotype:* Hacquebard (1967), pl. 3, fig. 15.
*Type locality:* Horton Group, Nova Scotia, Canada; Tourmaisan.

*Description:* Trilete pseudosaccate miospores with rounded-triangular equatorial outline. Exoexine separated from the intexine to form a pseudosaccus. The inner body rounded-triangular, and is conformable to the equatorial outline of the pseudosaccus.
Inner body occupies three fifths to four fifths of total miospore radius. Laesurae reach to the margin of the inner body, often accompanied by folding which may approach or reach the equatorial margin of the pseudosaccus. Pseudosaccus surface is granulate. Inner body is thin and almost indistinguishable from the thick pseudosaccus.

*Dimensions*: Total 70 (72) 75 (7 specimens; HF). Total 68 (71) 35 (9 specimens; Schulze and 2% KOH).

*Discussion*: *Discernisporites micromanifcestus* is also commonly found above the Cambriense Marine Band, despite having a published range of Viséan to Langsettian (McLean, pers. comms.). The Bristol representative of the species is also stratigraphically persistent in both coals and clastics, suggesting these are not simply reworked specimens.

*Comparison*: *Discernisporites* sp.1 is smaller, with a slightly more distinct body.

*Occurrence*: Harry Stoke B borehole to siltstones above Shortwood Hard coals (Winterbourne Formation to Farrington Member). Possibly in Bickley Wood (Mangotsfield Member).

*Known range*: Viséan to Langsettian (Sabry and Neves, 1971; Turner and Spinner, 1993).

**Discernisporites sp. 1**

*Plate 13, Figure 1*

*Description*: Trilete pseudosaccate miospores with a round to rounded-triangular equatorial outline. Exoexine separated from the intexine to form a pseudosaccus. The inner body may be round to rounded-triangular, and is conformable to the equatorial outline of the pseudosaccus. The inner body occupies three quarters to four fifths of the total miospore radius, and may have a slight darkening at the periphery. Laesurae extend
from three quarters to the full length of the radius of the inner body. Pseudosaccus surface is subtly granulate. Inner body is thicker, and therefore typically distinguishable from the saccus.

*Dimensions*: Total 44 (49) 55 (6 specimens; HF). Total 52 (2 specimens; Schulze and 2% KOH).

*Comparison*: *Discernisporites micromanifestus* is usually bigger, with a less distinct inner body.

*Occurrence*: Harry Stoke B borehole Huckford Quarry (Winterbourne Formation to Mangotsfield Member).

**Genus GRANDISPORA (Hoffmeister et al.) McGregor 1973**
Type species: *G. spinosa* Hoffmeister *et al.*, 1955.

*Description*: Trilete miospores with rounded to rounded-triangular equatorial outline. Exoexine separated to form a thin pseudosaccus. Intexine relatively much thicker than the pseudosaccus, forming a well-defined inner body which occupies over two thirds of the total miospore radius. The inner body may or may not be conformable in outline to the pseudosaccus. Laesurae greater than three quarters of the inner body radius, and may be accompanied by folds in the exoexine that may approach or reach the equatorial margin. Exoexine is ornamented with well-spaced coni, and subordinate spinae, which may have slightly bulbous bases. Ornament occurs on the distal surface and near the equatorial margin of the proximal face.

*Comparison*: The ornament in *Spinozonotriletes* is dominantly spinate, and the difference in thickness between the exoexine and intexine is much less.

*Affinity*: Unknown.
**Grandispora spinosa** Hoffmeister *et al.*, 1955

Plate 13, Figure 2

*Holotype:* Hoffmeister *et al.*, (1955), pl. 39, fig. 10,14.

*Type locality:* Hardinsburg Formation, Chester Series, Kentucky; Upper Mississippian.

*Description:* Trilete miospores with rounded to rounded-triangular equatorial outline. Exoexine separated to form a thin pseudosaccus. Intexine relatively much thicker than the pseudosaccus, forming a well-defined inner body which occupies over two thirds of the total miospore radius. The inner body may or may not be conformable in outline to the pseudosaccus. Laesurae greater than three quarters of the inner body radius, and may be accompanied by folds in the exoexine that may approach or reach the equatorial margin. Exoexine is ornamented with well-spaced coni and rarer spinae, 3-5 µm tall and around 2 µm wide at the base. The coni are variably spaced, with interstitial spaces ranging from 2-7 µm. Coni may or may not have bulbous bases. Ornament occurs on the distal surface and near the equatorial margin of the proximal face.

*Dimensions:* Total 90-100 (2 specimens; HF).

*Comparison:* *Spinozonotriletes uncatus* is generally slightly smaller, and has an inner body that occupies a larger proportion of the miospore radius. Although the ornament is a similar size in *S. uncatus*, it is much more slender and spinate in character.

*Occurrence:* Harry Stoke B (Winterbourne Formation).

Genus *SPINOZONOTRILETES* Hacquebard 1957

Type species: *S. uncatus* Hacquebard 1957

*Description:* Trilete miospores with rounded to rounded-triangular equatorial outline. Exoexine separated to form a pseudosaccus. Intexine relatively thicker than the pseudosaccus, forming a well-defined to poorly defined inner body which occupies over three quarters of the total miospore radius. The inner body may or may not be conformable in outline to the pseudosaccus. Laesurae greater than three quarters of the inner body radius, and may be accompanied by folds in the exoexine that may approach or reach the equatorial margin. Exoexine is ornamented with large spinae, which are fairly widely spaced. Ornament occurs mainly at the equator, and is reduced at the poles.

*Affinity:* Unknown.

*Spinozonotriletes cf. uncatus* Hacquebard 1957

Plate 13, Figure 3

*Holotype:* Hacquebard (1957), pl. 3, fig. 8-10.

*Type locality:* West Gore, Horton Group, Nova Scotia, Canada; Tournaisian

*Description:* Trilete miospores with rounded to rounded-triangular equatorial outline. Exoexine separated to form a pseudosaccus. Intexine relatively thicker than the pseudosaccus, forming a well-defined to poorly defined inner body which occupies over three quarters of the total miospore radius. The inner body may or may not be conformable in outline to the pseudosaccus. Laesurae greater than three quarters of the inner body radius, and may be accompanied by folds in the exoexine that may approach or reach the equatorial margin. Exoexine is ornamented with large spinae, 3-5 µm tall and around 1 µm in basal diameter. Ornament occurs mainly at the equator, and is reduced at the poles.

*Dimensions:* Total 60 (67) 72 (5 specimens; HF).
Comparison: *Grandispora spinosa* has a inner body which occupies relatively less of the total miospore radius, and is generally of a larger overall size. The ornament of *G. spinosa* is also distinctly conate, with generally wider based ornament. The Bristol specimens feature a body that occupies a greater portion of the total radius and shorter spines than *S. uncatus* and are therefore referred to *S. cf. uncatus*.

Occurrence: Harry Stoke B borehole (Winterbourne Formation).

Known range: Tournaisian (Higgs et al., 1988). Reworked.

**Genus KRAEUSELISPORITES (Leschik) Jansonius 1962**

Description: Trilete miospores with a rounded-triangular equatorial outline. Exoexine separated to form a bizonate cingulum/zona. Inner cingulum relatively wider than the outer zona. In total the bizonate cingulum occupies around a quarter to two fifths of the miospore radius. Laesurae reach into the cingulum or just into the zona, and are typically associated with prominent folds. Distal surface is ornamented with long and narrow spinae. Ornament is usually concentrated on the distal area of the inner body and cingulum, with only rare coni occurring in on the zona. Due to the height of the ornament, the tips of the spinae may project at the equatorial margin of the zona. Ornament absent on the proximal pole.

Comparison: The distal ornament of *Lundbladispora* is of much finer and conate projections, which are more densely and regular spaced across the inner body and the entire bizonate cingulum.

Affinity: Unknown.
Kraeuselisporites ornatus (Neves) Owens et al. 1976

Plate 13, Figure 4

1961  Cirratriradites ornatus Neves, p. 269.

Holotype: Neves (1961), pl. 33, fig. 3.
Type locality: Hipper Sick, Derbyshire; Namurian (Yeadonian).

Description: Trilete miospores with a rounded-triangular equatorial outline. Apices typically fairly well pointed. Bizonate equatorial structure formed by separation of the exoexine, comprising an inner cingulum surrounded by a thinner zona. Cingulum either equal to or slightly broader than the width of the zona. The bizonate cingulum occupies a quarter to two fifths of the miospore radius. Laesurae reach into cingulum or into zona, often accompanied by folds. Distal surface of miospore is ornamented with long and narrow spinae; 5-7 µm tall and 1.5-3 µm broad at the base. Spinae are concentrated on the distal surface of the inner body and the cingulum. Due to the length of the spinae their tips may project slightly at the equatorial margin of the zona, but the zona is typically devoid of ornament. Proximally the exine is laevigate.

Dimensions: Total 53 (64) 68 (4 specimens; HF).

Occurrence: Harry Stoke B borehole (Winterbourne Formation).

Known range: Namurian A to Langsettian (Clayton et al., 1977). Reworked.

Genus LUNDBLADISPORA (Balme) Playford 1965
Type species: L. wilmotti Balme 1963

Description: Trilete miospores with a rounded-triangular equatorial outline. Exoexine separated to form a bizonate cingulum/zona. Inner cingulum relatively narrower than the outer zona. In total the bizonate cingulum occupies around two fifths to half of the
miospore radius. Laesurae reach into the cingulum or just into the zona, and are typically associated with prominent folds. Distal surface is ornamented with coni and rarer verrucae. Ornament occurs over the inner body and the bizonate cingulum distally, being of fairly even size and disposition over the entire hemisphere. Ornament greatly reduced in size and density proximally, or absent.

*Comparison:* *Kraeuselisporites* is similar, but has long spinae which are less densely distributed. The ornament of *Kraeuselisporites* ornament is also restricted to the distal surface, but tends to occur only on the inner body.

*Discussion:* Playford (1965) emended the genus to exclude laevigate forms.

*Affinity:* Herbaceous lycopsid (J. Bek, pers. comms. 2011)

**Lundbladispora gigantea** (Alpern) Doubinger 1968

Plate 13, Figures 5-6

1958 *Lycospora gigantea* Alpern, p. 78.

*Holotype:* Alpern (1958), pl. 1, fig. 24.
*Type locality:* Unspecified borehole, Decize, France; Stephanian.

*Description:* Trilete miospores with a rounded-triangular equatorial outline. Shape may approach circular. Bizonate equatorial structure formed by separation of the exoexine, comprising of an inner cingulum surrounded by a thinner zona. Zona either equal to or slightly broader than the width of the inner cingulum. The bizonate cingulum occupies around two fifths to half of the miospore radius. Laesurae reach into cingulum or into zona, often accompanied by folds. Distal surface of miospore is ornamented with regular 1-2 μm coni, which occur evenly on both the inner body and the bizonate cingulum. The
coni project at the equatorial margin of the zona. Proximally the ornament appears reduced, or absent.

_Dimensions_: Total 52-57 (2 specimens; HF). Total 56-64 (2 specimens; Schulze and 2% KOH).

_Occurrence_: Frome Bank to Huckford Quarry, below and above Trench Coal (Mangotsfield Member to Farrington Member).

_Known range_: Asturian to Autunian (Clayton et al., 1977).

_Infraturma POLYPSEUDOSACCITI Smith and Butterworth 1967_  
_Genus ALATISPORITES (Ibrahim) Smith and Butterworth 1967_  
_Type species_: _A. pustulatus_ Ibrahim 1932

_Description_: Trilete miospores with a generally triangular equatorial outline, modified by three or more pseudosacci. Pseudosacci extend over much of the proximal surface, often reaching to or very close to the laesurae. Most of the distal hemisphere is free of pseudosacci. Pseudosacci number and size variable between species. Laesurae reach to or nearly to the equator, and may be open. Body may be laevigate, granulate or rugulate. Pseudosacci are granulate.

_Affinity_: Unknown.

_Alatisporites hoffmeisterii_ Morgan 1955  
_Plate 13, Figure 7_

_Holotype_: Morgan (1955), pl. 2, fig. 1.  
_Type locality_: Rowe Coal, Des Moines Series., Oklahoma, U.S.A.; Asturian.
Description: Trilete miospores with a rounded-triangular equatorial outline, modified by several pseudosacchi. Pseudosacchi oval to rounded in outline, 20-35 µm in diameter and generally of variable sizes on a specimen. 2-4 pseudosacchi occur in each interradial areas, with 7-9 pseudosacchi occurring in total on a specimen. Laesurae reach to or nearly to the equator, and may be open. Body ornamented with small verrucae of variable size. Pseudosacchi are granulate.

Dimensions: Body 68, total 85 (1 specimen; HF). Body 43-58, total 60-100 (2 specimens; Schulze and 2% KOH).

Comparison: The smaller Alatisporites pustulatus is tri-pseudosaccate and has a finer rugulate-verrucate body ornament. The irregular size, circular shape and comparatively high number of pseudosacchi make this species distinct from other member of the genus.

Occurrence: Harry Stoke B borehole to 65 The Dingle (Winterbourne Formation to Mangotsfield Member).

Known range: Bolsovian to Asturian.

*Alatisporites pustulatus* Ibrahim 1932

Plate 14, Figure 1

1933 *Alati-sporites pustulatus* Ibrahim, p. 32.

*Holotype:* Potonié and Kremp (1956), pl. 19, fig. 445.
*Type locality:* Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

Description: Trilete miospores with a rounded-triangular equatorial outline, modified by three pseudosacchi. Pseudosacchi extend over much of the proximal pole, often reaching to or very close to the laesurae. Most of the distal hemisphere is free of pseudosacchi. One phaseolate to oval pseudosaccus occurs in each interradial region. Folds on pseudosacchi generally occur along the radial length of the pseudosacchi, both where they overlie the
body and where they project from the equator. Laesurae reach to or nearly to the equator, and may be open. Body ornamented with fine verrucae and rugulae, which may coalesce to form an almost reticulate pattern. Pseudosacci are granulate.

*Dimensions:* Body 37 (39) 53, total 58 (68) 82 (5 specimen; HF).

*Comparison:* *A. hoffmeisterii* has a verrucate body which never appears rugulate or microreticulate, is generally larger and has more than three pseudosacci.

*Occurrence:* Harry Stoke B borehole to Dingle leaf bed (Winterbourne Formation to Mangotsfield Member).

*Known range:* Upper Langsettian to mid-Bolsovian.

**Alatisporites trialatus** Kosanke 1950

Plate 14, Figure 2

*Holotype:* Kosanke (1950), pl. 23, fig. 13-15.

*Type locality:* No. 5 Coal, Carbondale Group, Illinois, U.S.A.; Asturian.

*Description:* Trilete miospores with a rounded-triangular to concave-triangular equatorial outline, modified by three pseudosacci. Most of the distal and proximal surface is free of pseudosacci. One phaseolatoveal pseudosaccus occurs in each interradial region. Folds on pseudosacci generally occur along the radial length of the pseudosacci, both where they overlie the body and where they project from the equator. Laesurae reach to or nearly to the equator, and may be open. Body laevigate. Pseudosacci are granulate.

*Dimensions:* Body 50-54, total 61-88 (2 specimens; HF). Body 45 (53) 60, total 63 (79) 98 (6 specimens; Schulze and 2% KOH).
Comparison: The laevigate body and limited extent of the pseudosacci on the proximal surface of this miospore makes it distinct from *A. pustulatus*.

Occurrence: Frome Bank Gardens to Shortwood Hard Coal (Mangotsfield Member to Farrington Member).

Known range: Upper Bolsovian to Asturian.

**Alatisporites sp.1**  
Plate 14, Figures 3-4

Description: Trilete miospores with a rounded-triangular to concave-triangular equatorial outline, modified by three pseudosacci. Most of the distal and proximal surface is free of pseudosacci. One phaseolate pseudosaccus occurs in each radial region. Laesurae reach to or nearly to the equator, and may be open. Body laevigate. Pseudosacci are granulate.

Dimensions: Body 60, total 65 (1 specimen; Schulze and 2% KOH).

Discussion: Conforms to the genus *Alatisporites*, apart from that the pseudosacci are attached at the radial and not interradial regions.

Occurrence: Harry Stoke B borehole to 65 The Dingle (Winterbourne Formation to Mangotsfield Member).
*Turma MONOLETES Ibrahim 1933*

*Suprasubturma ACAVATOMONOLETESES Dettmann 1963*

*Subturma AZONOMONOLETESES Luber 1935*

*Infraturma LAEVIGATOMONOLETESES Dybová and Jachowicz 1957*

*Genus LAEVIGATOSPORITES Ibrahim 1933*

Type species: *L. vulgaris* Ibrahim 1933

*Description:* Monolette miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae half to four fifths of miospore long axis. Exine laevigate.

*Discussion:* There appears to be two size-delimited speciation schemes for *Laevigatosporites*. Smith and Butterworth (1967) favoured; *L. minimus* (<35 µm), *L. minor* (45-64 µm) and *L. vulgaris* (>64 µm). Alpern and Doubinger (1973) use a slightly alternate system; *L. perminutus* (<25 µm), *L. vulgaris* (30-90 µm) and *L. maximus* (>100 µm). Smith and Butterworth (1967) speciation limits were retained for the purposes of this study, as this makes palaeoecological interpretations easier (see below)

*Affinity:* Smaller forms (less than 35 µm) more typical of marattialean tree ferns (*Scolecopteris, Pecopteris, Zeilleria*) while larger forms are only found in the cones of sphenophylls (*Bowmanites*). (summary in Traverse, 2008; Balme, 1995).
**Laevigatosporites minor** Loose 1934

Plate 14, Figure 5

1932  *Sporonites vulgaris* Ibrahim in Potonié *et al.* Loose in part.
1933  *Laevigato-sporites vulgaris* Ibrahim in part.
1934  *Laevigatosporites vulgaris minor* Loose, p. 158.
1957a  *Laevigatosporites minor* (Loose) Potonié and Kremp; Bharadwaj, p. 109.

**Holotype:** Loose (1934), pl. 7, fig. 12.
**Type locality:** Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

**Description:** Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Long axis 35-64 µm. Laesurae half to three quarters of miospore long axis. Exine laevigate.

**Dimensions:** Total 43 (52) 64 (10 specimens; HF). Total 47-49 (2 specimens; Schulze and 2% KOH).

**Comparison:** Laevigate monolete specimens ranging between 35-64 µm will be assigned to *L. minor*, smaller specimens will be assigned to *L. minmus* and larger to *L. vulgaris*.

**Occurrence:** Harry Stoke B borehole to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

**Known range:** Namurian to Asturian.
Laevigatosporites minimus (Wilson and Coe) Schopf et al., 1944

Plate 14, Figure 6

1940    Phaseolites minimus Wilson and Coe, p. 183.
1944    Laevigatosporites minimus (Wilson and Coe); Schopf et al., p. 37.

Holotype: Wilson (1958), after Wilson and Coe (1940), pl. 1, fig. 5

Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Long axis <35 µm. Laesurae half to two fifths of miospore long axis. Exine laevigate.

Dimensions: Total 23 (31) 34 (4 specimens; HF). Total 26 (1 specimen; Schulze and 2% KOH).

Comparison: Distinguished from other Laevigatosporites by its smaller size (<35 µm).

Occurrence: Harry Stoke B borehole to Shortwood Hard Coal and roof of Parkfield Hard Coal, Bickley Wood to Hursley Hill borehole (Winterbourne Formation to Radstock Member).

Known range: Bolsovian to Asturian.
Laevigatosporites vulgaris Ibrahim 1933

Plate 14, Figure 7

Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Long axis >64 µm. Laesurae half to two fifths of miospore long axis. Exine laevigate.

Dimensions: Total 66 (76) 117 (8 specimens; HF). Total 71 (84) 115 (5 specimens; Schulze and 2% KOH).

Comparison: L. desmoinesensis was given a size range of 60-75 µm by Wilson and Coe (1940); this species being favoured in studies of the North American coalfields and is listed as a synonym in Alpern and Doubinger (1973).

Occurrence: Harry Stoke B borehole to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Duckmantian to Asturian.

Holotype: Potonié and Kremp (1956), pl. 19, fig. 429
Type locality: Ágir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian
**Infraturma SCULPTATOMONOLETES** Dybová and Jachowicz 1957

**Genus PUNCTATOSPORITES** (Ibrahim) Alpern and Doubinger 1973

Type species: *P. minutus* Ibrahim 1933.

*Description:* Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae three to four fifths of miospore long axis. Exine granulate.

*Comparison:* *Laevigatosporites* does not feature ornament, and *Speciososporites* is cingulate.


**Punctatosporites granifer** (Potonié and Kremp) Alpern and Doubinger 1973

Plate 14, Figure 8

*Holotype:* Potonié and Kremp (1956), pl. 19, fig. 442.

*Type locality:* Gliicksburg Seam, Ibbenburen, Germany; Bolsovian.

*Description:* Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae three to four fifths of miospore long axis. Exine ornamented by 0.5 µm grana, which may appear to have pointed apices.

*Dimensions:* Total 35-41 (2 specimens; HF). Total 33 (37) 51 (4 specimens; Schulze and 2% KOH).

*Comparison:* *P. minutus* has smaller grana.
Occurrence: Harry Stoke B borehole to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Bickley Wood to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Bolsovian to Asturian.

Punctatosporites minutus (Ibrahim) Alpern and Doubinger 1973

Plate 14, Figure 9

1933 Punctato-sporites minutus Ibrahim, p. 40.
1938 Azononoletes minutus (Loose); Luber in Luber and Waltz.
1957 Granulatosporites minutus (Ibrahim); Dybova and Jachowicz, p. 191.

Holotype: Ibrahim (1933), pl. 19, fig. 33.
Type locality: Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae three to four fifths of miospore long axis. Exine ornamented scabrate, barely discernible except under oil immersion.

Dimensions: Total 22 (24) 26 (4 specimens; HF). Total 19 (26) 34 (9 specimens; Schulze and 2% KOH).

Comparison: P. granifer has larger grana.

Occurrence: Harry Stoke B borehole to Westerleigh/Shortwood Hard Coal, Bickley Wood to Hursley Hill borehole (Winterbourne Formation to Radstock Member).

Known range: Langsettian to Asturian.
**Punctatosporites punctatus** (Kosanke) Alpern and Doubinger 1973

Plate 14, Figure 10

1958 *Speciosporites laevigatus* Alpern, p. 81.
1973 *Punctatosporites punctatus* (Kosanke); Alpern and Doubinger, p. 40.

**Holotype:** Kosanke (1950), pl. 5, fig. 3.
**Type locality:** Willis coal, Tradewater Group, Illinois, U.S.A; Asturian.

*Description:* Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae three fifths of miospore long axis; may show incipient trilete condition. Exine granulate. 3-4 µm wide pseudocingulum.

*Dimensions:* Total 40-44 (2 specimens; Schulze and 2% KOH).

*Discussion:* Includes forms indistinguishable from *Punctatosporites oculus* Smith and Butterworth 1967.

*Occurrence:* From Bank Gardens to below Westerleigh Hard Coal (Mangotsfield Member to Farrington Member).

*Known range:* Bolsovian to Asturian.

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**Genus THYMOSPORA** Wilson and Venkatachala 1963a

1950 *Verrucososporites* Knox
1963a *Thymospora* Wilson and Venkatachala

Type species: *T. thiessenii* (Kosanke) Wilson and Venkatachala 1963a
Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae half to three quarters of miospore long axis; may be obscured by ornament. Exine heavily ornamented with verrucae with coalescing bases which may form rugulae. Isolated coni may be present on the verrucae/rugulae.

Discussion: Verrucate/ruglate ornament differentiates this genus from other ornamented monolete genera.

Affinity: Marattialean tree ferns (Alpern and Doubinger, 1973).

Thymospora obscura (Kosanke) Alpern and Doubinger 1967

Plate 15, Figure 1

1950 Laevigatosporites obscurus Kosanke, p. 29.
1954 Verrucososporites obscurus (Kosanke); Potonié and Kremp, p. 166.
1963a Thymospora obscura (Kosanke); Wilson and Venkatachala, p. 76.

Holotype: Kosanke (1950), pl. 15, fig. 6.
Type locality: New Haven Coal, McLeansboro Group, Illinois, U.S.A.; Asturian-Cantabrian.

Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae half to three quarters of miospore long axis; may be obscured by ornament. Exine ornamented with 2–4 μm wide verrucae with coalescing bases which may form irregular and poorly developed rugulae with rounded apices. Ornament <2 μm tall when measured at the equator. Isolated coni may be present on the verrucae/rugulae.

Dimensions: Total 26 (38) 42 (8 specimens; Schulze and 2% KOH).
Comparison: Overlaps with *T. thiessenii*, but *T. thiessenii* is dominantly rugulate and *T. obscura* has confluent verrucae but not elongated rugulate sculpture. *T. pseudothiessenii* has coarse and more confluent ornament (generally $>5 \, \mu m$ wide).

Occurrence: Grove Cottage to Shortwood Hard Coal, Bickley Wood to Salridge Coal (Downend Member to Farrington Member).

Known range: Asturian.

*Thymospora pseudothiessenii* (Kosanke) Alpern and Doubinger 1967
Plate 15, Figure 2-3

1950  *Laevigato-sporites pseudothiessenii* Kosanke, p. 3.
1956  *Verrucososporites pseudothiessenii* (Kosanke); Potonié and Kremp, p. 144.
1963a  *Thymospora pseudothiessenii* (Kosanke); Wilson and Venkatachala, p. 78.

Holotype: Kosanke (1950), pl. 5, fig. 10.
Type locality: No. 5 Coal, Carbondale Group, Illinois, U.S.A.; Asturian.

Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseololate outline in equatorial view. Laesurae half to three quarters of miospore long axis; may be obscured by ornament. Exine ornamented with 2-7 $\mu m$ wide verrucae with coalescing bases which form irregular rugulae with rounded to pointed apices. Ornament $<5 \, \mu m$ tall when measured at the equator.

Dimensions: Total 38 (42) 45 (4 specimens; HF). Total 26 (34) 40 (11 specimens; Schulze and 2% KOH).

Comparison: Generally larger and with coarser ornament than *T. obscura*, where verrucae rarely exceed 2.5 $\mu m$ basal diameter and do not form elongate rugulae. *T. theiessenii* is smaller ($<25 \, \mu m$) and has a finer verrucate/rugulate ornament (typically not greater than 2 $\mu m$ in basal diameter).
Occurrence: Harry Stoke B to Shortwood Hard Coal, Bickley Wood (Winterbourne Formation to Farrington Member).

Known range: Asturian.

Thymospora thiessenii (Kosanke) Wilson and Venkatachala 1963

Plate 15, Figures 4

1958 Thymospora verrucosa Alpern, p. 80.
1958 Thymospora reticulata Alpern, p. 80.

Holotype: Kosanke (1943), pl. 125, fig. 1a–b.
Type locality: Pittsburg (No. 8) Coal, Hanna Strip Mine, Ohio, U.S.A. Asturian.

Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae half to three quarters of miospore long axis; may be obscured by ornament. Exine ornamented with 2 µm wide verrucae with coalescing bases which may form rugulae with rounded apices. Ornament <2 µm tall when measured at the equator.

Dimensions: Total 24 (1 specimen; HF).

Discussion: This species will be used for distinctly rugulate monolete miospores which are <25 µm. These size limit appears to effectively differentiate these small miospores with relatively smaller verrucae/rugulae, from large forms with coarser ornament (i.e T.pseudothiessenii). Due to sieving at 20 µm it is likely that these miospores will almost always be lost.

Occurrence: Harry Stoke B to shales associated with Shortwood Top Coal (Winterbourne Formation to Farrington Member).
Known range: Asturian-Stephanian B.

**Genus TORISPORA (Balme) Doubinger and Horst 1961**

Type species: *T. securis* Balme 1952.

*Description:* Monolete miospores with an oval equatorial outline in polar view, and an oval to slightly phaseolate outline in equatorial view. Laesurae half to three quarters of miospore long axis, typically around three quarters. Exine thickened on one side of the miospore, to form a sub-rectangular to crescentic crassitude. Exine laevigate, granulate or verrucate/rugulate.

*Comparison:* Would be attributed to *Laevigatosporites minutus/Punctatosporites spp. /Thymospora* in specimens where the crassitude has been lost.

*Discussion:* Position, shape and size of crassitude is highly variable.

*Affinity:* Marattialean tree ferns (Alpern and Doubinger, 1973).

**Torispora laevigata** Bharadwaj 1957

Plate 15, Figure 5

*Holotype:* Bharadwaj (1957a), pl. 30, fig. 5.

*Type locality:* Kohlback Seam, Göttelborn Mine, Saarland, Germany; Stephanian B.

*Description:* Monolete miospores with an oval equatorial outline in polar view, and an oval to slightly phaseolate outline in equatorial view. Laesurae half to three quarters of miospore long axis, typically around three quarters. Sub-rectangular to crescentic crassitude at one extremity of the miospore. Exine laevigate.
**Dimensions:** Body 26 (28) 30 (4 specimens; HF). Body 24 (28) 30 (4 specimens; Schulze and 2% KOH).

**Comparison:** Specimens which have lost the crassitude would be referred to *Laevigosporites minimus*. Differentiated from other species of *Torispora* by having a laevigate exine.

**Occurrence:** Harry Stoke B to siltstones above Shortwood Hard Coal, below Trench Coal (Winterbourne Formation to Farrington Member).

**Known range:** Bolsovian to Asturian.

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**Torispora securis** (Balme) Alpern et al. 1965

Plate 15, Figures 6-7

1957a *Torispora recta* Dybova and Jachowicz, p. 197.
1957a *Torispora speciosa* Dybova and Jachowicz, p. 198.
1957a *Torispora undulata* Dybova and Jachowicz, p. 197.
1958 *Crassosporites punctatus* Alpern, p. 81.
1958 *Crassosporites trileloides* Alpern, p. 81.

**Lectotype:** Balme (1952), fig, 3a.

**Type locality:** Big Vein Seam, Bristol and Somerset Coalfields, England; Asturian.

**Description:** Monolete miospores with an oval equatorial outline in polar view, and an oval to slightly phaseolate outline in equatorial view. Laesurae half to three quarters of miospore long axis, typically around three quarters. Sub-rectangular to crescentic crassitude at one extremity of the miospore. Exine granulate.

**Dimensions:** Body 27 (29) 32 (4 specimens; HF). Body 26 (1 specimen; Schulze and 2% KOH).

**Comparison:** *T. securis* is here used exclusively for specimens with a granulate exine. Smith and Butterworth (1967) used this species to include all monolete miospores with a
Torispora-type crassitude at one extremity; whether they are laevigate, granulate or verrucate.

Occurrence: Harry Stoke B to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Bickley Wood to below Trench Coal (Winterbourne Formation to Farrington Member).

Known range: Bolsovian to Asturian.

Genus SPINOSPORITES Alpern 1958
Type species: S. spinosus Alpern 1958.

Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae three quarters of miospore long axis. Exine spinose.

Comparison: Similar ornament to Acanthotriletes (trilete, triangular equatorial outline)

Affinity: Marattialean tree ferns (Alpern and Doubinger, 1973).

Spinosporites exigus Upshaw and Hedlund 1967
Plate 15, Figure 8

Holotype: Upshaw and Hedlund (1967), pl. 4, fig. 17-19.
Type locality: Coffeyville Coal Clay, Oklahoma, U.S.A.; Stephanian.

Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae three quarters of miospore long axis; typically faint. Exine ornamented with minute <1 μm tall spinae.
**Dimensions:** Total 16-17 (2 specimens; Schulze and 2% KOH).

**Discussion:** Noted as having a first occurrence in lowermost Bolsovian in Illinois, eastern Kentucky and eastern Tennessee (Peppers, 1996)

**Comparison:** This species is smaller (<20 µm) than *S. spinosus* (typically over 30 µm), and has shorter spinae. However, due to sieving at 20 µm it is likely that these miospores will almost always be lost.

**Occurrence:** Harry Stoke B (Winterbourne Formation).

**Known range:** Bolsovian (Peppers, 1996) to Stephanian.

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**Spinosporites spinosus** Alpern 1958

Plate 15, Figure 9

**Holotype:** Alpern (1958), pl. 2, fig. 41.

**Type locality:** Sondage Saint-Aubin II, Auvergne, France.; Autunian.

**Description:** Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae half to three fifths of miospore long axis. Exine ornamented with closely spaced spineae, up to 2 mm long and <1 µm wide at the base.

**Dimensions:** Total 34 (1 specimen; HF). Total 30 (34) 37 (3 specimens; Schulze and 2% KOH).

**Comparison:** This species is larger than *S. exiguus*, and features longer and more closely spaced spinae.

**Occurrence:** Harry Stoke B to 65 The Dingle (Winterbourne Formation to Mangotsfield Member).
Known range: Asturian to Stephanian (Clayton et al., 1977).

**Genus COLUMINISPORITES Peppers 1964**

Type species: *C. ovalis* Peppers 1964

Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae difficult to distinguish against ornament. Several prominent ridges encircle the miospore, parallel to the long axes, which may branch. Finer parallel ridges and grooves ornament the spore body between the ridges; running more or less perpendicular to the coarser, branching ridges.

Discussion: Will become *Laevigatosporites minor* if outer perine layer is detached.

Affinity: Sphenophylls (Riggs and Rothwell, 1985).

**Columinisporites ovalis** Peppers 1964

Plate 15, Figure 10

*Holotype:* Peppers (1964), pl.1, fig. 11.

*Type locality:* Fithian cyclothem, McLeansboro Group, Illinois, U.S.A.; Asturian-Cantabrian

Description: Monolete miospores with an oval equatorial outline in polar view, and an oval to phaseolate outline in equatorial view. Laesurae difficult to distinguish against ornament. 3-4 prominent ridges, 2-3 µm wide, encircle the miospore parallel to the long axes, which may branch. Finer parallel ridges and grooves ornament the spore body between the ridges; running more or less perpendicular to the coarser, branching ridges.

*Dimensions:* Total 43 (50) 66 (15 specimens; HF).
Occurrence: Harry Stoke B to shales below Westerleigh Hard Coal, Bickley Wood to Hursley Hill (Winterbourne Formation to Radstock Member).


Suprasubtura CAVATOMONOLETES Oshurkova and Pashkevich 1990
Subtura ZONOCAVATOMONOLETES Oshurkova and Pashkevich 1990
InfraTurma ARCHAEOSACCITI Oshurkova and Pashkevich 1999
Genus PALEOSPORA Habib 1966
Type species: P. fragila Habib 1966

Description: Monolete monosaccate pollen with a broadly oval to lenticular equatorial outline. Body oval to lenticular; distinct and markedly darker than the saccus. Laesurae usually totally obscured by a longitudinal fold that often extends to the equatorial outline. Long axis of body conformable to that of the long axis of the saccus; occupying half of the total diameter of the long axis. Saccus may be infrareticulate, and is narrow. Around the body and saccus is a flange, slightly wider than the saccus it encircles.

Comparison: Differentiated from Potonieisporites by its flange and long longitudinal furrow.

Discussion: Originally assigned to Turma Saccites (InfraTurma Vesiculomonoraditi) by Habib (1966). This genus is clearly pseudosaccate, and so cannot be assigned to a Turma for monolete saccate pollen. The present author proposed allocation within InfraTurma Archaeosacciti, with the structurally similar Archaeoperisaccus (Naumova) Potonié 1958, which is monolete and pseudosaccate.
**Affinity:** Sub-arborescent lycopsid. Recovered from Asturian *Spencerites*, along with *Spencersporites* (Leisman and Stidd, 1967). *Spencerites leismanii* described as a sub-arborescent lycopsid (Bek et al., 2009a).

**Paleospora fragila** Habib 1966

Plate 15, Figure 11

*Holotype:* Habib (1966), pl. 103, figs. 1-2.

*Type locality:* Lower Kittanning Coal, Allegheny Series, western Pennsylvania, U.S.A.; Asturian.

*Description:* Monolete monosaccate pollen with a broadly oval to lenticular equatorial outline. Body oval to lenticular; distinct and markedly darker than the saccus. Laesurae usually totally obscured by a longitudinal fold that often extends to the equatorial outline. Long axis of body conformable to that of the long axis of the saccus; occupying half of the total diameter of the long axis. Saccus infrareticulate and narrow, around 9-18 µm wide. Around the body and saccus is a flange, 11-22 µm, slightly wider than the saccus it encircles.

*Dimensions:* Total 180 (1 specimen; Schulze and 2% KOH).

*Occurrence:* 65 The Dingle (Mangotsfield Member).

*Known range:* Langsettian to Asturian (Ravn, 1986)
Genus VESTISPORA (Wilson and Hoffmeister) Wilson and Venkatachala 1963

Type species: V. profunda Wilson and Hoffmeister 1956

Description: Trilete miospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body is attached only near the edge of operculum. Inner body laevigate. Outer body may be laevigate, foveolate, costate or reticulate.

Comparison: The only other operculate genus, Pteroretis, features prominent wing-like structures.

Affinity: Sphenophylls (Bowmanites).

Vestispora costata (Balme) Spode in Smith and Butterworth 1967

Plate 16, Figures 1-2

1952 Endosporites costatus Balme, p. 178.
1957b Vestispora costata (Balme); Bharadwaj, p. 118.
1958 Glomospora costata (Balme); Butterworth and Williams, p. 385.

Lectotype: Smith and Butterworth (1967), pl.25, fig.1.
Type locality: Seam at 719 ft. 3 in., Manton Colliery, Yorkshire Coalfield, England; Bolsovian.

Description: Trilete miospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body
is attached only near the edge of operculum. Inner body laevigate. Outer body encircled by 2-3 µm wide costae, which seem to radiate from a point near the distal pole. Costae rounded to slightly pointed in profile and are spaced 9-18 µm and rarely branch.

Dimensions: Total 59 (71) 88 (5 specimens; HF). Total 65-78 (2 specimens; Schulze and 2% KOH).

Discussion: According to Smith and Butterworth (1967), the operculum of Vestispora costata are represented by the “less elaborately costate form” of Reticulatasporites facetus (Ibrahim) Potonié and Kremp 1955 and R. taciturnus (Ibrahim) Potonié and Kremp 1955.

Comparison: The costate ornament of V. tortuosa branches more frequently than the typically spiral costata of V. costata. V. pseudoreticulata has a secondary reticulum between its primary costae.

Occurrence: Harry Stoke B to Huckford Quarry, Golden Valley to Bickley Wood (Winterbourne Formation to Mangotsfield Member).

Known range: Duckmantian to Bolsovian.

Vestispora fenestrata (Kosanke and Brokaw) Spode in Smith and Butterworth 1967

Plate 16, Figure 3

1954  Microreticulitasporites fenestrateus (Kosanke and Brokaw); Butterworth and Williams, p. 755.
1955  Foveolaiispories fenestrateus (Kosanke and Brokaw); Bharadwaj, p. 126.
1963b  Vestispora fenestratea (Kosanke and Brokaw); Wilson and Venkatachala, p. 99.

Holotype: Kosanke (1950), pl. 1, fig. 6.

Type locality: No. 6 Coal, Carbondale Group, Illinois, U.S.A.; Asturian.
Description: Trilete miospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body is attached only near the edge of operculum. Inner body laevigate. Outer body foveolate; diameters of fovea 1-2 µm and oval to circular in shape. Fovea are spaced around 2 µm apart.

Dimensions: Total 34 (58) 88 (10 specimens; HF). Total 56 (68) 88 (8 specimens; Schulze and 2% KOH).

Discussion: Fits the description in Smith and Butterworth (1967); "Miospores having a thick exoexine which is perforated by numerous foveolae less than 3 microns in diameter and less than 3 microns apart”

Comparison: V. fenestrata has smaller foveae and muri than V. luminata.

Occurrence: Harry Stoke B to Shortwood Hard Coal and roof of Parkfield Hard Coal, Bickley Wood to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Bolsovian to Asturian.

Vestispora laevigata Wilson and Venkatachala 1963b

Plate 16, Figures 4-5


Holotype: Wilson and Venkatachala (1963b), pl.1, fig. 8.

Type locality: Croweburg Coal, Des Moines Series, Oklahoma, U.S.A.; Asturian.

Description: Trilete miospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body is attached only near the edge of operculum. Inner body laevigate. Outer body laevigate.

Dimensions: Total 56 (64) 74 (6 specimens; HF). Total 69 (70) 87 (6 specimens; Schulze and 2% KOH).
**Comparison:** Exine is unornamented (or very faintly ornamented) and is much thicker than other species.

**Occurrence:** Harry Stoke B to Shortwood Hard Coal, below Salridge Coal (Winterbourne Formation to Farrington Member).

**Known range:** Bolsovian to Asturian.

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**Vestispora luminata** Ravn 1979

Plate 16, Figure 6

*Holotype:* Ravn (1979), pl. 17, figs. 4.

*Type locality:* Unnamed seam, CP-19-4 borehole, lower Cherokee Gourp, Iowa, U.S.A.; Asturian (late Atokan/early Desmoinesian).

**Description:** Trilete miospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body is attached only near the edge of operculum. Inner body laevigate. Outer body foveolate; diameters of fovea 2-4 µm and oval to circular in shape. Foveolae are spaced around 2-3 µm apart.

**Dimensions:** Total 57 (67) 101 (5 specimens; Schulze and 2% KOH).

**Comparison:** Fovea and muri are consistently larger than *V. fenestrata*.

**Occurrence:** Harry Stoke B to 65 The Dingle, below Salridge Coal (Winterbourne Formation to Mangotsfield Member).

**Known range:** Langsettian to Asturian.
**Vestispora pseudoreticulata** Spode in Smith and Butterworth 1967

Plate 17, Figures 1-2

1952 *Reticulatisporites tortuosus* Balme (in part), p. 179
1964 *Vestispora pseudoreticulata* (Spode) Neves, p. 1233.
1965 *Vestispora pseudoreticulatus* (Spode) Laveine, p. 2556.

**Holotype:** No holotype has been given

**Type locality:** Barnsley Seam, Yorkshire Coalfield, England; Duckmantian.

**Description:** Trilete miospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body is attached only near the edge of operculum. Inner body laevigate. Outer body with coarse 2-3 µm muri with a pointed to occasionally rounded profile, which range from branching costae to frequently branching forming a pseudoreticulum with elongate polygonal lumina. This coarser primary reticulum encloses a finer secondary reticulum; with 2 µm wide muri enclosing 2-6 µm diameter polygonal lumina.

**Dimensions** Total 54-59 (2 specimens; HF). Total 48 (68) 86 (7 specimens; Schulze and 2% KOH).

**Discussion:** According to Smith and Butterworth (1967), the operculum of *Vestispora costata* are represented by the “less elaborately costate form” *Reticulatasporites facetus* (Ibrahim) Potonié and Kremp 1955 (pl. 11, fig. 104) and *R. taciturnus* (Ibrahim) Potonié and Kremp 1955 (pi. 11, figs. 105a, b. The costate nature or ornament was not specifically noted by Smith and Butterworth (1967), but the coarse primary muri in the Bristol specimens ranged from costate (like *V.tortuosa*, more branching than in *V. costata*) to form with pseudoreticulum (as in *V. tortuosa*).

**Comparison:** *V. costata and V. tortuosa* have no secondary reticulum between the primary muri, which are of a costate form. In *V. magna* the primary muri are much coarser and the areas between are more irregularly reticulate. Forms approaching the coarse reticulum of *V. magna* were encountered but were not deemed to be sufficiently different, in this case, to be separated out of *V. pseudoreticulata*. The reticulum of *V.*
*Vestispora reticulata* is similar to the secondary reticulum of *V. pseudoreticulata*, but lacks the coarser primary reticulum.

**Occurrence:** Harry Stoke B to siltstones above with Shortwood Hard Coal, Bickley Wood (Winterbourne Formation to Farrington Member).

**Known range:** Langsettian to lower Asturian.

**Vestispora reticulata** (Laveine) Loboziak 1971
Plate 17, Figure 3

1971 *Vestispora reticulata* (Laveine) Loboziak, p. 81.

*Holotype:* Laveine (1965), pl.1, fig. 21.
*Type locality:* No 12 Seam, Faiseau d’Ernestine, Auchel-Bruay, France; lower Bolsovian.

**Description:** Trilete miospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body is attached only near the edge of operculum. Inner body laevigate. Outer body with closely spaced 1-2 µm muri which define a regular reticulum of lumina 1-7 µm wide, which are elongated roughly parallel to the equator.

**Dimensions:** Total 62-110 (2 specimens; HF).

**Comparison:** Lacks the coarse primary reticulum of *Vestispora pseudoreticulata*, but ornamentation is similar to the secondary reticulum of that species. V. sp.1 features closely spaced costae that seldom branch and therefore do not define rugulae polygonal lumina.

**Occurrence:** Harry Stoke B to Shortwood Top Coal (Winterbourne Formation to Farrington Member).
Known range: Duckmantian to Asturian.

**Vestispora tortuosa** (Balme) Spode in Smith and Butterworth 1967

Plate 17, Figure 4

1952  *Reticulatisporites tortuosus* Balme (in part)
1957b *Vestispora tortuosa* (Balme); Bharadwaj, p. 119.
1957a *Cancelatisporites cancellatus* Dybova and Jachowicz, p. 111.

**Lectotype:** Chosen by Balme, at Sheffield Coal Survey Lab (T 72/1).
**Type locality:** Wheatworth Seam, Yorkshire Coalfield, England; Upper Duckmantian

*Description:* Trilete miospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body is attached only near the edge of operculum. Inner body laevigate. Outer body with coarse 2-3 µm wide muri with a generally pointed profile. Muri appear to have a faintly costate habit, but branch frequently to produce a reticulum of slightly elongate polygonal lumina.

*Dimensions:* Total 62-77 (2 specimens; Schulze and 2% KOH).

*Comparison:* Muri branch more regularly and have more well developed carination than *V. costata*. Absence of a weak secondary reticulum differentiates this species from *V. pseudoreticulata*.

*Occurrence:* Harry Stoke B to Grove Cottage, Golden Valley (Winterbourne Formation to Downend Member).

*Known range:* Upper Langsettian to mid-Bolsovian.
**Vestispora sp. 1**
Plate 17, Figures 5-6

*Description:* Trilete miospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body is attached only near the edge of operculum. Inner body laevigate. Outer body with closely spaced 2-3 µm wide costae which encircle the miospore almost parallel to the equator (when viewed in equatorial compression). At the distal pole costae branch more frequently and some specimens show a poorly defined reticulum may form in this localised region. Costae seldom branch, and are spaced 1-2 µm apart.

*Dimensions:* Total 52-64 (2 specimens; HF). Total 46 (55) 62 (4 specimens; Schulze and 2% KOH).

*Discussion:* *V. colchesterensis* Peppers is broadly similar, but has muri which have very low relief and are barely discernible at the spore outline, where they appear to merge into the exine. *V. profunda* Wilson and Hoffmeister has a more distinct distal reticulum, but it is not clear from the description if the ornament features comparable costae as they are described as “reticulations by Wilson and Hoffmeister (1956)

*Comparison:* *V. reticulata* features a distinctly reticulate ornament, with elongate polygonal lumina.

*Occurrence:* Shortwood Great Coal and roof of Parkfield Great Coal to Shortwood Top Coal/roof of Coalpit Heath Hollybush Coal (Farrington Member).

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**Genus PTERORETIS (Felix and Burbridge) McLean et al. 2006**

Type species: *P. primum* (Felix and Burbridge) McLean et al. 2006

*Description:* Trilete miospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body...
laevigate. Equatorial and distal surfaces of mioospores ornamented by two fold muri. Coarse primary muri encircle the distal hemisphere of the mioospore, and are crossed almost perpendicularly by the finer secondary muri. Round the equator the encircling ridge is expanded into a dramatic, fragile wing-like structure supported by ribs. There may be a second, smaller wing-like equatorial extension on the distal side of the main equatorial wing (a “cuppa” sensu McLean et al. (2006)). Proximal surface is laevigate, with a prominent ridge encircling the operculum.

Discussion: A structural re-interpretation of the genus is illustrated in McLean et al. (2006). As the equatorial wing(s) are almost always found irregularly torn and laying over the spore body; it is often very difficult to discern this structure from the limited number of Bristol specimens, but it still fits the specimens well.

Affinity: Sphenophylls (Bowmanites) (Bek et al., 2009c)

**Pteroretis primum** (Felix and Burbridge) McLean et al. 2006
Plate 18, Figure 1

*Lectotype:* Felix and Burbridge (1961), pl.1, fig.2.

*Type locality:* Sun Oil Company Theresa Wright #1 Well, Texas, U.S.A.; Namurian.

Description: Trilete mioospores with a circular to oval equatorial outline. Trilete-bearing inner body encased in a thick outer body with proximal operculate opening. Inner body laevigate. Equatorial and distal surfaces of mioospores ornamented by two fold muri. Coarse 3-5 µm wide primary muri encircle the distal hemisphere of the mioospore; spaced 13-16 µm apart. These are crossed almost perpendicularly by the finer secondary muri; around 2 µm wide and 3-6 µm spaced. Round the equator the encircling ridge is expanded into a dramatic, fragile wing-like structure which is supported by ribs. In between ribs the wing is typically narrower which may be a product of damage.
Measured at the strengthening ribs the wing reaches a maximum width of 25 µm. Proximal surface is laevigate, with a prominent ridge encircling the operculum.

*Dimensions:* Total 108-128 (specimens; HF).

*Discussion:* It is not usually possible to determine the smaller wing-like equatorial extension on the distal side of the main equatorial wing ("cuppa" *sensu* McLean *et al.* (2006)) due to the wings being often torn and irregularly folded.

*Occurrence:* Harry Stoke B (Winterbourne Formation). Possibly in Hursley Hill borehole (Publow Member).

*Known range:* Typically Viséan (Sabry and Neves, 1971) to Langsettian (McLean, 1991). However, *Pteroretis primum* is present just above the Bolsovian Bay Marine Band (=Cambriense Marine Band) in North Staffordshire (McLean *et al.*, 2006)

**Anteturma POLLENITES Potonié 1931**

**Turma SACCITES Erdtman 1947**

**Subturma MONOSACCITES (Chitaley) Potonié and Kremp 1954**

**Infraturma ALETESACCITI Leschik 1955**

**Genus FLORINITES Schopf et al. 1944**

Type species: *F. pellucidius* (Wilson and Coe 1940) Wilson 1958 [?synonym of *F. mediapudens* (Loose) Potonié and Kremp].

*Description:* Alete monosaccate pollen with a broadly oval equatorial outline. Body oval to circular, and may be indistinct from the saccus in its colour or dark and distinct. Long axis of body conformable to that of the long axis of the saccus. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at distal pole, with proximal surface of the body being free of saccus. Folding typical around the margins of the body.
Comparison: *Wilsonites* is typically circular, with a faint but consistent trilete mark. *Cordaitina* does have a similar oval equatorial outline but the body has a very indistinct outline, due to the saccus encompassing the entire body, and is often paler than the saccus. The body of *Cordaitina* also typically occupies a much large proportion of the total diameter than in *Florinites*, and may bear a faint trilete mark. *Potoniesporites* is clearly monolette, and the saccus is proximally attached with the distal side of the body being free. The saccus of *Guthrlisporites* differs in its reverse attachment of the saccus (saccus covers entire distal pole but not the proximal face, where it attached to the body). *Guthrlisporites* is also distinctly trilete. As this structural distinction is difficult, it is deemed not meaningful to make a distinction between the genera for the purposes of this study.

Discussion: This study uses a similar species division as Smith and Butterworth (1967); based on total diameter of long axis, whether the body is distinct or indistinct and the size of the body in relation to the total diameter of the long axis. For pollen with an indistinct body; <51 µm *F. millotti*, 51-75 µm *F. florini*, 76-100 µm *F. pumicosus*, >100 µm *F. visendus*. Where the body is dark and distinct, and occupies >50% on the total diameter of the long axis; <70 µm *F. mediapudens*, >70 µm *F. similis*. Where the body is dark and distinct, and occupies <50% on the total diameter of the long axis; *F. junior* (50-90 µm).

Affinity: Cordaitales.

*Florinites florini* Imgrund 1960

Plate 18, Figure 2

*Holotype:* Imgrund (1960), pl. 16, fig. 94.

*Type locality:* Seam 4, Kaiping Basin, China; Lower Permian.
**Description:** Alete monosaccate pollen with a broadly oval equatorial outline. Body oval to circular; pale and indistinct from the saccus. Long axis of body conformable to that of the long axis of the saccus. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at distal pole, with proximal surface of the body being free of saccus. Folding typical around the margins of the body.

**Dimensions:** Total 52 (59) 70 (5 specimens; HF), Total 53 (1 specimen; Schulze and 2% KOH).

**Discussion:** These are possibly the saccus of *F. mediapudens*.

**Occurrence:** Harry Stoke B to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

**Known range:** Langsettian to Asturian.

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**Florinites junior** Potonié and Kremp 1956

Plate 18, Figure 3

*Holotype:* Potonié and Kremp (1956), pl. 21, fig. 94.

*Type locality:* Baldur Seam, Ruhr Coalfield, Germany; Lower Bolsovian.

**Description:** Alete monosaccate pollen with a broadly oval equatorial outline. Body oval to circular; dark and distinct from saccus and occupying less than half of the total diameter of the pollen long axis. Long axis of body conformable to that of the long axis of the saccus. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at distal pole, with proximal surface of the body being free of saccus. Folding typical around the margins of the body.

**Dimensions:** Total 52 (62) 80 (13 specimens; HF).
Discussion: *F. mediapudens* and *F. similis* overlap these size ranges, but have a body that is half or greater than half of the diameter of the total long axis of the pollen grain.

Occurrence: Harry Stoke B to Westerleigh/Shortwood Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Bolsovian to Asturian.

**Florinites mediapudens** (Loose) Potonié and Kremp 1956

Plate 18, Figure 4

1934  *Reticulata-sporites mediapudens* Loose, p. 158.
1956  *Florinites mediapudens* (Loose); Potonié and Kremp, p. 169.
1957a *Endosporites mediapudens* (Loose); Dybova and Jachowicz, p. 207.


Type locality: Bismarck Seam, Ruhr Coalfield, Germany; Upper Duckmantian.

Description: Alete monosaccate pollen with a broadly oval equatorial outline. Body oval to circular; dark and distinct from saccus and occupying half or slightly more of the total diameter of the pollen long axis. Long axis of body conformable to that of the long axis of the saccus. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at distal pole, with proximal surface of the body being free of saccus. Folding typical around the margins of the body.

Dimensions: Total 51 (63) 73 (8 specimens; HF).

Discussion: Smith and Butterworth (1967) noted *F. antiquus* and the synonymous *F. pellucidus* overlap in size with *F. mediapudens*, suggesting there is little justification for treating these three species separately.
Comparison: *F. junior* has a body <50% the width of the saccus along the long axis of the miospore. *F. junior* is also larger (70-90μm). Pollen >70μm will be assigned to *F. similis*.

Occurrence: Harry Stoke B to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Langsettian to Asturian.

**Florinites millotti** Butterworth and Williams 1954

Plate 18, Figure 5

*Holotype:* Butterworth and Williams (1954), pl. 26, fig 9.

*Type locality:* Upton borehole, Oxfordshire, England; Asturian.

Description: Alete monosaccate pollen with a broadly oval equatorial outline. Body oval to circular; pale and indistinct from the saccus. Long axis of body conformable to that of the long axis of the saccus. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at distal pole, with proximal surface of the body being free of saccus. Folding typical around the margins of the body.

*Dimensions:* Total 43 (46) 49 (4 specimens; HF).

Occurrence: Harry Stoke B to Westerleigh/Shortwood Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Duckmantian to Asturian.
**Florinites pumicosus** (Ibrahim) Schopf et al., 1944

Plate 18, Figure 6

1933 *Reliculata-sporites pumicosus* Ibrahim, p. 38.
1938 *Zonaletes pumicosus* (Ibrahim); Luber in Luber and Waltz, pi. 8, fig. 110.
1944 *Florinites? pumicosus* (Ibrahim); Schopf, Wilson, and Bentall, p. 59.

**Holotype:** Potonié and Kremp (1955), pl. 21, fig. 472. After Ibrahim preparation.

**Type locality:** Ägir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

**Description:** Alete monosaccate pollen with a broadly oval equatorial outline. Body oval to circular; pale and indistinct from the saccus. Long axis of body conformable to that of the long axis of the saccus. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at distal pole, with proximal surface of the body being free of saccus. Folding typical around the margins of the body.

**Dimensions:** Total 75 (80) 88 (3 specimens; HF).

**Occurrence:** Harry Stoke B to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

**Known range:** Langsettian to Asturian.

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*Florinites similis* Kosanke 1950

Plate 18, Figure 7

**Holotype:** Kosanke (1950), pl. 12, fig. 2.

**Type locality:** No. 8 Coal, McLeansboro Group, Illinois, U.S.A.; Asturian-Cantabrian.
Description: Alete monosaccate pollen with a broadly oval equatorial outline. Body oval to circular; dark and distinct from saccus and occupying half or slightly more of the total diameter of the pollen long axis. Long axis of body conformable to that of the long axis of the saccus. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at distal pole, with proximal surface of the body being free of saccus. Folding typical around the margins of the body.

Dimensions: Total 77 (98) 115 (6 specimens; HF).

Comparison: Pollen <76µm will be assigned to *F. mediapudens*.

Occurrence: Harry Stoke B to Westerleigh/Shortwood Hard Coal and roof of Parkfield Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Langsettian to Asturian.

*Florinites visendus* (Ibrahim) Schopf *et al.*, 1944

Plate 19, Figure 1

1944 *Florinites visendus* (Ibrahim); Schopf, Wilson, and Bentall, p. 60.

Holotype: Potonié and Kremp (1956), pl.21, fig. 477. After Ibrahim preparation.

Type locality: Ágir Seam, Ruhr Coalfield, Germany; uppermost Duckmantian.

Description: Alete monosaccate pollen with a broadly oval equatorial outline. Body oval to circular; pale and indistinct from the saccus. Long axis of body conformable to that of the long axis of the saccus. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at distal pole, with proximal surface of the body being free of saccus. Folding typical around the margins of the body.
Dimensions: Total 105-135 (2 specimens; HF). Total 100-132 (2 specimens; Schulze and 2% KOH).

Occurrence: Harry Stoke B to Westerleigh/Shortwood Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Publow Member).

Known range: Langsettian to Asturian.

Infraturma VESICULOMONORADITI (Pant) Bharadwaj 1956
Genus VESTIGISPORITES (Balme and Hennelly) Hart 1960
Type species: V. rudis Balme and Hennelly 1955.

Description: Monolete to incipient trilete monosaccate pollen with a generally oval equatorial outline. Laesurae indistinct to distinct, occupying around half of the body diameter. Body circular to slightly oval; occupying two fifths to three fifths of total diameter. Saccus infrareticulate and proximally attached. Saccus features prominent radial folds, which originate where the saccus attaches to the body on the proximal surface. Folds typically reach or nearly reach the equatorial outline of the shorter axis, and terminate around three quarters of the way towards the long axis. Constriction of the saccus occurs along the short axis of the pollen, to produce and almost diploxynoid outline in most specimens.

Comparison: Potonieisporites has a more consistent and distinct monolete mark, and lacks the characteristic radial saccus folds of Vestigesporites.

Affinity: Gymnosperm.
**Vestigisporites sp. 1**
Plate 19, Figure 2

*Description:* Monolette to incipient trilete monosaccate pollen with a generally oval equatorial outline. Laesurae indistinct to distinct, occupying around half of the body diameter. Body circular to slightly oval; occupying two fifths to three fifths of total diameter. Saccus infrareticulate and proximally attached; overlaps body up to 10 µm on proximal face. Saccus features prominent radial folds, which originate where the saccus attaches to the body on the proximal surface. Folds typically reach or nearly reach the equatorial outline of the shorter axis, and terminate around three quarters of the way towards the long axis. Constriction of the saccus occurs along the short axis of the pollen, to produce and almost diploxyloid outline in most specimens.

*Dimensions:* Total 48 (55) 74 (4 specimens; HF). Total 74-83 (2 specimens; Schulze and 2% KOH).

*Discussion:* Similar to *Vestigisporites* sp.1 from the Missourian-aged Henshaw Formation of Illinois (Peppers, 1970).

*Occurrence:* Harry Stoke B, Stonehill unnamed coal to below Salridge Coal (Winterbourne Formation to Grovesend Member). Possibly above Trench Coal (Farrington Member).

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**Genus POTONIEISPORITES (Bharadwaj) Bharadwaj 1964**

Type species: *P. novicus* Bharadwaj 1954.

*Description:* Monolette monosaccate pollen with a broadly oval equatorial outline. Body oval to circular; distinct and markedly darker than the saccus. Laesurae may be monolette, monolette with median inflexion, or monolette with median inflexion showing a faint and very short third arm (incipient trilete). Long axis of body conformable to that of the long axis of the saccus; occupying between half and two thirds of the total
diameter of the long axis. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at proximal pole, with distal surface of the body being free of saccus. Folding typical around the margins of the body.

Comparison: Florinites is alete and may have a very indistinct body, and has a distally fused saccus with the proximal surface of the body being free.

Affinity: Coniferales (Voltzialean/Walachian).

**Potonieisporites novicus** Bharadwaj 1954

Plate 19, Figure 3

*Holotype:* Bharadwaj (1954), fig. 10.
*Type locality:* Grenzkohlen Seam, Breitenbacher Schichten, Saarland, Germany; Stephanian C.

*Description:* Monolete monosaccate pollen with a broadly oval equatorial outline. Body oval to circular; distinct and markedly darker than the saccus. Laesurae usually open and may be monolete, monolete with median inflexion, or monolete with median inflexion showing a faint and very short third arm (incipient trilete). Long axis of body conformable to that of the long axis of the saccus; occupying between half and two thirds of the total diameter of the long axis. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at proximal pole, with distal surface of the body being free of saccus. Saccus onlap onto body may produce an annular to oval thickening around the margins of the body. Folding typical around the margins of the body.

*Dimensions:* Total 73 (89) 128 (16 specimens; HF). Total 83 (85) 88 (3 specimens; Schulze and 2% KOH).

*Occurrence:* Harry Stoke B to Westerleigh Hard Coal and roof of Parkfield Hard Coal, Bickley Wood to Hursley Hill borehole (Winterbourne Formation to Publow Member).
Known range: Asturian to Stephanian.

**Infraturma TRILETISACCITI Leschik 1955**  
Genus **CORDAITINA Samoilovich 1953**

Type species: *Zonaletes (Latensina) uralensis* Luber

**Description:** Trilete monosaccate pollen with a broadly oval equatorial outline. Laesurae typically indistinct. Body oval to circular; outline of body indistinct so that no clear line demarking the transition is seen, but saccus is much more robust and slightly darker than the body. Long axis of body conformable to that of the long axis of the saccus and occupies around three quarters of the long axis. Saccus with robust infrareticulate structure. Saccus encompasses entire inner body.

**Comparison:** Outline of the body is very indistinct compared with *Florinites*. The distinct body outline in *Florinites* is due to the fusing of the saccus to the distal surface of the body, whereas in Cordaitina the saccus encompasses the body. *Florinites* also doesn’t exhibit a trilete mark, and features a comparatively thinner saccus.

**Discussion:** Due to the variable nature of the appearance of the trilete mark, both apparently alete and faintly trilete forms were included in this genus as at least partial trilete marks can always be discerned. This means that *Latensina trileta*, often cited as a stratigraphically useful taxa, would not be specifically recorded but would be included within this genus. Samoilovich (1953) states that the saccus totally encompasses the inner body, which would account for the indistinct body outline (cf. *Florinites*). Samoilovich (1953) states that the body occupies around half of the total spore axis, which is considerably less than the two thirds to three quarters observed in the Bristol specimens.

**Affinity:** Cordaitales (Vojnvkyaceae and Rufloriaceae).
**Cordaitina uralensis** (Luber) Samoilovich 1953

Plate 19, Figures 4-5

1941  *Zonaletes (Latensina) uralensis* Luber in Luber and Waltz, p.62.
1953  *Cordaitina uralensis* Samoilovich, p. 27.
1955  *Cordaitozonaletes uralensis* (Luber) Luber, p. 73.

*Holotype:* Waltz (1941), pl. 13, fig. 214.
*Type locality:* Kungur Deposits, Solikamsk, Russia; Permian.

*Description:* Trilete monosaccate pollen with a broadly oval equatorial outline. Laesurae typically indistinct. Body oval to circular; outline of body indistinct so that no clear line demarking the transition is seen, but saccus is much more robust and slightly darker than the body. Long axis of body conformable to that of the long axis of the saccus and occupies around three quarters of the long axis. Saccus with robust infrareticulate structure. Saccus encompasses entire inner body.

*Dimensions:* Total 55 (61) 72 (3 specimens; HF). Total 50 (61) 75 (4 specimens; Schulze and 2% KOH).

*Discussion:* Grade into forms identical to *Latensina triplicata*.

*Occurrence:* Frome Bank Gardens to Parkfield Great Coal and roof of Coalpit Heath Hollybush Coal, Bickley to above Trench Coal (Downend Member to Farrington Member).

*Known range:* Upper Bolsovian to Triassic.
Genus PLICATIPOLLENTITES (Potonié and Sah) Foster 1975
Type species: P. malabarensis (Potonié and Sah) Foster 1975.

Description: Trilete monosaccate pollen with a circular to slightly oval equatorial outline. Laesurae indistinct to distinct, occupying less than half of the body diameter, and may be open. Body circular to slightly oval and concordant with equatorial outline; occupying three fifths to four fifths of total diameter. Distal annular thickening continuous around the edge of the body, appears to be a product of saccus onlap. Saccus infrareticulate and distally attached.

Comparison: Similar to Wilsonites, but has a clear and continuous fold where the saccus is attached to the sub-equatorial region of the distal surface.

Affinity: Coniferales.

Plicatipollenites cf. malabarensis (Potonié and Sah) Foster 1975
Plate 19, Figure 6

1960 Cannanoropolis malabarensis Potonié and Sah, p. 128.
1964 Plicatipollenites indicus Lele, p. 152.
1964 Plicatipollenites diffusus Lele, p. 156.
1975 Plicatipollenites malabarensis (Potonié and Sah) Foster, p. 142.

Holotype: Potonié and Sah (1960), p. 2. fig. 5.
Type locality: Cannanore Beach, Malabar Coast, Tertiary.

Description: Trilete monosaccate pollen with a circular to slightly oval equatorial outline. Laesurae indistinct to distinct, occupying less than half of the body diameter, and may be open. Body circular to slightly oval and concordant with equatorial outline; occupying three fifths to four fifths of total diameter. 3-7 μm wide distal annular
thickening continuous around the edge of the body, appears to be a product of saccus onlap. Saccus infrareticulate and distally attached.

*Dimensions* Total 55-62 (2 specimens; HF). Total 49 (53) 71 (6 specimens; Schulze and 2% KOH).

*Discussion:* Smaller than the 103-146 µm quoted by Potonié and Sah (1960). This size discrepancy may in part be due to differing maceration techniques.

*Comparison:* *Cordaitina triplicata* Pittau is very similar. Pittau (2008) explains that saccus onlap on the distal surface produces the distal thickening. By definition the body of *Cordaitina* is fully encompassed by the saccus, but this description does match *Plicatipollenites malabarensis*. It is proposed that *Cordaitina triplicata* Pittau is a junior synonym.

*Occurrence:* Harry Stoke B to roof of Parkfield Hard Coal, Bickley Wood to below Salridge Coal (Winterbourne Formation to Farrington Member).

*Known range:* Not found in Euramerica. This is a Gondwanan species which is typical of the Stephanian and Permian, rarely in Bolsovian.

**Genus WILSONITES Kosanke 1950**

Type species: *Wilsonia vesicatus* Kosanke 1950.

*Description:* Trilete monosaccate pollen with a circular equatorial outline. Body circular and concordant with equatorial outline of saccus; may be pale or dark but always has an indistinct outline. Laesurae may be indistinct or distinct; extending for half to two thirds of the radius of the body. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at proximal pole, with proximal surface of the body being free of saccus. Folding of bladder may occur.
Comparison: *Endosporites* has a more distinct body, sub-triangular amb and granulate bladder ornament. Differs from *Florintes* in being always trilete and generally circular.

Affinity: Pteridosperm.

**Wilsonites delicatus** Kosanke 1950
Plate 19, Figure 7

*Holotype:* Kosanke (1950), pl.14, fig. 4.
*Type locality:* No. 6 Coal, Carbondale Group, Illinois, U.S.A; Asturian.

**Description:** Trilete monosaccate pollen with a circular equatorial outline. Body circular and concordant with equatorial outline of saccus; may be pale or dark but always has an indistinct outline. Laesurae may be indistinct or distinct; extending for half to two thirds of the radius of the body. Saccus infrareticulate, with a laevigate or slightly granulate external ornament. Saccus and body fused at proximal pole, with proximal surface of the body being free of saccus. Folding of saccus may occur.

*Dimensions:* Total 63-72 (2 specimens; HF). Total 54 (68) 89 (10 specimens; Schulze and 2% KOH).

Comparison: Forms with similar pale body as illustrated by Kosanke (1950) and Smith and Butterworth (1967) as well as those with a darker body, similar to those figured by Clayton *et al.* (1977) and Peppers (1970). Specimens consistently have an indistinct body outline.

**Occurrence:** Harry Stoke B to Westerleigh Hard Coal and roof of Parkfield Hard Coal, Stonehill unnamed coal to Hursley Hill borehole (Winterbourne Formation to Publow Member).

**Known range:** Upper Langsettian to Bolsovian.
**Subtursma DISACCITES Cookson 1947**

*Genus ALISPORITES (Daugherty) Jansonius 1971*

Type species: *A. opii* Daugherty 1941

**Description:** Alete bisaccate with oval haploxynoid equatorial outline. Body roughly oval to rounded tetragonal shape, with long axis orientated perpendicular to the long axis of the pollen grain. Body may be faintly granulate. Sacci typically hemispherical, rarely crescent shape, with infrareticulation. Sacci overlap around half of the pollen body on the distal surface.

**Comparison:** Alisporites differs from Illinites by its lack of any laesurae.

**Affinity:** Pteridosperm.

**Alisporites zapfei** (Potonié and Klaus) Jizba 1962

Plate 19, Figures 8-9

1954  *Pityosporites zapfei* (Klaus) Potonié and Klaus, p.538.

**Holotype:** Potonié and Klaus (1954), pl. 10, fig. 9.

**Description:** Alete bisaccate with oval haploxynoid equatorial outline. Body roughly oval to rounded tetragonal shape with long axis orientated perpendicular to the long axis of the pollen grain, occupying half to two thirds of the long axis. Sacci typically hemispherical, rarely crescent shape, with infrareticulation. Sacci overlap around half of the pollen body on the distal surface.

**Dimensions:** Total 43 (47) 55 (4 specimens; HF). Total 45-55 (2 specimens; Schulze and 2% KOH).
Comparison: Similar in shape and size to *Illinites unicatus*, but *Alisporites zapfei* is apparently alete. This species is often not preserved as well as *Illinites unicatus*, and the lack of a monolete mark may be preservational.

Occurrence: Harry Stoke B to 65 The Dingle, below Trench Coal to Hursley Hill borehole (Winterbourne Formation to Publow Member). Possibly in Golden Valley (Winterbourne Formation).

Known range: Late Stephanian to Permian.

*Infraturma STRIATITI* Pant 1954

*Genus PROTOHAPLOXYPINUS* (Samoilovich) Morbey 1975

Type species: *P. latissimus* Luber 1941

Description: Alete bisaccate with oval dihaploxynoid equatorial outline. Body roughly oval to rounded tetragonal shape, with long axis orientated perpendicular to the long axis of the pollen grain. Body taeniate. Sacci hemispherical, with infrareticulation. Sacci overlap over half of the pollen body on the distal surface.

Comparison: Taeniae are similar to *Illinites unicatus* var. *striata*, but *Protohaploxypinus* is not trilete and there is no oval taenia encircling the striated portion of the inner body in proximal view.

Affinity: Pteridosperm.
Protohaploxypinus sp. 1
Plate 20, Figure 1

Description: Alete bisaccate with oval dihaploxynoid equatorial outline. Body roughly oval, occupying around half of the long axis of the pollen grain, with long axis orientated perpendicular to the long axis. Body taeniate, 5-6 taenia encircle the body parallel to the long axis of the pollen grain. Sacci hemispherical, with infrareticulation. Sacci overlap over the body by around 8 \( \mu \text{m} \); roughly half of the pollen body on the distal surface.

Dimensions: Total 90 (1 specimen; HF).

Occurrence: Above Trench Coal (Farrington Member).

Infracurma DISACCIATRILETI (Leschik) Potonié 1958

Genus ILLINITES (Kosanke) Potonié and Kremp 1954

Type species: I. unicatus Kosanke 1950

Description: Monolete to incipient trilete bisaccate with oval haploxynoid to diploxynoid equatorial outline. Laesurae extend two thirds to three quarters of the body. Body roughly oval to rounded tetragonal shape with long axis orientated perpendicular to the long axis of the pollen grain, occupying half to two thirds of the long axis; may be granulate. Body may have several striations (taeniae) encircling the body, parallel to the long axis of the pollen, which may branch. Sacci typically hemispherical or crescent shape, with infrareticulation. Sacci overlap around half of the pollen body on the distal surface.

Comparison: The bladders are not inclined distally as in Pityosporites or modern pollen, and are as wide as or wider than the body. Alisporites is alete. Taeniae are similar to
those in *Protohaploxypinus*, but the taenia which encircles the pollen body differentiates *Illinites*.

**Affinity:** Coniferales. Recovered from Triassic *Aethophyllum*; a herbaceous conifer (Rothwell *et al.*, 2000).

**Illinites elegans** (Kosanke) Peppers 1970

Plate 20, Figure 3

1955 *Kosankeisporites elegans* (Kosanke) Bharadwaj, p. 137.
1962 *Complexisporites polymorphus* Jizba, p. 869.
1970 *Kosankeisporites elegans* (Kosanke) Peppers, p. 133.

**Description:** Monolete to incipient trilete bisaccate with oval haploxynoid to diploxynoid equatorial outline. Laesurae two thirds to three quarters of the body. Body roughly oval to rounded tetragonal shape with long axis orientated perpendicular to the long axis of the pollen grain, occupying half to two thirds of the long axis; may be granulate. Body may have 3-6 striations (taeniae) encircling the body, parallel to the long axis of the pollen, which may branch. Oval taenia encircles the striated portion of the inner body in proximal view forming a gutter-like feature around the body. Sacci typically hemispherical or crescent shape, with infrareticulation. Sacci overlap around half of the pollen body on the distal surface.

**Dimensions:** Total 46 (58) 80 (4 specimens; Schulze and 2% KOH).

**Discussion:** Helby (1966) proposed striated forms of *Illinites* are synonymous with *Kosankeisporites* Bharadwaj, *Complexisporites* Jizba and *Striatosporites* Jizba. Azcuy (2002) emended *Illinites unicatus* to include these proposed synonymies. Striated forms of *Illinites* are rare in the Bristol Coalfield preparations, but were logged as *Illinites*
*Illinites unicatus* (Kosanke) Helby 1966

Plate 20, Figure 2


_Holotype:_ Kosanke (1950), pl.1, figs. 1-2.
_Type locality:_ McLeary’s Bluff Seam, Bond Formation, Illinois; Stephanian.

_Description:_ Monolete to incipient trilete bisaccate with oval haploxynoid to diploxynoid equatorial outline. Laesurae two thirds to three quarters of the body. Body roughly oval to rounded tetragonal shape with long axis orientated perpendicular to the long axis of the pollen grain, occupying half to two thirds of the long axis; may be granulate. Sacci typically hemispherical or crescent shape, with infrareticulation. Sacci overlap around half of the pollen body on the distal surface.

_Dimensions:_ Total 56-58 (2 specimens; HF). Total 49-55 (2 specimens; Schulze and 2% KOH).

_Discussion:_ See discussion for *Illinites elegans._

*elegans* in order to retain as much information on the diversity of palynomorphs as possible.

_Comparison:_ *Illinites unicatus* does not have a striated body. These two species are often viewed as synonymous.

_Occurrence:_ 65 The Dingle, below Salridge Coal (Downend Member to Mangotsfield Member).

_Known range:_ Langsettian to Stephanian.
Comparison: *Illinites elegans* features a striated body. These two species are often viewed as synonymous.

Occurrence: Harry Stoke B to 65 The Dingle, below Salridge Coal to above Trench Coal (Winterbourne Formation to Farrington Member).

Known range: Langsettian to Stephanian.

**Illinites sp. 1**

Plate 20, Figure 4

Description: Monolete to incipient trilete bisaccate with oval haploxynoid to diploxynoid equatorial outline. Laesurae two thirds to three quarters of the body. Body roughly oval to rounded tetragonal shape with long axis orientated perpendicular to the long axis of the pollen grain, occupying half to two thirds of the long axis; may be granulate. Sacci typically hemispherical or crescent shape, with infrareticulation. Sacci overlap around half of the pollen body on the distal surface.

Dimensions: Total 68 (78) 90 (4 specimens; HF). Total 70-78 (2 specimens; Schulze and 2% KOH).

Comparison: This species is consistently larger that *Illinites unicatus*.

Occurrence: Harry Stoke B to 65 The Dingle, above Trench Coal (Winterbourne Formation to Farrington Member).
Genus PARASPORITES Schopf 1938

Type species: P. maccabei Schopf 1938

Description: Monolete to incipient trilete bipseudosaccate pollen with oval haploxynoid to diploxynoid equatorial outline. Body roughly oval to rounded tetragonal shape with long axis orientated parallel to the long axis of the pollen grain, occupying two thirds to four fifths of the long axis. Body ornament of spore body consists of a network of interconnecting, convolute rugulae which may almost abut together and are separated by narrow v-shaped furrows. Laesurae half to two thirds of pollen body diameter. Pseudosacci, lacking infrareticulation, crescent shaped attached to the distal surface of the pollen body.

Affinity: Medullosalean pteridosperm.

Parasporites maccabei Schopf 1938

Plate 20, Figure 5

Holotype: Schopf (1938), pl. 7, fig. 1-3.

Type locality: Herrin (No. 6) Coal, Carbondale Group, Illinois, U.S.A.; Asturian.

Description: Monolete, with median deflection to incipient trilete bisaccate with oval haploxynoid to diploxynoid equatorial outline. Body roughly oval to rounded tetragonal shape with long axis orientated perpendicular to the long axis of the pollen grain, occupying half to two thirds of the long axis; may be granulate. Sacci typically hemispherical or crescent shape, with infrareticulation. Sacci overlap around half of the pollen body on the distal surface.

Dimensions: Total 179 (209) 246 (13 specimens; Schulze and 2% KOH).

Occurrence: 65 The Dingle (Mangotsfield Member).
Known range: Asturian (Schopf, 1938)

Turma PLICATES (PLICATA Naumova 1937,1939) Potonié 1962
Subturma PRAECELPATES Potonié and Kremp 1954
Infraturma Praecolpali Potonié and Kremp 1954
Genus ZONALOSPROITES (Ibrahim) Ravn 1986
Type species: Z. vittatus Ibrahim 1933

1933 Zonalosporites Ibrahim, p. 40.

Description: Monolete pollen, oval in equatorial outline. Laesurae may be indistinct or distinct, two thirds to four fifths of pollen long axis, and may feature a median deflection. Convex nature of the distal surface often leads to longitudinally orientated compression folds on the distal surface. Typically there are two of these; one each side of the distal convexity. Exine is laevigate to punctate.

Discussion: Median deflection of the monolete mark is similar to that seen in Parasporites; another pteridosperm pollen. Zonalosporites priority over Schopfipollenites, has been recognised by several authors (Potonié, 1970; Kaiser, 1976; Ravn, 1986).

Affinity: Medullosalean pteridosperm.
Zonalosporites ellipsoides (Ibrahim) Ravn 1986

Plate 20, Figure 6

Description: Monolete pollen, oval in equatorial outline. Laesurae may be indistinct or distinct, two thirds to four fifths of pollen long axis, and may feature a median deflection. Convex nature of the distal surface often leads to longitudinally orientated compression folds on the distal surface. Typically there are two of these; one each side of the distal convexity. Exine is laevigate to punctate.

Dimensions: Total 179 (209) 2460 (13 specimens; HF). Total 295 (350) 420 (13 specimens; Schulze and 2% KOH).

Occurrence: Harry Stoke B to roof of Parkfield Hard Coal, Golden Valley to Hursley Hill borehole (Winterbourne Formation to Radstock Member).

Known range: Namurian B to Asturian.

Subturma MONOCOLPATES (Monosulcites) Potonié 1970

Infraturma QUASILAEVIGATI Potonié 1970

Genus CYCADOPITES Wodehouse ex Wilson and Webster 1946
Type species: C. follicularis Wilson and Webster 1946
Description: Monosulcate pollen grains with an oval to lenticulate equatorial outline. Sulcus extends for full length of pollen grain. Lip-like thickenings may border the sulcus. Exine laevigate.

Discussion: Comparable Carboniferous monocolpate pollen are typically referred to *Cheiledonites* Doubinger 1957. However, this genus is junior to the more stratigraphically persistent *Cycodopites* Wodehouse ex Wilson and Webster 1946.

Affinity: Cycadales.

**Cycadopites sp. 1**
Plate 20, Figure 7

Description: Monosulcate pollen grains with an oval to lenticulate equatorial outline. Sulcus extends for full length of pollen grain. Lip-like thickenings may border the sulcus. Exine laevigate.

Dimensions: Total 95 (102) 117 (7 specimens; HF).

Discussion: A comparable specimen is figured in Clayton *et al.*, (1977) (Plate 22, fig 26).

Comparison: Larger than *Cycadopites* sp.2.

Occurrence: Harry Stoke B to roof of Coalpit Heath Hollybush Coal and shales associated with Shortwood Top Coal, Bickley Wood to below Trench Coal (Winterbourne Formation to Farrington Member).
Cycadopites sp. 2
Plate 20, Figure 8

**Description:** Monosulcate pollen grains with an oval to lenticulate equatorial outline. Sulcus extends for full length of pollen grain. Lip-like thickenings may border the sulcus. Exine laevigate.

**Dimensions:** Total 58 (61) 65 (3 specimens; HF).

**Discussion:** A comparable specimen is figured in Clayton *et al.*, (1977) (Plate 22, fig 26).

**Comparison:** Smaller than *Cycadopites* sp.1.

**Occurrence:** Harry Stoke B to below Westerleigh Hard Coal and roof of Parkfield Hard Coal, Bickley Wood to above Trench Coal (Winterbourne Formation to Farrington Member).
3.3 Biostratigraphy and correlation

3.3.1 Miospore biozonation of the Bristol Coalfield

A new biozonation scheme was produced from the stratigraphical ranges of the Bristol Coalfield; range charts of stratigraphically important taxa were constructed for the Coalpit Heath Basin (Figure 33) and for the southern limb of the Kingswood Anticline (Figure 34). Range charts of all recorded taxa are included in Appendix 2 and Appendix 3. Reworked taxa are discussed in ‘3.3.4 Reworked taxa’.

Several key species have range tops within the Mangotsfield Member, with the lowermost ~125 m of this unit; Acanthotriletes spp., Alatisporites hoffmeisterii, Alatisporites pustulatus, Apiculatisporis spinososaetosus, Convolutispora varicosas, Cristatisporites indignabundus, Cristatisporites solaris, Dictyotriletes muricatus, Lophotriletes gibbosus, Lophotriletes mosaicus, Planisporites cf. granifer, Raistrickia fulva, Reticulatisporites reticulatus, Reticulitriletes clatriformis, Reticulitriletes falsus, Spinosporites exigus, Spinosporites spinosus, Triquitrites cf. sculptilis. Verrucosiporites microverrucosus, Verrucosiporites sifati, Vestispora costata, Vestispora luminata, Vestispora tortuosa and Westphalensisporites irregularis. Several stratigraphically important species also appear over this interval within the Coalpit Heath Basin; Alatisporites trialatus, Cadiospora magna, Cadiospora sp. 1, Cirratriradites annulatus, Cirratriradites annuliformis, Cordaitina uralensis, Microreticulatisporites sulcatus, Mooreisporites inusitatus, Mooreisporites lucidus, Parasporites maccaei, Punctatosporites punctatus, Raistrickia aculeata, Savitrisporites majus, Thymospora obscursa, Triquitrites subspinosus and Vestispora sp. 1.

Generally, the biostratigraphy of the southern limb of the Kingswood Anticline is broadly similar to that of the northern basin. Lundbladispora gigantea and Westphalensisporites irregularis range into the Farrington Member; these taxa are last recorded in the lower half of the Mangotsfield Member in the Coalpit Heath Basin. Several species which have range bases within the lower Mangotsfield Member have
slightly earlier records within the southern basin. *Cirratiradiates annuliformis, Mooreisporites inusitatus, Savitrisporites majus* and *Thymospora obscura* are first recorded in the uppermost Downend Member, from localities within Bickley Wood.

*Thymospora pseudothiessenii* is first recorded from the Winterbourne Formation, almost always in clastic environments, at very low abundances (typically only 1-2 specimens per sample). *Cristatisporites* spp. are common in the lower half of the Winterbourne Formation, representing up to a quarter of the total palynoflora, but are rare (<1.5%) components in the upper Winterbourne Formation and the Pennant Sandstone Formation. *Laevigatosporites minimus, Punctatosporites* spp. *Thymospora* spp. become more abundant components of the palynoflora in both the coals and clastics of the Farrington Member.
Figure 33 – Range chart of stratigraphically important taxa in the Warwickshire Group of the Coalpit Heath Basin. A larger range chart of all encountered taxa is included in Appendix 2. Locality numbers are shown in blue text. WF= Winterbourne Formation; FM=Farrington Member.
Figure 34 - Range chart of stratigraphically important taxa in the Warwickshire Group of the southern limb of the Kingswood Anticline. A larger range chart of all encountered taxa is included in Appendix 3. Locality numbers are shown in blue text. WF= Winterbourne Formation; FM=Farrington Member.
3.3.2 Correlation to published biozonation schemes

3.3.2.1 Details of published biozonation schemes

Several key miospore biozonation schemes have been published for the late Carboniferous (Figure 35). The early schemes of Coquel et al. (1976) and Smith and Butterworth (1967) will not be discussed specifically in this study, as much of this work has been amalgamated and expanded on in subsequent publications. The Bristol biostratigraphy outlined in ‘3.3.1 Miospore biozonation of the Bristol Coalfield’, and associated figures, will be compared to published schemes for onshore (Clayton et al., 1977 and revisions) and offshore (McLean et al., 2005) western Europe to allow biostratigraphic dating of the Warwickshire Group. For brevity, only taxa which were found in the Bristol Coalfield will be discussed in this section.
Figure 35 – Correlation of western European Carboniferous miospore zonal schemes discussed. Dashed lines in the Biozone columns reflect uncertainty in the positioning of a Biozone boundary. Marine band bands highlighted in blue (A= Aegiranum Marine Band, C= Cambriense Marine Band).
3.3.2.1.1 Clayton et al. (1977) revisions – notes on progress

Clayton et al. (1977) is in the process of being revised, and is currently in draft form (Clayton et al., in preparation). This revised scheme includes Sub-Biozones based on data from McLean et al. (2005) and Clayton et al. (2003) as well more recent on-going work. A preliminary version of this biozonation is included in Figure 35, and key Biozone correlation and emendation details are outlined below.

There are several important changes in the revised Clayton et al. (1977) scheme. The base of the Torispora securis – T. laevigata (SL) Biozone of Clayton et al. (1977) is stated as lying close to the Aegiranum Marine Band, indicating an age approximating the Duckmantian-Bolsovian boundary. The bottom of the revised SL Biozone proposed by Clayton et al. (in preparation) is stratigraphically higher, approximately at the level of or slightly below the Cambriense Marine Band (mid-Bolsovian). This revision makes the SL Biozone equivalent to other notable Biozones; X Biozone (Smith and Butterworth, 1967), W6 Biozone (McLean et al., 2005) and Vestispora fenestrata Biozone (Clayton et al., 2003). The base of the Clayton et al. (1977) SL Biozone therefore equates to; W5a-W5b Sub-Biozone boundary (McLean et al., 2005) and the Microreticulatisporites nobilis – Triquitrites sculptilis Biozone boundary. The revised SL Biozone includes definition of two Sub-Biozones; Torispora securis (Ts) and Latensina trileta (Lt), which correlate to the Torispora securis and Raistrickia aculeata Sub-Biozones of (Clayton et al., 2003) and the W6a and W6b Sub-Biozones of (McLean et al., 2005). Where the SL Biozone is mentioned in this text, it shall be in reference to the revised Biozone.

As well as this change to the stratigraphical position of the base of the SL Biozone, another new Biozone has been added between the SL Biozone and the proceeding NJ Biozone; the Vestispora magna – Triquitrites sculptilis (MS) Biozone, which is equivalent to the IX Biozone (Smith and Butterworth, 1967) and the W5 Biozone (McLean et al., 2005). The new MS Biozone also comparable to the total range of the
Vestispora magna Sub-Biozone and Triquitrites sculptilis Biozone (Clayton et al., 2003).

The third revision proposed is a simple renaming of the Thymospora obscura – T. thiessenii (OT) Biozone (Clayton et al., 1977), to the Thymospora obscura - T. pseudothiessenii (OP) Biozone. This is because Thymospora thiessenii is typically very rare in British material, and Thymospora pseudothiessenii is therefore considered to be better suited as an index taxon. The OP Biozone correlates with XI (Smith and Butterworth, 1967), Thymospora pseudothiessenii Biozone (Clayton et al., 2003) an W7 (McLean et al., 2005). The OP Biozone is also split into three Sub-Biozones, from base to top; Thymospora pseudothiessenii – T. verrucosa (pv) Subzone, Schopfites dimorphus (Sd) Subzone and Savitrisporites camptotus (Sc) Subzone. These correlate with W7a, W7b, W7c Sub-Biozones (McLean et al., 2005).

3.3.2.1.2 Western Europe (onshore)

Several important monolete taxa appear at the base of the Torispora securis – T. laevigata (SL) Biozone, including both index taxa (Clayton et al., in preparation). The distinctive operculate miospore Vestispora fenestrata also have a range base coincident with the base of this Biozone. The base of the acme of Punctatosporites spp. and the appearance of Westphalensisporites irregularis occurs just above the base of the Biozone. The range tops of Apiculatisporis spinosaetosus, Alatisporites pustulatus, Reticulatisporites reticulatus, Savitrisporites nux and Vestispora tortuosa occur in roughly the middle of the Biozone, defining the top of the Torispora securis (Ts) Sub-Biozone. The upper half of the SL Biozone, Latensina trileta (Lt) Sub-Biozone, is marked by the first appearance of the index taxa and Raistrickia aculeata. Latensina trileta would be included within Cordaitina uralensis in this study (see relevant systematics entry for this species). The top of the SL Biozone coincides with the range tops of Cingulizonates loricatus and Dictyotriletes bireticulatus. Vestispora costata and Acanthotriletes triquetrus have range tops within the upper portions of the SL Biozone (Smith and Butterworth, 1967).
Generally, SL Biozone assemblages feature abundant *Lycospora, Laevigatosporites, Punctatosporites, Torispora, Triquitrites, Densosporites* and/or *Crassispora kosankei*; dominance-diversity patterns being driven by differing factors such as substrate and ecology of the vegetation on a location-by-location basis. Association of *Cirratriradites saturni, Crassispora kosankei, Cristatisporites solaris*, *Florinites junior, Microreticulatisporites nobilis, Punctatosporites* spp., *Triquitrites sculptilis* and *Vestispora costata* are common in this Biozone.

The base of the *Thymospora obscura - T. pseudothiessenii* (OP) Biozone is marked by the first appearance of one of the index taxa, *Thymospora pseudothiessenii*. *Thymospora obscura* appears slightly stratigraphically higher, in the middle of the *Thymospora pseudothiessenii – T. verrucosa* (pv) Sub-Biozone. *Cadiospora magna* also appears at the base of the Biozone; extending into roughly the middle of the pv Sub-Biozone. Smith and Butterworth (1967) also reported that *Mooreisporites inusitatus, Alatisporites trialatus* and *Cirratriradites annuliformis* have a range base in the latest Bolsovian/basal Asturian: a horizon which likely correlates to the base of the OP Biozone.

The top of the pv Sub-Biozone is defined as the last occurrences of *Cristatisporites solaris, Reinschospora speciosa, Reticulitriletes falsus, Triquitrites tribullatus* and *Vestispora magna*. The first occurrence of *Cirratriradites annulatus* and *Lundbladispora gigantea* occur at the base of the *Schopfites dimorphus* (Sd) Sub-Biozone. Several notable species have last occurrences within this Sub-Biozone: *Florintes junior, Vestispora pseudoreticulata* and *Westphalensisporites irregularis* disappear roughly in the middle of this Sub-Biozone; *Vestispora laevigata, Alatisporites hoffmeisterii* and *Endosporites zonalis* have range tops which define the upper limit of the Sub-Biozone. The uppermost OP Biozone division, the *Savitrisporites camptotus* (Sc) Subzone, marks the first occurrence of *Savitrisporites camptotus* (*S. majus*).

OP Biozone assemblages, like those of the proceeding SL Biozone, may be dominated by *Lycospora, Laevigatosporites, Punctatosporites, Torispora* and/or *Triquitrites*. High levels of *Thymospora* are also a common feature of these assemblages, and may be used
to differentiate the two Biozones. Association of *Crassipora kosankei*, *Endosporites globiformis*, *Florinites junior*, *Punctatosporites* spp, *Raistrickia aculeata*, *Thymospora* spp. and *Vestispora* spp. are typical of this biozone.

### 3.3.2.1.3 North Sea

McLean *et al.* (2005) produced a biozonation scheme for the North Sea, which correlates well with onshore British and western European scheme(s) discussed above. This scheme recognised 18 biozones, divided into 40 Sub-Biozones, ranging from Tournaisian to Asturian in age. The mid- to late Bolsovian is represented by the W6 Biozone, which is succeeded by the W7 Biozone of latest Bolsovian to Asturian age. The range bases of *Torispora securis* and *Vestispora fenestrata* mark the base of the W6 Biozone; the base of the Biozone also correlates with the Cambriense (Winterbourne) Marine Band. *Alatisporites pustulatus*, *Vestispora tortuosa*, *Savitrisporites nux* and *Apiculatisporis spinososaetosus* have range tops which define the top of the W6a Sub-Biozone. *Raistrickia aculeata* and *Latensina trileta* appear at the base of the W6b Sub-Biozone. *Raistrickia fulva* and *Verrucosispornites microverrucosus* have last occurrences in W6b, disappearing near the top of this Sub-Biozone. The W6-W7 transition is marked by the first occurrence of *Thymospora pseudothiessenii*, with *Thymospora obscura* appearing slightly above this level, and the last occurrences of *Cingulizonates loricatus* and *Dictyotrilites bireticulatus*. *Cristatisporites solaris*, *Alatisporites triquetrus*, *Reticulitritles falsus*, *Reinschospora speciosa* and *Triquitrites tribullatus* have range tops which define the upper limit of the W7a Sub-Biozone; this Sub-Biozone straddles the Bolsovian-Asturian boundary. *Cirrattriradites annulatus* and *Lundbladispora gigantea* appear at the base of the W7b Sub-Biozone. Many notable species have last occurrences within W7b: *Florinites junior*, *Westphalensisporites irregularis* and *Vestispora pseudoreticulata* have range tops in the lower within the lower half of this biozone; *Vestispora laevigata*, *Endosporites zonalis*, *Alatisporites hoffmeisterii* and *Zonalosporites* spp. have range tops that mark the top of this Sub-Biozone. The final Sub-Biozone of McLean *et al.* (2005), W7c, marks the first occurrence of *Savitrisporites (camptotus) majus.*
3.3.2.1.4 North America – brief comparison

Peppers (1996) provided a summary of miospore biostratigraphic ranges for various North American coal basins, but did not formally erect Biozones. The Atokan and Desmoinesian can be broadly considered to equivalent to the Bolsovian and combined Asturian-Cantabrian, respectively.

Generally, the biostratigraphic ranges are broadly comparable with those observed in western Europe. *Alatisporites pustulatus*, *Cingulizonates loricatus*, *Cristatisporites indignabundus*, *Dictyotriletes bireticulatus* and *Savitrisporites nux* have range tops at end Atokan or in the earliest Desmoinesian (~Bolsovian-Asturian boundary) in all North American basins, comparable to the western European ranges of these taxa. *Alatisporites trialatus* extends from the late Atokan to the end of the Desmoinesian, which is comparable to a latest Bolsovian to Asturian occurrence. *Verrucosisporites sifati* ranges from early Atokan to mid-Desmoinesian, therefore having a range top which also equates to its Asturian limit in western Europe. *Mooreisporites inusitatus* and *Cadiospora magna*, important index taxa for the Asturian, have range bases which roughly coincide with the base of the equivalent Desmoinesian in all the North American basins.

*Vestiispora laevigata* has a range top at the end of the Desmoinesian or earliest Missourian. *Vestiispora pseudoreticulata* disappears at the end of the Atokan in Illinois and the Appalachian regions, and early Desmoinesian in Eastern Kentucky and middle Desmoinesian in the Western Interior. *Westphalensisporites irregularis* has a range top at the end of the Desmoinesian in Illinois, but is known to extend into the mid-Missourian in the Appalachian region. These three species have a longer range than in western Europe, where they have range tops in the mid-Asturian. *Lycospora* spp. dominance continues until the end of the Desmoinesian (~end of Cantabrian) in North America, whereas these taxa typically become much rarer in the Asturian and are further reduced in abundance by Cantabrian and Stephanian.
3.3.2.2 Biostratigraphic dating of the Bristol Coalfield

The Winterbourne Formation features a diverse assemblage of miospores which clearly match the SL Biozone (mid- to latest Bolsovian), featuring; *Acanthotretilates triquetrus, Apiculatisporis spinosasaetosus, Alatisporites pustulatus, Cingulizonates loricatus, Cirratriradites saturni, Cristatisporites solaris, Crassispora kosankei, Dictyotretilates bireticulatus, Florinites junior, Microreticulatisporites nobilis, Punctatosporites spp., Reticulatisporites reticulatus, Savitrisporites nux, Torispora securis, Torispora laevigata, Triquitrites sculptilis, Verrucosisporites microverrucosus, Vestispora costata, Vestispora tortuosa, Vestispora fenestrata and Westphalensisporites irregularis*. Dominance patterns (Table 4) also correspond well to this Biozone, with *Lycospora, Laevigatosporites, Punctatosporites, Torispora, Triquitrites*, and *Crassispora kosankei* being common components of the palynoflora. These assemblages continue on into the Downend Member, and into the lower half of the Mangotsfield Member.

The Grovesend Formation features assemblages typical of the OP Biozone (latest Bolsovian to Asturian). Samples feature abundant *Lycospora, Laevigatosporites, Punctatosporites* and *Triquitrites*, similar to the proceeding SL Biozone, with high levels of *Thymospora* (Table 4). The following taxa association are typical of the OP Biozone; *Alatisporites trialatus, Alatisporites hoffmeisterii, Cadiospora magna, Cirratriradites annulatus, Cirratriradites annuliformis, Crassispora kosankei, Endosporites globiformis, Florinites junior, Lundbladispora gigantea, Mooreisporites inusitatus, Vestispora laevigata, Savitrisporites majus, Punctatosporites spp, Raistrickia aculeata, Thymospora spp. Vestispora fenestrata, Vestispora laevigata and Vestispora pseudoreticulata.*
<table>
<thead>
<tr>
<th>Stratigraphy</th>
<th>Common (5-9.5%)</th>
<th>Abundant (10-40%)</th>
<th>Dominant (&gt;40%)</th>
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<tr>
<td>Grovesend Formation</td>
<td>Alisporites zapfei</td>
<td>Calamospora spp.</td>
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<td></td>
<td>Endosporites globiformis</td>
<td>Crassispora kosankei</td>
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<tr>
<td></td>
<td>Laevigatosporites spp. (&gt;)35 µm</td>
<td>Florinites spp.</td>
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<td></td>
<td></td>
<td>Lycospora spp.</td>
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<tr>
<td>Farrington Member</td>
<td>Calamospora spp.</td>
<td>Crassspora kosankei</td>
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<tr>
<td></td>
<td>Cyclogranisporites spp.</td>
<td>Florinites spp.</td>
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<tr>
<td></td>
<td>Laevigatosporites spp. (&lt;35 µm)</td>
<td>Laevigatosporites spp. (&gt;)35 µm</td>
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<tr>
<td></td>
<td>Thymospora spp.</td>
<td>Lycospora spp.</td>
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<td></td>
<td>Triquitrites spp.</td>
<td>Punctatosporites spp.</td>
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<td>Vestispora spp.</td>
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<td>Mangotsfield Member</td>
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<td>Convolutispora spp.</td>
<td>Crassspora kosankei</td>
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<tr>
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<td>Cyclogranisporites spp.</td>
<td>Densosporites spp.</td>
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<td>Densosporites spp.</td>
<td>Florinites spp.</td>
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<tr>
<td></td>
<td>Endosporites globiformis</td>
<td>Laevigatosporites spp. (&gt;)35 µm</td>
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<tr>
<td></td>
<td>Punctatosporites spp.</td>
<td>Lycospora spp.</td>
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<td></td>
<td></td>
<td>Torispora spp.</td>
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<td>Downend Member</td>
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<td>Crassspora kosankei</td>
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<tr>
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<td>Densosporites spp.</td>
<td>Florinites spp.</td>
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<tr>
<td></td>
<td>Punctatosporites spp.</td>
<td>Laevigatosporites spp. (&gt;)35 µm</td>
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<td></td>
<td></td>
<td>Lycospora spp.</td>
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<td>Winterbourne</td>
<td>Calamospora spp.</td>
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<td>Formation</td>
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<td>Calamospora spp.</td>
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<tr>
<td></td>
<td>Cyclogranisporites spp.</td>
<td>Converrucosisporites spp.</td>
<td></td>
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<tr>
<td></td>
<td>Punctatosporites spp.</td>
<td>Crassspora kosankei</td>
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<tr>
<td></td>
<td></td>
<td>Cristatisporites spp.</td>
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<td></td>
<td></td>
<td>Florinites spp.</td>
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<td></td>
<td></td>
<td>Laevigatosporites spp. (&gt;)35 µm</td>
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<td></td>
<td></td>
<td>Lycospora spp.</td>
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<td></td>
<td></td>
<td>Torispora spp.</td>
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<td></td>
<td></td>
<td>Triquitrites spp.</td>
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<tr>
<td></td>
<td></td>
<td>Vestigisporites sp.1</td>
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</tbody>
</table>

Table 4 – Taxa dominance patterns within the Warwickshire Group.
There is no clear-cut boundary between SL and OP Biozone assemblages, but it is clear that the transition occurs gradually over the lower ~100 m of the Mangotsfield Member in the Coalpit Heath Basin (Figure 33). *Parasporites maccabbei*, a pteridosperm pollen only previously known from Asturian-equivalent strata of North America, is also recorded at this horizon. Few horizons in the upper Downend Member were available for sampling from the Coalpit Heath Basin, but several assemblages were recovered from Bickley Wood in the southern limb of the Kingswood Anticline (Figure 34). In these assemblages *Cadiospora magna* and *Savitrisporites majus* were recorded just below the Salridge Coal, from the uppermost Downend Member (assuming the lithostratigraphical correlation of the two sub-basins proposed by this study). This occurrence is 50-100 m lower than observed in the Coalpit Heath Basin, this has a two-fold effect on the biostratigraphical interpretation; a) the observed stratigraphical range of the SL-OP transition is extended from ~100 m to ~150-200 m, and b) the transition is now interpreted as having its base in the uppermost 50 m of the Downend Member, rather than within the lowermost Mangotsfield Member. The transitional nature of this boundary is commonly seen in practice, but it rarely emphasised in published biozonational schemes (McLean, pers. comms. 2012).

Sub-Biozones of McLean *et al.* (2005) and Clayton *et al.*, (in preparation) are also not readily discernible in the Bristol biostratigraphy. The first possible explanation is that there is substantial reworking between the Warwickshire Group assemblages, blurring the boundaries as taxa range tops are extended into subsequent strata. This is a distinct possibility in these coarse-grained fluvial systems, as several reworked pre-Bolsovian assemblages were identified within the Pennant Sandstone Formation (discussed in 3.3.4 Reworked taxa). A second possibility is that the these species are not reworked, and the Bristol Coalfield taxa indeed have subtly different ranges. This study consists of samples derived from unusual depositional settings, such channel abandonment facies and localised peat mires within a braided fluvial system. As palynoflora is dictated by vegetational assemblages, it is highly likely that these substrates were home to subtly
differing ecological succession than those of the establish peat mires (economic coals) and fringing clastic swamps (roof shales) that are typically studied in biostratigraphy. There is some palynological evidence to suggest the Farrington Member may be mid-Asturian in age. *Cristatisporites solaris, Reinschospora speciosa* and *Reticulitrilites falsus* have range tops in the latest Bolsovian/early Asturian pv/W7a Sub-Biozone; these species occur in the Winterbourne and Pennant Sandstone formations but were not recorded from the Grovesend Formation. *Alatisporites hoffmeisterii* and *Westphalensisporites irregularis*, which have reported range tops in the mid-Asturian (Sd/W7b Sub-Biozone), are also not recorded above the Pennant Sandstone Formation. There are several species recorded which suggest this formation doesn’t extend into the late Asturian sc/W7c Sub-Biozone; *Vestispora pseudoreticulata* and *Vestispora laevigata* are reported to have range tops in the mid- and late Sd/W7b Sub-Biozone, respectively.

Key features, and major deviations, from previous biozonation schemes are summerised below;

1. The Winterbourne Formation and (most of the) Downend Member feature assemblages indicative of the mid- to latest Bolsovian SL Biozone, while the Grovesend Formation features taxa corresponding the latest Bolsovian to Asturian OP Biozone.

2. There is some palynological evidence to indicate that the Farrington Member of the Grovesend Formation may be mid-Asturian in age (Sd/W7b Sub-Biozone).

3. The SL-OP Biozone boundary is transitional, occurring over the lower ~100 m of the Mangotsfield Member in the Coalpit Heath Basin and may extend downwards into the uppermost 50 m of the Downend Member in the southern limb of the Kingswood Anticline. This basal discrepancy is almost certainly due to a lack of sampling horizons within the uppermost Downend Member from the Coalpit Heath Basin.
4. There is no evidence of Sub-Biozones within the SL Biozone. However, the position of the Ts-Lt Sub-Biozone boundary likely lies in the Downend Member, a member that has very few available sample localities.

5. The transitional nature of the SL-OP boundary, as well as the lack of Sub-Biozones, may due to one (or both) of the following factors; a) reworking of underlying Warwickshire Group assemblages causing a blurring of assemblages, or b) the nature of the atypical facies of the Bristol Coalfield driving differing vegetation assemblages (and correspondingly different palynofloras).

6. There are several taxa that occur throughout the Grovesend Formation (OP Biozone), which are typically reported as having range tops within the SL Biozone, these are; Cingulizonates loricatus, Dictyotriletes bireticulatus, Lophotriletes commissuralis, Lophotriletes microsaetosus and Savitrisporites nux. Explanations for these apparently extended ranges are discussed in 5).

7. Raistrickia aculeata has a reported range base in the middle of the SL Biozone (base of the Lt/W6b Sub-Biozone), but is associated with the SL-OP transition in the lower half of the Mangotsfield Member. This likely relates to the lack of sampling points, as discussed in 4).

8. Cadiospora magna is previously reported as only occur in the lowermost Asturian (pv Sub-Biozone), but occurs in the Farrington (which is likely mid-Asturian in age, Sd Sub-Biozone).

9. Cirratriradites annulatus has a previously reported range base in mid-Asturian (Sd/W7b Subzone), but appears in lower Mangotsfield Member in association with the transitional SL-OP boundary. This difference in range could possibly due to the differing facies of the Bristol Coalfield, and correspondingly different
vegetational assemblages, of the Bristol Coalfield compared to previously studied areas.

10. *Savitrisporites* (*camptotus*) *majus*, index taxon for the late Asturian Sc/W7c Sub-Biozone, also occurs at the SL-OP transition. This difference in range could possibly due to the differing facies of the Bristol Coalfield, and correspondingly different vegetational assemblages, of the Bristol Coalfield compared to previously studied areas.

11. *Lundbladispora gigantea* is reported from Winterbourne and Pennant Sandstone formations (SL Biozone), but not from Grovesend Formation (OP Biozone). This taxon has a previously reported range base within the middle OP Biozone (Sd/W7b Sub-Biozone). This difference in range could possibly due to the differing facies of the Bristol Coalfield, and correspondingly different vegetational assemblages, of the Bristol Coalfield compared to previously studied areas.

12. *Thymospora pseudothiessenii* and *Thymospora thiessenii* are typical of OP Biozone assemblages, but are recorded from the Winterbourne and Pennant Sandstone formations (SL Biozone). Again, this may be an effect of the atypical facies of the Bristol Coalfield. *Thymospora obscura* has a range base slightly higher, occurring in the lowermost Mangotsfield Member in association with the SL-OP transitional boundary.

13. New *Vestispora* and *Cadiospora* species are described in this study. These taxa are recorded only from the Farrington Member, making this biostratigraphically useful taxa.
3.3.3 Scolecodonts from the Cambriense (Winterbourne) Marine Band

The lowermost three samples (09jlp1-3) from the Winterbourne Formation contain an interesting assemblage of scolecodonts (Plate 21).

3.3.4 Reworked taxa

Reworked taxa are common in the Winterbourne and Pennant Sandstone formations (Appendix 4 and Appendix 5). These include; Tournaisian to Langsettian miospores, Middle and Upper Devonian miospores (Plate 22, figures 1-5) and Cambrian-Tremadoc acritarchs (Plate 22, figures 5-12; Plate 23). Generally reworked taxa are generally only found in non-peat forming environments. Peat mires, where clastic input is very low, typically represent the vegetation growing in and around the margins of these pools. Reworked palynomorphs are typically fluvially transported within clastic material and this, combined with the high input and preservation of locally sourced palynoflora with peat mire, suitably explains their prevalence in clastic material and relative dearth within coals.

Palynomorph colour can often be used as a proxy for thermal maturity, with increasing thermal maturity being reflected by darker exine (Legall et al., 1981). In this case, this proxy can only be tentatively utilised due to the disparate nature and age of the reworked assemblages. Reworked miospores from the Tournaisian-Langsettian show no greater thermal maturity than the miospores inferred as being generated by the vegetation of the Warwickshire Group. This can be tentatively interpreted to suggest that both of this assemblage was sourced from areas with low deformation, and little igneous intrusions. Tournaisian-Langsettian miospore assemblages are found with both Cambrian-Tremadoc acritarchs, and also associated with the Devonian miospore assemblages. However, assemblages containing Devonian miospores are typically not found in the same samples than those containing Cambrian-Tremadoc acritarchs, with the exception of Baltisphaeridium. This suggests that the Baltisphaeridium in these
samples may also be Devonian in age. The thermal maturity of the Devonian miospore assemblage is also vastly greater than observed in the other assemblages, suggesting that the two pre-Carboniferous assemblages were indeed sourced from areas with differing thermal histories. *Baltisphaeridium* found in association with Devonian miospores also illustrate differing thermal maturity to those found associated with the Cambrian-Tremadoc acritarchs. McLean (1995) recorded Middle/Upper Devonian miospores and Tremadoc acritarchs reworked into Langsettian-aged rocks near Sheffield, in the Pennine Basin. In this case, all assemblages showed the same levels of thermal maturity and Devonian miospores were found in association with Tremadoc acritarchs. In this study, multiple phases of reworking were inferred; firstly of Tremadoc acritarchs into Devonian sediments, with both assemblages then reworked into Langsettian-aged rocks. In the Bristol Coalfield, which was isolated from the Pennine Basin by the Wales-Brabant High, it is possible multiple phases of reworking also occurred.

The source region of the Bristol sediments switched from a north/north-easterly direction during deposition of the Winterbourne Formation to a south/south-easterly source in the Pennant Sandstone Formation; it would therefore be expected that this dramatic switch in source would manifest in a difference between reworked assemblages between the formations. Generally the Winterbourne Formation features more diversity, but both the Winterbourne and Pennant Sandstone formations feature taxa which are exclusive of the other formation (Table 5). The Coalpit Heath Basin features a greater diversity than the southern limb of the Kingswood Anticline, but this may in part be due to a higher sampling density in the northern basin.
<table>
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<tr>
<th>Pennant Sandstone Formation only</th>
<th>Cambrian-Tremadoc acritarchs</th>
<th>Middle/Upper Devonian miospores</th>
<th>Tournaisian-Langsettian miospores</th>
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<tr>
<td>Multiplicisphaeridium ramispinosum</td>
<td>‘Granulate spore’ spp.</td>
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<td></td>
<td>‘Galeate acritarch’ sp. 1</td>
<td>Kraeuelisporites ornatus</td>
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<td></td>
<td>Impluviculus multiangularis</td>
<td>Oswaldispora xenika</td>
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<td></td>
<td>Neovervchachium? sp. 1</td>
<td>Rugospora sp. 1</td>
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<td></td>
<td>Vulcanispheara turbata</td>
<td>Spinozonotriletes cf. unicus</td>
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<tr>
<td></td>
<td>Veryhachium spp.</td>
<td>Trinidulus diamphidios</td>
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Table 5 - List of reworked taxa, which have a range restricted to the Winterbourne Formation, or the Pennant Sandstone Formation

Several of the Tournaisian-Langsettian miospores appear in both clastic and coal samples; Knoxisporites pristinus, Microreticulatisporites punctatus, Secarisporites remotus, Tripartites trilinguis and Waltzispora spp. It is possible that small-scale peat generating environments in close association with the fluvial system, such as the one at Grove Cottage and 65 The Dingle where some of these species occur, received input of clastic material during their relatively short accumulation times. In this situation, it would be likely these taxa are indeed reworked. However several taxa also appear in several economic scale coal seams, which represent long-term and well-established peat generating environments (Secarisporites remotus and Waltzispora spp.). In these situations, it is perfectly possible that these taxa were sourced from the peat mire vegetation contemporaneously with their formation.
The only reworked taxon seen in the Grovesend Formation is *Radiizonates aligerens*; this miospore is usually indicative of Langsettian-aged assemblages from the RA Biozone of Clayton *et al.* (1977). This taxon is only ever recorded in clastic samples throughout the Warwickshire Group, which suggests that Langsettian-aged sediments were constantly reworked into the Bristol Coalfield throughout the entire interval.


3.4 Palaeoecology

Using semi-quantitative palynomorph counts, interpretations of vegetational assemblages can be made. Using available published records, the parent plant affinity of each genus is reproduced in Table 6 (summarised from ‘3.2 Systematic part’, where full details and discussion can be found within generic descriptions). These parent plant affinities were used throughout this section in palaeoecological interpretations.

See ‘3.1.5.3.1 Relating palynological and vegetation assemblages’ for important caveats to bear in mind when interpreting vegetational successions from palynological data.
<table>
<thead>
<tr>
<th>Lycopsid</th>
<th>Herbaceous</th>
<th>Sub-arborescent</th>
<th>Arborescent</th>
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<tbody>
<tr>
<td></td>
<td>Cirratriradites</td>
<td>Chaloneria</td>
<td>Endosporites</td>
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<td>Lundbladispora</td>
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<td>Sphenopsid</td>
<td>Sphenophyll</td>
<td>Sphenophyte</td>
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<td>Columinisporites</td>
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<td>Pteroretis</td>
<td>Elaterites</td>
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<td></td>
<td>Vestispora</td>
<td>Laevigatosporites (&gt;35um)</td>
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<tr>
<td>Fern</td>
<td>Small fern (mainly tedelacean, gleichenacean, sphenopterid)</td>
<td>Tree fern (Marattialean)</td>
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<td>Coniferales</td>
<td>Protohaploxypinus</td>
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<td></td>
<td>Hymenospora</td>
<td>Reinschospora</td>
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Table 6 – Details of parent plant affinity assignment of miospore genera used in palaeoecological interpretations
3.4.1 Statistical investigation of the vegetational succession from Harry Stoke B borehole (Winterbourne Formation)

Harry Stoke B provided a sequence of well-preserved samples, which covered the full stratigraphical range of the Winterbourne Formation. From semi-quantitative counts of palynomorph genera, several statistical analyses were undertaken. See ‘3.1.5.3.2 PAST: PAleontological STatistics’ for more details on these statistical methods. As previously discussed, the Winterbourne Formation represents poorly-drained coastal plain deposits (grey clastics), succeeded by periodically well-drain alluvial plains in the upper parts (grey and red clastics, with conglomerate deposits). Generic counts of palynomorphs, grouped by parent plant affinity, are included in Appendix 6 in full tabulated format, and graphically in Figure 37.

Figure 36 – Unconstrained seriation matrix of semi-quantitative palynomorph generic counts from the Winterbourne Formation of the Harry Stoke B borehole.
Figure 37 – Graphical representation of dominance-diversity patterns for the Winterbourne Formation. Data derived from semi-quantitative palynomorph generic counts. Locality number key and lithological key is reproduced in Figure 42.
Figure 38 - Cluster analysis dendrogram of semi-quantitative palynomorph generic counts from the Winterbourne Formation of the Harry Stoke B borehole. Unconstrained and paired group algorithm used, with several coefficients (a-d). Matrix was ordered by seriation (Figure 36), as sample order in the matrix can affect the position/length of the nodes/branches within the dendrogram.
Several palynoflora assemblage associations are highlighted in both cluster analysis (Figure 38) and DCA (Figure 39). These can be classified as reflecting nine different vegetational associations which are described and interpreted below. Measurements are borehole depths, unless otherwise noted.

**Lepidodendraceae associations**

These assemblages feature the highest levels (>17.5%) of the Lepidodendraceae miospore, *Lycospora*. There are two distinct associations within this group:

a) **Lepidodendraceae association I**

This association occurs in one sample; a coal residue from the National Coal Board material, record as being derived from a seam at 47.8-49 m depth. The borehole logs indicate this 1.2 m seam features a soft 94 cm coal overlying a 25 cm hard coal, with a 2.5 cm intervening coaly shale band. The sample depth suggests this assemblage was derived from the lower, hard coal. The assemblage is dominated by Lepidodendraceae miospores, which represent 58% of the palynoflora. Subordinate palynoflora can be attributed to sphenophytes (14%), ferns (4%) and tree ferns (10.5%). Cordaite pollen input is low in this assemblage (9%).

This association is interpreted as a topogenous peat mire with Lepidodendraceae; these are likely *Lepidophloios*-type, which are thought to have been more well adapted to waterlogged peat mires (DiMichele and Phillips, 1985; DiMichele and Phillips, 1994). This coal appears above the first red beds with associated conglomerates at 74.8-77.7 m, suggesting this peat mire was part of the alluvial plain facies (during a poorly-drained interval following the well-drained, red-bedded interval).

b) **Lepidodendraceae association II**

This association is found in several horizons, always in close association with coals; siliciclastics underlying and overlying the thick coal at 47.8-49 m, coaly
shales between 59.03-60.12 m and from a 0.5 m clastic-rich coal at 142.95 m. These assemblages have consistently high *Lycospora* (17.5-37.5%) and are typically co-dominated by miospores from one or more other plant groups; cordaites (17.5-37.5%), sphenophytes (7-30.5%) or ferns (6.5-16.5%). On two of the dendrograms (Figure 38a,c) this association plots some distance away from Lepidodendraceae association I, despite both assemblages having similarly (relatively) high levels of *Lycospora*. This is due to the co-dominance of cordaite pollen within this association, which is causing these assemblages to plot close to other cordaite-rich assemblages in cluster analysis. Cordaites were traditionally thought to be sourced from extra-basinal or ‘upland’ areas, their monosaccate pollen being wind-blown into lowland basin such as Bristol. However, it is now known that these plants grew in a variety of habitats within fluvial systems, including clastic swamps and peat-forming mires.

This association is interpreted are representing clastic swamps, with a diverse vegetation of Lepidodendraceae, cordaites, sphenophytes and ferns. These swamps were associated with short lived peat mires, or in close proximity to larger mires, as indicated by this association also appearing in coaly shales/clastic-rich thin coals.

**Sub-arborescent lycopsid association**

This association is found in a 0.25 m thick coal, at 110.64 m, sourced from National Coal Board material. This assemblage is dominated by miospores derived from *Omphalophloios*-type sub-arborescent lycopsids (36.5%), with representation of a wide range of ‘Densospore Group’ taxa; *Cingulizonates* (3.5%), *Cristatisporites* (25.5%), *Densosporites* (6.5%) and *Radiizonates* (1%). Subordinate plant groups are represented by tree fern (25%) and sphenophyte (12.5%) miospores.

High concentrations of sub-arborescent lycopsids are often interpreted as indicating ombrogenous mires, where low nutrients often resulted in this type stunted vegetation (Smith, 1962; Smith and Butterworth, 1967; Greb et al., 2006). As ombrogenous mires
typically form at the climax of long-term peat accumulation, assemblages rich in sub-
arborescent lycopsid miospores are usually associated with the upper portions of thick
(metre-scale) coal seams. This has been demonstrated recently by Jasper et al. (2010a; 2010b), who also found these assemblages also occur in association with layers of
increased clastic material within the coal. ‘Densospore Group’-rich assemblages have
also been recovered from thin coals which contain interbedded clastic layers, which are
not thought to have developed into ombrogenous mires (Strehlau, 1990; Opluštil et al.,
1999).

Given the thin nature (0.25 m) of this coal, it seems unlikely that this assemblage can be
interpreted as an ombrogenous mire. As many of the thinner coals recorded on the
borehole log have high levels of interleaved clastic material, it seems likely to interpret
this assemblage as being derived from a similar facies. This assemblage is therefore
interpreted as representing a nutrient-poor peat mire, with high levels of clastic input,
dominated by Omphalophloios-type sub-arborescent lycopsid. It is also possible that this
level of the Winterbourne Formation was still part of a coastal plain facies, as
Omphalophloios-type sub-arborescent lycopsid have also found in association with
coastal and brackish environments (see below).

**Sigillarian- sub-arborescent lycopsid association**

This association is found in the lowermost three clastic samples. The palynoflora is
dominated by miospores derived from Sigillariaeaceae (24.5-28.5%), with subordinate
Omphalophloios-type sub-arborescent lycopsid miospores (15-19.5%) and cordaite
pollen (17-28.5%). The sub-arborescent lycopsid miospores are derived from a wide
range of ‘Densospore Group’ genera; Cingulizonates (1-1.5%), Cristatisporites (12.5-
17%), Densosporites (1-2%) and Radiizonates (0-0.5%). Subordinate members of the
palynoflora can be linked to sphenophytes (8.5-10.5%) and fern (7.5-14%). The high
levels of Omphalophloios-type sub-arborescent lycopsid miospores differentiate this
assemblage from other Sigillariaceae-rich assemblages.
These assemblages reflect coastal plain clastic swamps dominated by Sigillariaceae and *Omphalophloios*-type sub-arborescent lycopsid. These assemblages clearly had some marine influence, due to the associated scolecodonts and other marine fauna within all three samples. Similarly, Densospore-producing sub-arborescent lycopsids have also previously been linked with coastal brackish conditions, as well as salt-marsh type habitats (Eble and Grady, 1990; Wagner et al., 2003).

**Sigillarian – fern/tree fern association**

This association was recovered from four clastic samples, from; 128.73 m, 104.70 m, 104.57 m, 64.35 m. These assemblages feature the highest portions of Sigillariaceae miospores (36-45%). Subordinate miospores types are a mixture of cordaite pollen (11.5-24.5%), and fern (0.5-24.5%), tree fern (3-9%) and/or sphenophyte miospores (5-14%).

This assemblage is interpreted as a clastic swamp dominated by Sigillariaceae, with cordaite, ferns, tree ferns and/or sphenophytes as subordinate components. As all three of these plant groups were better adapted to more well-drained areas of swamp, this assemblage likely represents the more well-drained areas of clastic swamp.

**Fern/tree fern-herbaceous lycopsid association**

This association occurs in a clastic sample from 39.17 m. This assemblage is dominated by tree fern (24.5%) and fern (25%) miospores, with subordinate cordaite pollen (15%) and sphenophyte (14.5%) and herbaceous lycopsid (*Cirratriradites*; 14.5%) miospores. Lepidodendraceae miospores form 6% of the palynoflora.

High concentrations of *Cirratriradites* (herbaceous lycopsid) and *Laevigatosporites* (>35 μm; sphenophyte) in peat mires is typical of “Transition” and “Incursion” phases of Smith (1962). The “Transition Phase” occurs as topogenous mire assemblages (Lepidodendraceae-dominated) are replaced with ombrogenous mire assemblages (sub-arborescent lycopsid and fern dominated), as groundwater levels fall. The “Incursion Phase” occurs in mires where a subsequent influx of freshwater/rise in groundwater
level causes an ombrogenous mire assemblages to be replaced, once again, by Lepidodendraceae-dominated topogenous mire assemblages. This generally leads to an inverse relationship between herbaceous miospores and those derived from Lepidodendraceae (Smith, 1962; Kosanke, 1973; Kosanke, 1988a; Kosanke, 1988b; Opluštil et al., 1999). This suggests that herbaceous lycopsids existed in transitional environments, where larger lycopsids were unable to colonise. Alternatively the apparent increase in abundance of herbaceous lycopsids in these settings may simply be due to a lack of input from the larger lycopsids, which are known to have produced abundant miospores, which typically ‘drowned out’ input from other plant groups.

This association is interpreted as a tree fern and fern dominated clastic swamp within an alluvial plain setting. This area of the plain was possibly moderately- to well-drained, prohibiting colonisation by arborescent lycopsids and allowing ecological niches to be filled by other vegetation types.

**Cordaite – tree fern association**

This association was recovered from two coals near the top of the Winterbourne Formation, at 32.61 m and 12.01 m. The sample at 32.61 m, taken from a thin (<5 cm) coal, lies just below the level where red clastic intervals become more persistent and frequent. The sample at 12.01 m was derived from a 0.56 m coal within this red clastic-dominated interval, and immediately underlies a series of purple and red mudstones. Both samples feature high levels of cordaite pollen (37.5-41%) and tree fern miospores (23-24.5%). Lepidodendraceae miospores are comparatively rare, representing 7.6% of the palynoflora from the thin seam at 32.61 m and being absent in the seam at 12.01 m. The assemblage from 32.61 m also features quite high proportions of herbaceous lycopsid miospores (3.5%).

This assemblage is interpreted as a peat mire within a well-drained alluvial plain with high levels of cordaites and tree ferns. Tree ferns likely inhabited ecological niches left vacant by the arborescent lycopsids, which appear to be comparatively scarce in these assemblages.
Cordaite associations
These assemblages feature the highest levels (>40%) of the cordaite pollen, *Florinites*. There are two distinct associations within this group:

Cordaite association I

The association is found in several clastic samples, which always occur a few metres above a coal seam; 136.47 m, 125.50 m, 58.62 m and 57.15 m. Cordaite pollen represent most of the palynoflora (44-55.5%), with subordinate Sigillariaceae (10-17.5%), sphenophyte (9-13%), fern (5.5-9.5%) and tree fern (5.5-8%) miospores. Lepidodendraceae miospores make up on 1-7.5% of the palynoflora. The sample at 125.50 m also contains the highest abundance of medullosalean pteridosperm pre-pollen recorded from the Winterbourne Formation (11%).

This association is interpreted as representing a vegetational assemblage of cordaites, Sigillariaceae and sphenophytes growing in and around clastic swamps. Medullosalean pteridosperms may also be present in localised thickets.

Cordaite association II

This association is found in clastic samples from 94.34 m, 87 m and 35.92 m. This association is vastly dominated by cordaite pollen (56-71%), to an even greater extent than cordaite association I, with subordinate representation of fern (4-25%), tree fern (0.5-6.5%) or sphenophyte miospores (5-11.5%). Lepidodendraceae miospores make up <3% of the total palynoflora. The sample from 94.34 m features the highest levels of the non-cordaite monosaccate gymnosperm pollen (*Vestigisporites*; 12.5%).

Like cordaite association I, this palynoflora represents a clastic swamp vegetational assemblage that is characterised by high levels of cordaites. Ferns, tree ferns or sphenophytes were also present as subordinate components.
Figure 39 – Detrended correspondence analysis (DCA) plot of semi-quantitative palynomorph generic counts from the Winterbourne Formation of the Harry Stoke B borehole. Eigenvalues: 0.299 axis 1, 0.1958 axis 2 and 0.09828 axis 3.
Figure 40 – Ternary diagrams of illustrating vegetation relationships within the Winterbourne Formation between selected growth habits and plant groups; a) vegetation type, b) vegetation growth habit, c) lycopsid growth habit and d) arborescent vegetation type. All data derived from generic level palynomorph semi-quantitative counts.

Other key features of the Winterbourne Formation which can be interpreted from Figure 37 to Figure 40:

1) The thinner coals seem to represent mixed fern-lycopsid-sphenophyte vegetation, whereas the thick coal (47.8-49 m depth) is much more heavily dominated by
Lepidodendraceae lycopsids. This is the opposite of what has been recorded in the Bolsovian coals from Dobrudzha Coalfield (Makedonka Formation), where thinner coals were observed to have higher proportions of Lepidodendraceae lycopsids, and thicker coals were dominated by a mixed fern and lycopsid vegetation (Dimitrova and Cleal, 2007). This difference in vegetational succession between these two contemporaneous successions of coal measures may be due to two factors; a) the geographically distant and tectonically isolated nature of these two basins, b) the slightly higher elevation in Dobrudzha at the time, and/or c) differing depositional facies/substrate types.

2) Cordaite pollen is present in all samples, in both clastic and coal settings (typically 10-40% of palynoflora; >50% in five samples). The high concentration of pollen corroborates the growing body of evidence suggesting these plants were not purely restricted to extra-basinal areas, and were significant components of the vegetation in at least some lowland depositional settings.

3) Axis 1 of the DCA (Figure 39) gives the “Densopore Group” (*Cingulizonates*, *Cristatisporites*, *Densosporites* and *Radiizonates*) a high weighing, along with some specific tree fern miospores (*Laevigatosporites* <35 µm, *Torispora* and *Reticulatisporites*). Taxa given a low weighting are *Columinisporites* (sphenophyll), *Plicatisporites* (conifer), *Triquitrites* (tree fern), *Camptotrilites* (fern) and *Discernisporites* (unknown affinity).

4) Axis 2 of the DCA gives the highest weightings to an assortment of gymnosperm pollen (*Vestigisporites*, *Cycadopites*, *Alisporites*, *Illinites* and *Plicatisporites*), and low weighting to *Lycospora* (Lepidodendraceae lycopsid). In between these two end members, lie assemblages characterised by a mixed palynoflora derived from Sigillariaceae, tree ferns and ferns. This likely relates differing ecologies that are driven by drainage/substrate moisture gradients, from more waterlogged (Lepidodendraceae lycopsid assemblages) through to well-drained settings (gymnosperm dominated)
5) Axis 3 of the DCA gives the highest weightings to several member of the ‘Densospore Group’ (*Cingulizonates, Cristatissporites* and *Radiizonates*), as well as fern (*Dictyotriletes*), tree fern (*Savitrisporites*), sub-arborescent lycopsid miospores (*Chaloneria*-type; *Endosporites*), and *Alatisporites* and *Spackmanites*. Low weightings were assigned to sphenophyll miospores (*Columinisporites* and *Pteroretis*) and gymnosperm pollen (*Cycadopites* and *Illinites*). There may also be a slight stratigraphical gradient, with assemblages from lower in the Winterbourne Formation generally having higher weighing than those from further up the sequence.

6) The Winterbourne Formation assemblages are strongly influenced by substrate type and fluctuations in drainage, resulting in a complex series of vegetational associations (Figure 40a). Miospores attributed to arborescent plants are the most abundant in the Winterbourne Formation, representing >70% of the palynoflora (Figure 40b). This is almost certainly partially a result of the greater dispersal potential inherent with an arborescent habit. It is also logical that as arborescent forms are larger than herbaceous/sub-arborescent forms, they would be capable of generating more miospores.

7) Miospores derived from arborescent lycopsids are typically the most abundant lycopsid miospores observed in these assemblages (Figure 40c), which is almost certainly partially related to the high level of production of this plant group, as well as the greater dispersal potential of arborescent forms. However, in most assemblages the majority of palynomorphs attributed to arborescent groups are derived from non-lycopsid arborescent plants (i.e cordaites, tree ferns and sphenophytes) (Figure 40d).
3.4.2 Vegetational assemblages and successions of the Warwickshire Group

3.4.2.1 Dominance-diversity patterns in the Warwickshire Group

Dominance-diversity patterns within the palynofloras of the Pennant Sandstone and Grovesend formations were also studied. Semi-quantitative palynomorph generic counts were used for this investigation, and interpreted using the same parent plant affinities listed in Table 6. Winterbourne Formation is discussed, in detail, in the previous section (3.4.1 Statistical investigation of the vegetational succession from Harry Stoke B borehole (Winterbourne Formation)) this section will deal with the Pennant Sandstone and Grovesend formations.

Downend Member (Pennant Sandstone Formation)

a) Coalpit Heath Basin

Grove Cottage provided the only Downend Member samples from this basin. The siltstones, interpreted as relating to channel abandonment facies, are dominated by cordaite pollen (23.5-28%), with subordinate Sigillariaceae (16.5-19%), fern (10-11.5%) and sphenophyte miospores (14-14.5%). Sub-arborescent lycopsids also represent 10-12% of the palynoflora (mainly Omphalophloios-type). A small, lenticular coal at the same locality is dominated by Lepidodendraceae miospores (50%), with high levels of fern (21%) and sphenophyte miospores (16%). Cordaite pollen represents only 3% of the assemblage. This coal is interpreted as being deposited in a localised area of peat accumulation, associated with a point bar-type setting. Alternatively, given the geometry of this coal bed and the sedimentology of the surrounding exposure it is possible this coal is allochtonous and represents a dislodged peat mat which has come to rest within this point bar.
It can be inferred that the siltstone assemblage was derived from plants colonising the abandoned channel in a clastic swamp, as well as from the surrounding levee/channel margin areas. Vegetation features typical riparian groups (cordaites, *Sigillaria*, ferns and sphenophytes). The coal is interesting, as it presents a clearly different vegetational signal; Lepidodendraceae with ferns and sphenophytes, but low input from cordaites. Given the nature of this coal (<5 cm thick, ~1 m wide and lenticular), the most logical interpretation is that this localised peat accumulated nearby to Lepidodendraceae, ferns and sphenophytes within a point bar-type setting. High levels of Lepidodendraceae may have been sourced from an adjacent peat mire or clastic swamp. It is possible, as previously mentioned, that this coal may represent a dislodge peat mat from a distal setting.

b) **Southern limb of the Kingwood Anticline**
The coal recovered from the A4174 at Stonehill features an assemblage vastly dominated by cordaite pollen (72.5%), with subordinate sphenophyte miospores (11%). Arborescent lycopsid miospores are low in abundance (Sigillariaceae 6.5%; Lepidodendraceae 5.5%). This is an exceptionally high abundance of cordaite pollen for a moderately thick coal seam, and suggests that cordaites were abundant on the margins of this peat mire as well as possibly within the mire. What is interesting is the lack of typical peat mire flora such a Lepidodendraceae. The dominance of cordaites and sphenophytes may be explained by frequent disturbances of the mire substrate, as indicated by frequent interleaved clastic-rich layers within the coal, which may have prohibited a more ‘normal’ vegetational succession.

The assemblage recovered from abandoned channels in Bickley Wood are very similar to those from the Grove Cottage siltstones; cordaite pollen is abundant (29%), with subordinate Sigillariaceae (17.5%), fern (11.5%), sphenophyte (11.5%) and 12% *Omphalophloios*-type sub-arborescent lycopsid miospores.
Mangotsfield and Salridge Coal (Pennant Sandstone Formation)

a) Coalpit Heath Basin (Mangotsfield coals)

The Mangotsfield Coal sample is dominated by sphenophyte miospores (30%) and cordaite pollen (27.5%), with subordinate Lepidodendraceae (16%) and fern (8%) miospores. It is unusual for a Westphalian age coal to be dominated by sphenophytes and cordaites, as these taxa are more typical of clastic substrates. Cordaite-dominated coals are more typical of Stephanian or Permian. It is possible that this coal featured interleaved clastic beds, indicative of disturbed environments, which would account for this atypical vegetational assemblage. A similar assemblage was recovered from a clastic-rich coal from the Downend Member at Stonehill. Unfortunately, no exposure of the Mangotsfield coals are available to corroborate this hypothesis.

b) Southern limb of the Kingwood Anticline (Salridge Coal)

Three samples obtained from the 0.85 m Salridge Coal, although none yielded miospores in sufficient quantities to allow semi-quantitative counting.

The 7.3 m seat earth below the Salridge Coal produced only one specimen that was deemed to have an assemblage with suitable preservation for semi-quantitative counts. This siltstone was sampled ~1.2 m below the first thin coal in the sequence of minor coals that underlie the Salridge Coal. This siltstone palynoflora features highly abundant Lepidodendraceae miospores (88%), with subordinate sphenophyte (5.5%) and fern miospores (4%). Cordaite pollen represents only 1% of the palynoflora. Thin coals from ~2.3 m below the Salridge Coal are dominated by Lepidodendraceae (62.5-77.5%) miospores, with subordinate sphenophyte (10-16.5%), cordaite (6-8.5%) tree fern (0.5-13.5%) and fern (2-11%) palynomorphs.

Thin coals and associated seat earth underlying the Salridge Coal feature palynoflora indicative of high levels of Lepidodendraceae with sphenophytes, tree ferns and cordaites. The Mangotsfield Coal assemblage can be interpreted as containing a palynoflora indicative of better drained conditions (sphenophytes and cordaites) than the Salridge Coal in the south (Lepidodendraceae-dominated).
Mangotsfield Member (Pennant Sandstone Formation)

a) Coalpit Heath Basin

The siltstone-filled abandoned channels from Winterbourne Down have assemblages dominated by Sigillariaceae miospores (15.5-35%), with subordinate cordaite (13-26.5%), tree fern (10.5-12%), fern (7-11.5%) or sphenophyte palynomorphs (8.5-16.5%). All these plant groups are well-adapted for clastic substrates, particularly those fluctuating water tables. Thymospora (tree fern) miospores start to appear in semi-quantitative counts (1.5-3.5%). Sub-arborescent lycopsid miospores, mainly Omphalophloios-type, are also common (7.5-17.5%). These vegetational group patterns are broadly comparable with those from similar abandoned channel facies of the underlying Downend Member.

The coal lens in the garden of 65 The Dingle contains a drastically different assemblage to the previously discussed clastics, despite occupying a similar abandoned channel setting and occurring in close geographical area and stratigraphical horizon. Tree fern miospores make up most of the palynoflora (29.5-31.5%), with subordinate sphenophyte (20.5-23%) and fern miospores (17.5-20.5%) and cordaite pollen (6.5-10.5%). Thymospora only represents <0.5% of palynoflora in one sample, and is absent from the other coal samples.

The clastic-filled abandoned channel facies of the Mangotsfield Member, like the Downend Member, continue to be colonised by Sigillaria, cordaites, ferns, tree ferns and sphenophytes; the palynomorphs being derived from plants colonising clastic swamps within the channel, as well as from the surrounding levee/channel margin areas. Thymospora begin to appear in semi-quantitative counts in the Mangotsfield Member clastic environments but continue to remain very rare in peat-forming environments. Where peat-generating environments became establish in these settings, the vegetation was dominated by tree ferns with subordinate sphenophytes and ferns.
b) **Southern limb of the Kingwood Anticline**

No Mangotsfield Member assemblages were obtained from this area due to a lack of exposure.

**Farrington Member (Grovesend Formation)**

a) **Coalpit Heath Basin – Coalpit Heath collieries**

The High Coal, the lowermost of the Farrington Member coals in this area, was sampled from a temporary exposure in the basement of the Old Vicarage. This partial exposure of the High Coal likely represents the upper parting of the coal seam, corresponding with the Hollybush Coal of Parkfield. These 3 samples are co-dominated by tree fern and sphenophyte miospores. The proportion of tree fern miospores decreases from 63.5% of the total palynoflora at the base of the exposure, to 42.5% at the top; fern miospores also decrease from 16% at the base of the coal to 9.5% at the top. There is a corresponding increase in sphenophyte miospores (from 14.5 to 39.5%), and slight increase in Lepidodendraceae (from 0 to 5.5%) miospores between the base and top of the exposure. This is the first horizon where tree fern miospores make up >50% of the palynoflora.

The uppermost Farrington Member coal, the Hard Coal, and underlying siltstones were sampled from the Westerleigh railway cutting. The underlying siltstone features a palynoflora co-dominated by Sigillariaceae (29.5%) and sphenophyte (29%) miospores, with subordinate cordaite pollen (13%) and tree fern miospores (7.5%). This association is typical of clastic swamps. The Hard Coal is dominated by *Omphalophloios*-type subarborescent lycopsid miospores (54.5%), with subordinate sphenophyte (21%) and Lepidodendraceae miospores (11%). The Hard Coal is a thick economic coal, therefore representing a well-establish and laterally continuous mire community. It is possible that these coal fragments were therefore sourced from an ombrogenous mire community, from the upper portions of the coal seam. Unfortunately these samples were collected from ex situ material, so this hypothesis cannot be tested.
b) **Coalpit Heath Basin – Parkfield collieries**

A collection of the 4 Parkfield coals was collected from temporary exposures and dislodged material along the A4174 at Shortwood. For the purposes of this section, the geographically close Parkfield and Shortwood successions will be considered as a unified data set to enable comparison with Coalpit Heath further to the north.

The lowest coal, the Great Coal, contains assemblages vastly dominated by tree fern miospores (61%), with *Thymospora* representing 7.5% of the palynoflora. Subordinate miospores are derived from sphenophyte (17.5%) and Lepidodendraceae (9%). Cordaite pollen only represents 2% of the assemblage.

The roof of this coal, sampled from palaeobotanical museum specimens, is dominated by sphenophyte miospores (40%), with subordinate Lepidodendraceae (22.5%), sphenophyll (13.5%), cordaite (10%) and tree fern palynomorphs (6%). This illustrates a sphenophyte-dominated clastic swamp; these plants favoured the unstable and clastic substrates fringing the peat mires (Pfefferkorn *et al.*, 2001).

The Hollybush Coal is co-dominated by Lepidodendraceae (40%) and tree fern miospores (30%, 6.5% *Thymospora*), with subordinate sphenophyte (17%). The assemblages from the coal in the basement of the Old Vicarage are dissimilar, and are co-dominated by tree fern and sphenophyte miospores with little Lepidodendraceae input. A similar relationship was noted between the Salridge Coal (south) and Mangotsfield coals (north), with the southern assemblages having high levels of Lepidodendraceae and northern assemblages featuring assemblages indicative of better drained conditions.

The Top Coal is dominated by tree fern (33%) with subordinate fern (22.5%), sphenophyte (16%), sphenophyll (11.5) and Lepidodendraceae (10.5%). The Hard Coal is also dominated by tree ferns (40%) with subordinate sphenophytes (27.5%), but features cordaite pollen (11.5%) instead of sphenophyll miospores. This coal also has similar levels of Lepidodendraceae miospores (9%). The Hard Coal roof shale is
dominated by Sigillariaceae miospores (35.5%) and cordaite pollen (27%). Tree fern (6.5%), sphenophyte (7.5%), sub-arborescent lycopsid (7.5%), Lepidodendraceae miospores (7.5%) and fern (7%) miospores are also present as subordinate components.

In conclusion, most peat generating environments feature palynofloras indicative of high levels of tree ferns with subordinate sphenophytes. Roof shale assemblages are more variable in composition, with dominance of sphenophytes, cordaites and *Sigillaria* instead of tree ferns. The Parkfield Hollybush Coal features a different palynofloras to the other Farrington Member coals, being Lepidodendraceae-dominated. The equivalent coal from the Coalpit Heath basin (Old Vicarage basement) features a tree fern-dominated assemblage, which is comparable to the other Farrington Member coals. The different assemblage from the Parkfield Hollybush Coal could be sourced from a localised area of differing vegetation, possibly due to subtle differences in drainage or clastic input, which enabled colonisation of more Lepidodendraceae instead of the typical Farrington Member tree fern and sphenophyte association. A similar phenomenon was described between the Salridge Coal and its northern equivalent, the Mangotsfield Coal. Assemblages from this stratigraphically earlier coal are also Lepidodendraceae-rich in the south, and also feature a palynoflora seemingly derived from plants adapted to thrive in better drained conditions dominating the northern areas of the mire.

c) **Southern limb of the Kingwood Anticline**

Siltstones from above and below the Trench Coal were obtained from the Brislington School boreholes. This coal is the second of four coals, which stratigraphically suggests it is equivalent to the Parkfield Hollybush Coal and the upper portion of the Coalpit Heath High Coal. All the assemblages feature dominance of Lepidodendraceae miospores (48.5-56.5%), with cordaite pollen (25.5-30.5%) and sphenophyte miospores (4-7.5%).

Interestingly, this is comparable with the assemblages from the Parkfield Hollybush Coal (both Lepidodendraceae-rich) but dissimilar from the tree fern and sphenophyte
assemblages from the equivalent coal at Coalpit Heath near the northern edge of the basin.

**Radstock and Publow members (Grovesend Formation)**

a) **Coalpit Heath Basin**

These members are not present in the Bristol Coalfield, either due to non-deposition or erosion.

b) **Southern limb of the Kingwood Anticline**

A clastic sample from the uppermost Radstock Formation of the Hursley Hill Borehole yielded an assemblage co-dominated by Sigillariaceae (32%), and sphenophyte miospores (25.5%) and cordaite pollen (28%).

Two more clastic samples, from above and below a coal according to borehole records, were taken from the middle of the Publow Member. The sample from below the coal is dominated by Lepidodendraceae miospores (72.5%), with subordinate cordaite pollen (13%). Sub-arborescent lycopsid miospores, from *Chaloneria*-type plants, make up 9.5% of the palynoflora. The sample from above the same coal is dominated by cordaite pollen (60%) with subordinate Sigillariaceae miospores (22.5%). The Publow Member is dated as Cantabrian, using macrofloral biozonation (Pendleton *et al.*, 2012).
Figure 41 – Graphical representation of dominance-diversity patterns for the Pennant Sandstone Formation of the Coalpit Heath Basin, and Grovesend Formation from the Coalpit Heath collieries. For the Grovesend Formation from the Parkfield collieries, see Figure 42. Data derived from semi-quantitative palynomorph generic counts. Locality number key and lithological key is reproduced in Figure 42.
Figure 42 - Graphical representation of dominance-diversity patterns for the Grovesend Formation from the Parkfield collieries. Data derived from semi-quantitative palynomorph generic counts.

Key for dominance-diversity plots:

**Lithostratigraphy and sampling**
- red measures
- mainly grey mudstones
- mainly sandstones
- coal seam
- M-M-marine band
- WF Winterbourne Formation
- FM Farrington Member

**Localities**
1. Harry Stoke B borehole
2. Coombe Brooke
3. Staple Hill Drainway
4. Grove Cottage
5. Church Lane Colliery
6. Red Pool
7. Frome Bank Gardens
8. Winterbourne Down railway cutting
9. Dingle leaf bed
10. 65 The Dingle
11. Huckford Quarry
12. Farrington Member
13. Golden Valley
14. A4174 at Stonehill
15. Bickley Wood A
16. Bickley Wood B
17. Salside Vein near Keynham
18. Brislington 3 borehole
19. Brislington 1 borehole
20. Hurley Hill Borehole
Figure 43 - Graphical representation of dominance-diversity patterns for the Pennant Sandstone Formation and Grovesend Formation from the southern limb of the Kingswood Anticline. Data derived from semi-quantitative palynomorph generic counts. Locality number key and lithological key is reproduced in Figure 42.
Key features of the vegetational signals of the Pennant Sandstone and Grovesend formations, and their evolution, are described below. The Winterbourne Formation is summarised at the end of the previous section (3.4.1 Statistical investigation of the vegetational succession from Harry Stoke B borehole (Winterbourne Formation)).

1. Siltstone assemblages from the Downend Member are derived from plants colonising the abandoned channel in clastic swamps, as well as from the surrounding levee/channel margin areas. Vegetation features typical riparian groups (cordaites, *Sigillaria*, ferns and sphenophytes). *Omphalophloios*-type sub-arborescent lycopsids are also a typical component of the vegetation, but quantitatively less significant in the palynofloras.

2. Some of these Downend Member abandoned channels hosted peat-generating environments, which were colonised by Lepidodendraceae with tree ferns and sphenophytes.

3. Palynofloras recovered from a moderately thick (~0.5 m) Downend Member coal are overwhelmingly dominated by cordaite pollen; this coal also features pervasive interleaved clastic beds, which suggests that high levels of cordaites inhabited peat-generating environments where disturbances were frequent, and typical Lepidodendraceae mires could not develop.

4. Clastic substrates within Mangotsfield Member abandoned channels continue to feature similar vegetation to those in the Downend Member; abundant *Sigillaria*, cordaites, ferns and sphenophytes with *Omphalophloios*-type sub-arborescent lycopsid also typically represented in the palynoflora. *Thymospora*-producing marattialean tree ferns begin to rise in abundance within Mangotsfield Member clastic environments, and a there is a general increase in total tree fern miospores in these settings.
5. A peat-generating environment within a Mangotsfield Member abandoned channel hosted tree ferns, sphenophytes, ferns and cordaites. This environment featured a constant supply of clastics, with fluctuations in supply likely seasonality-driven, which would have prevented lycopsid colonisation.

6. Most peat-generating environments from the Farrington Member feature high levels of tree ferns and sphenophytes. This is likely due to these plants occupying niches left vacant by Lepidodendraceae and other lycopsids, as they declined in abundance during the Asturian. Roof shale assemblages are more variable in composition, with dominance of sphenophytes, cordaites and **Sigillaria** instead of tree ferns.

7. Clastic environments from the Radstock and Publow members also typically feature **Sigillaria** and cordaite vegetation, with sphenophytes making a significant contribution to one palynological assemblage.

8. A clastic sample taken from below a coal within the Publow Member illustrates that at least localised pockets of Lepidodendraceae-dominated flora occurred into the early Cantabrian of Bristol. Dimitrova *et al*. (2005) recorded high levels of lycopsid miospores (55%) in the Llanwit No. 2 Coal, which is also early Cantabrian in age (Cleal, 2007).

9. Two basin-scale peat-generating environments highlight a difference in vegetational successions between northern and southern areas of the basin. This was observed in the Mangotsfield Coal and its southern equivalent, the Salridge Coal, which represents the division between the Downend and Mangotsfield members. This gradient was also seen between the Coalpit Heath High Coal (north) and the Parkfield Hollybush Coal, through to the clastics closely associated with the equivalent Trench Coal in the southern limb of the Kingswood Anticline. At both of these horizons, there is a change from more vegetation indicative of well-drained environments (tree fern and sphenophyte
coals) at the northern side of the basin, to assemblages indicative of poorer drainage (Lepidodendraceae-dominated) towards the south. This drainage disparity is also supported by the lithostratigraphy; red beds occur at several stratigraphical positions in the Coalpit Heath area but no red beds have been recorded from the southern limb of the Kingswood Anticline. This can also be extrapolated southwards into Somerset, where there is also a lack of reports of red beds outside of the Barren Red Member. There were several areas of elevated terrain around the northern edge of the basin; Usk Anticline, Lower Severn Axis, Malvern Axis and Wales-Brabant High. These pre-existing structures shaped deposition of the Bristol coal measures, demarking the northern-most limit of the Warwickshire Group sediments. It seems logical that fluctuations in drainage would be more pronounced at these northern basin margins, rather than in the thicker successions towards the south, especially if these structures were periodically rejuvenated and uplifted during the on-going Variscan compression.

10. Marattialeans appear in semi-quantitative counts from clastic environments (Grove Cottage, upper Downend Member) stratigraphically lower than in peat generating environments (65 The Dingle, middle Mangotsfield Member). This may suggest that this group originated in clastic environments, and only later moved into peat generating environments to occupy niches left vacant as lycopsids began to decline. A clastic origin for marattialeans has also been proposed by Cleal et al. (2007)

3.4.2.2 Extinction, origination and diversity throughout the Warwickshire Group

Extinction-origination and diversity curves provide another method of visualising the palaeoenvironments of the Bristol Coalfield. Palynomorph extinction, origination and diversity clearly reflect changes in vegetation. Key features of these curves from the Coalpit Heath Basin (Figure 44 and Figure 45) are discussed below for each
stratigraphical unit. It should be kept in mind that ‘extinction’ and ‘origination’ refers to the last stratigraphical occurrence and first stratigraphical occurrence of a species within the Bristol stratigraphy only.

**Winterbourne Formation**
Species diversity gradually increases over the lower half of the Winterbourne Formation (Figure 45), as vegetation colonised the Bristol area as the sea regressed (due to uplift and/or eustatic sea level fall). Peak origination rates in the Winterbourne Formation peat-generating environments (between 110.6 m and 60 m borehole depth; 20 and 23 new species, respectively) likely coincides with more widespread peat mires beginning to develop as coastal plains were replaced by alluvial plains (Figure 44). Origination rates in these 2 coals exceed the 95% confidence interval for the null model, suggesting these rates are indeed significantly higher than would be expected. These high origination rates leads to the highest species diversity within the Winterbourne Formation coals (86 species), in the assemblage from ~60 m depth. Total species diversity is reduced in the uppermost ~30 m of the Winterbourne Formation, where persistent red beds become the dominant lithology. The corresponding peak in extinction rate (10 species in the coal at 60 m depth) may interpreted in two ways; a) vegetation that inhabited the peat-generating areas of the coastal plains were not suitably adapted to these new depositional environments and were replaced by new vegetation, and b) certain plant groups declined as the alluvial plain began to experience periods of enhanced drainage (producing persistent red beds from ~30 m).

Clastic environments responded differently to the changing environments of the Winterbourne Formation, with origination rates peaking at ~120 m borehole depth and then generally declining throughout the rest of the Winterbourne Formation. Extinction rates generally fall within the 95% confidence intervals of the model, but are at the lowermost limit of the model which leads to the tentative interpretation of low extinction rates over most of the Winterbourne Formation clastic environments. Extinction rates can also be tentatively inferred to slightly increase within the uppermost ~45 m. The overall effect is that species diversity in clastics environments rises
throughout the lower Winterbourne Formation, with peak diversity occurring at around ~45 m borehole depth (112 species) before dropping (106 species). This represents the highest diversity assemblage within clastic environments of the entire Warwickshire Group. This peak in species diversity occurs ~15 m lower in peat-forming environments, and the corresponding sharp decrease in peat-mire species diversity occurs contemporaneously with the peak diversity within clastic environments. This suggests that the periods of increased drainage within the later stages of the Winterbourne Formation alluvial plain caused diversity loss within the peat mires slightly earlier than in clastic environments.

**Downend Member and Mangotsfield coals**

Origination and extinction rates fall below the lower 95% confidence interval for the null model in coals, indicating generally low by constant levels of turnover in peat-generating settings. Within clastic environments origination and extinction rates lay within the 95% confidence levels of the null model, suggesting level comparable to a model of constant background turnover. Correspondingly, total species diversity remains constant throughout both clastic (104 species) and peat-generating environments (80-82 species) during deposition of the Downend Member (Figure 45). However, only there are only 2 data points over the ~420 m Downend Member so any inferences made are tenuous.

**Mangotsfield Member**

Within a peat-generating environment within the lower half of the Mangotsfield, around 120 m above the Mangotsfield coals, a significant change in palynomorph composition is identifiable. Peaks in both extinction rates (42 species) and origination rates (21 species) occur at this horizon, with both of these values exceeding the upper limit of the 95% confidence interval of the null model. This indicates a statistically significant vegetation turnover at this horizon. This locality also contains the most diverse assemblages (103 species) observed in the Warwickshire peat-forming environments.
Within clastic environments, where there are more sample points, more detail can be seen. Origination rates remain within the 95% confidence intervals of the null model, with a subtle peak within the lower 70 m of the Mangotsfield Member (within the samples directly below the coal sample discussed above). Combined with low extinction rates within the Downend and lowermost Mangotsfield Member, peak Pennant Sandstone Formation in clastic settings diversity occurs ~40 m below the peak in peat-forming settings. This may be an artefact of sampling; only one coal was sampled compared to several clastic lenses. However, it can be seen that the extinction peak in clastic environment occurs within a narrow stratigraphical range, over ~20 m, and at a level which closely correlates to the coal lens.

Whereas the peat-generating environment experienced vegetation turnover and an increase in overall diversity, this nearby clastic environment experienced little change in diversity compared to the preceding Downend Member assemblages. This horizon, 100-120 m above the Mangotsfield Coals, marks the start of a gradual decline in species diversity in both clastic and peat-generating habitats (Figure 45). This turnover event is also discussed from a biostratigraphic angle in ‘3.3.1 Miospore biozonation of the Bristol Coalfield’, and can be seen in Figure 33, where this horizon is concluded to correspond to the SL-OP Biozone transition, which slightly predates the Bolsovian-Asturian boundary (Clayton et al., 1977). This overturn is related to a rise in abundance of tree ferns and loss of other vegetation components as substrates began to dry out in the latest Bolsovian and early Asturian. An increase in the abundance of tree fern miospores in the lower half of the Mangotsfield Member in is highlighted in ‘3.4.2.1 Dominance-diversity patterns in the Warwickshire Group’ and can be seen in Figure 41 and Figure 42.

**Farrington Member**
Species diversity within the Farrington Member is much lower, within both clastic and peat-forming environments, than the underlying Mangotsfield Member. There is a minor spike in diversity in the upper portion of the Coalpit Heath High Coal and the equivalent Parkfield Hollybush (Figure 45), which correlates with small pulse of species origination.
(Figure 44). This may be an artefact of high level of sampling within the Coalpit Heath High Coal, or be a reflection of the more diverse assemblages caused by a north-south drainage gradient (discussed in ‘3.4.2.1 Dominance-diversity patterns in the Warwickshire Group’). Origination rates within Farrington Member coals are low, below the lower limit of the 95% confidence level of the null model. Origination rates in clastics remain within the 95% confidence level of the null model, but lie towards the lower limits. Elevated extinction levels occur in the Parkfield Top and Coalpit Heath Hollybush, as well as the clastics above.
Figure 44- Extinction-origination curves for the Warwickshire Group of the Coalpit Heath Basin.
Figure 45 – Species diversity curves for the Warwickshire Group of the Coalpit Heath Basin.
4 Palynology – megaspores

Megaspore assemblages from the Warwickshire Group were recovered as part of this palynological investigation (see ‘3.1.2.2.3 Combined megaspore and miospore preparation’, for more detail on the megaspores extraction process). These were reported in Pendleton and Wellman (2012), where these Bristol assemblages were compared with the well-documented, and partly coeval, sequence from the nearby Forest of Dean. The aims of this paper were to; 1) provide the first published records of megaspore assemblages from the Bristol Coalfield, 2) produce a new megaspore biostratigraphy, 3) investigate the megaspore assemblages in a facies context, to highlight differing palaeoecological settings, and 4) make a comparison with the well-documented, and partly coeval, sequence in the nearby Forest of Dean Coalfield. This paper was based on data collected by the present author, and was assembled and predominantly written by the present author. A copy of the manuscript is included in Appendix 8.
5 Palaeobotany

During the course of this study the palaeobotany of the Bristol Coalfield was fully reviewed in a series of three papers. The first paper, Falcon-Lang et al. (2011), reviewed permineralised (calcified) plant assemblages from the Winterbourne Formation conglomerates from Staple Hill. These specimens were originally collected by Bolton in 1926, and later examined by Lillie (Lillie, 1910b) and later by Crookall (Crookall, 1927). This paper highlights: 1) a calcified cordaite-dominated assemblage, with subordinate pteridosperms and possible sigillarian lycopsids, 2) erratic growth interruptions in the woody fossil axes and 3) possible reworked caliche deposits within the conglomerate bands of the upper Winterbourne Formation. It is therefore interpreted that during the deposition of the Winterbourne Formation, the alluvial plains underwent pronounced periods of water deficit, either due to tectonically-induced water table fluctuations or seasonal subhumid tropical climate.

The permineralised fossil assemblages of the Bristol Coalfield were fully reviewed in Falcon-Lang et al. (2012), which also included new specimens which expanded on the Winterbourne Formation assemblages previously reported by Falcon-Lang et al. (2011). This paper described assemblages from ten permineralised fossil assemblages from the Pennant Sandstone of the Bristol Coalfield, as well as assemblages from the Severn and South Wales coalfields to the west. Like the assemblages from the Winterbourne Formation, the permineralised wood is found within conglomerate bands. Similarly, this large data set is also overwhelmingly dominated by cordaites (87%, n=72-77) which feature growth interruptions in their wood. The Pennant Sandstone Formation cordaites therefore also experienced periods of water deficit. These assemblages may represent flora that grew within the braided fluvial system, either growing in elevated interfluve areas with fluctuating water tables or reflecting vegetation which grew during drier climatic intervals. As the Variscan Deformation Front was only a few tens of kilometres from the south, these water-worn permineralised plant fragments could have been sourced from these upland habitats. A printed copy of these papers are included in Appendix 9 and Appendix 10.
All palaeobotanical work was originally intended to be published as a single paper. As the paper progressed, it became clear that the permineralised material would be best presented separate spin-off publication(s). The sedimentological, stratigraphical and geological information underpinning Falcon-Lang (2011;2012) was therefore provided by the present author, or re-written from early drafts of Pendleton et al. (2012). All these papers also use the Salridge Coal-Mangotsfield Coals correlation proposed in the present study. The present author also provided overviews of palynological assemblages and general input into palaeoecological interpretations within these papers, as well as much of the material from previously unreported Mangotsfield Member localities around Hambrook and Winterbourne Down reported in (2012).

Pendleton et al. (2012) reviewed the adpressed and sandstone-cast palaeobotanical record, based on a full reinvestigation of all previously collected material and integration of new collections made by the present author. This paper was predominantly written and assembled by the present author, with the exception of ‘5.2. Taxonomic notes on biostratigraphically-important taxa’ and ‘7.2. Correlation with South Wales and adjoining areas’, which was written by Chris Cleal. Chris Cleal also provided extensive support with identification of adpressed fossils, and taxonomic updating. With this taxonomically updated data set, a new system of biozonation was produced for the coalfield. This biozonation highlighted a stratigraphical gap between the Pennant Sandstone and Grovesend formation. This hiatus is interpreted as being associated with the Leonian Phase of tectonic activity which is manifested by similar hiatuses in the eastern South Wales Coalfield as well as European coalfields (Cleal, 1978; Cleal, 2007; Cleal et al., 2009; Cleal et al., 2011), and correlates with the onset of coal-bearing deposition in other coalfields in southern Britain (Cleal, 1986; Cleal, 1987; Cleal, 1997). The second aim was to consider the assemblages both in a stratigraphical and facies context to elucidate palaeoecology of the different depositional environments of the Warwickshire Group. A printed copy of this paper is included in Appendix 11. Supplementary data, in the form of taxa lists for each locality, is included within Appendix 12 of this thesis.
6 Conclusions

6.1 Biostratigraphy

1. The Warwickshire Group of the Bristol Coalfield, as demonstrated using this multidisciplinary biostratigraphic approach, is mid-Bolsovian to early Cantabrian in age.

2. The Winterbourne Formation and Downend Member feature assemblages corresponding to the SL palynological Biozone (Clayton et al., 1977; Clayton et al., in preparation) and *Laveineopteris rarinervis* megafloral Subzone (Cleal, 1991; Cleal and Thomas, 1996), indicating a mid- to late Bolsovian age for these units.

3. The transition between SL and OT palynological Biozones (Clayton et al., in preparation) occurs near the top of Pennant Sandstone Formation, over the lowermost ~120 m of the Mangotsfield Member. This closely corresponds to stratigraphical level of the first recorded *Anthraconauta tenuis* non-marine bivalves by Moore and Trueman (1937); this species is typically cited as having a first occurrence just below the base of the Asturian. This strongly suggests that the uppermost Pennant Sandstone Formation is early Asturian in age.

4. Megafloral assemblages from the Farrington Member assemblages indicate a late Asturian age (*Dicksonites plukenetii* Subzone). This highlights a stratigraphical gap between the Pennant Sandstone and Grovesend formations, encompassing the early to mid-Asturian. This hiatus is interpreted as being associated with the Leonian Phase of tectonic activity which is manifested by similar hiatuses in the eastern South Wales Coalfield as well as European coalfields, and correlates with the onset of coal-bearing deposition in other coalfields in southern Britain.
5. Cantabrian-aged megafloral assemblages (*Odontopteris cantabrica* Zone) are found in the Radstock Member, the uppermost division of the Grovesend Formation.

### 6.2 Temporal and spatial vegetational changes

1. A diverse patchwork of plant communities were highlighted by a detailed palynological palaeobotanical study.

2. Bolsovian peat mires of the Winterbourne and Pennant Sandstone formations were dominated by lepidodendrids and ferns, and were replaced by tree fern and fern mires in the late Asturian Grovesend Formation. High diversity pteridosperm, sphenophyte and fern clastic swamps fringed and infiltrated these mires.

3. Bolsovian braided fluvial systems created disturbed riparian niches that were colonised by low diversity pteridosperm-sphenophyte communities and Sigillaria-sphenophyte-cordaitalean communities. Ferns were also abundant, as indicated by palynological assemblages, but are typically not robust enough to be preserved in the macrofloral record in these depositional settings.

4. Cordaite pollen are typically abundant, and may be dominant, in both clastic and peat generating environments, indicating that these plants were important components of the vegetation within a wide range of lowland depositional environments. This adds to the growing body of evidence against this group being restricted to ‘upland’ or extra-basinal areas. It is likely that cordaites colonised peat mires which were too flood disturbed for Lepidodendraceae-type lycopsids.
5. An increase in marattialean tree fern miospores is recorded within the clastic environments from the upper Downend Member; a comparable increase is not seen in peat-generating environments until the lower Mangotsfield Member. This supports the hypothesis that this group originated in clastic environments, and only later moved into peat generating environments to occupy niches left vacant as lycopsids began to decline.
7 Acknowledgements

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8 References


9 Plates
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1. *Trihyphaecites triangulatus* Peppers 1970 (09jlp7.4 x22-3)
2. *Trihyphaecites triangulatus* Peppers 1970 (09jlp40.1ox j45-4)
3. *Leiotriletes levis* (Kosanke) Potonié and Kremp1955 (09jlp128.2 u28-1)
4. *Leiotriletes parvus* Guennel 1958 (09jlp 62.3 r30-4)
5. *Leiotriletes sphaerotriangulus* (Loose) Potonié and Kremp 1954 (09jlp 93.1 s36)
7. *Leiotriletes tumidus* Butterworth and Williams 1958 (09jlp 111.1 d52)
8. *Punctatisporites aerarius* Butterworth and Williams 1958 (09jlp 42.3 l23)
9. *Punctatisporites minutus* Kosanke 1950 (09jlp 1.4 u55)
11. *Punctatisporites obesus* (Loose) Potonié and Kremp 1955 (09jlp 17.2 154-2)
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1. *Punctatisporites cf. obesus* (Loose) Potonié and Kremp 1955 (09jlp2.2 s40)
2. *Punctatisporites punctatus* Ibrahim 1932 (09jlp 1.2 l40)
3. *Calamospora breviradiata* Kosanke 1950 (09jlp 2.2 u42)
4. *Calamospora microrugosa* Schopf *et al.* 1944 (09jlp 13.1 k50-2)
5. *Calamospora microrugosa* Schopf *et al.* 1944 (09jlp 17.5 u35-3)
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1. *Trinidulus diamphidios* Felix and Paden 1964 (09jlp 3.4 m28-2)
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3. *Elaterites triferens* Wilson 1934 (09jlp 4.1 p29-4)
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7. *Cyclogranisporites aureus* (Loose) Potonié and Kremp 1955 (09jlp 77.1 h37)
8. *Cyclogranisporites multigranus* Smith and Butterworth 1967 (09jlp 77.2 v39)
9. *Converrucosisporites armatus* (Dybová and Jachowicz) Smith and Butterworth 1967 (09jlp 68.1ox s48-1)
10. *Converrucosisporites mosacoides* (Imgrund) Potonié and Kremp 1955 (09jlp 17.3 f53-2)
11. *Converrucosisporites sp.1* (09jlp 18.5 p51-2)
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1. Verrucosisporites donarii Potonié and Kremp 1955 (09jlp125.1 m28)
2. Verrucosisporites microtuberosus (Loose) Smith and Butterworth 1967
   09jlp76.2 p24-4)
3. Verrucosisporites microverrucosus Ibrahim 1933 (09jlp76.1 q24-2)
4. Verrucosisporites sifati (Ibrahim) Smith and Butterworth 1967 (09jlp76.2 e38-2)
5. Cadiospora magna Kosanke 1950 (09jlp103.1 h37-2)
6. Cadiospora sp.1 (09jlp103.1 n37-3)
7. Lophotrilletes commissuralis (Kosanke) Potonié and Kremp 1955 (09jlp13.1 h50-2)
8. Lophotrilletes gibbosus (Ibrahim) Potonié and Kremp 1954 (09jlp18.6 p30)
9. Lophotrilletes microsaetosus (Loose) Potonié and Kremp 1955 (09jlp13.1 g50-4)
10. Lophotrilletes mosaicus Potonié and Kremp 1955 (09jlp2.4 q29)
11. Waltzispora planiangulata Sullivan 1964 (09jlp24.1 j46)
12. Waltzispora polita (Hoffmeister et al.) Smith and Butterworth 1967 (09jlp42.2 t29-1)
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1. Apiculatasporites spinulistratus (Loose) Ibrahim 1933 (09jlp107.2ox w48)
2. Apiculatisporis abditus (Loose) Potonié and Kremp 1955 (09jlp76.2 k32)
3. Apiculatisporis aculeatus (Ibrahim) Smith and Butterworth 1967 (09jlp110.1 o38-1)
4. Apiculatisporis spinososaetosus (Loose) Smith and Butterworth 1967 (09jlp13.1 t31-2)
5. Apiculatisporis spinososaetosus (Loose) Smith and Butterworth 1967 (09jlp2.4 q40-1)
6. Planisporites cf. granifer (Ibrahim) Knox 1950 (09jlp76.1 o40-3)
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8. Acanthotriletes triquetrus Smith and Butterworth 1967 (09jlp13.2 l52-4)
9. Ibrahimisporos brevispinosus Neves 1961 (09jlp2.2 j32)
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1. **Raistrickia aculeata** Kosanke 1950 (09jlp77.4 r38-2)
2. **Raistrickia fulva** Artüz 1957 (09jlp124.1ox o49-2)
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5. **Raistrickia cf. pistillata** Hacquebard 1957 (09jlp2.1 j44)
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7. **Raistrickia saetosa** (Loose) Schopf et al. 1944 (09jlp72.1 o31-3)
8. **Raistrickia cf. superba** (Ibrahim) Schopf et al. 1944 (09jlp2.1 m37)
9. **Spackmanites habibii** Ravn 1986 (09jlp2.1 u43)
10. **Sinuspores sinuatus** (Artüz) Račn 1986 (09jlp 62.3ox h42-2)
11. **Camptotriletes triangularis** Peppers 1970 (09jlp77.2 j43)
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1. **Convolutispora ampla** Hoffmeister et al., 1955 (09jlp3.1 v55-2)
2. **Convolutispora finis** Love 1960 (09jlp13.4 s43-4)
3. **Convolutispora florida** Hoffmeister et al. 1955 (09jlp48.3 ox e24)
4. **Convolutispora usitata** (Playford) Smith and Butterworth 1967 (09jlp77.2 o43-4)
5. **Convolutispora varicosa** Butterworth and Williams 1958 (09jlp77.2 v40-2)
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7. **Microreticulatisporites nobilis** (Wicher) Knox 1950 (09jlp25.3 m37-3)
8. **Microreticulatisporites punctatus** Knox 1950 (09jlp76.4 g27-3)
9. **Microreticulatisporites sulcatus** (Wilson and Kosanke) Smith and Butterworth 1967 (11jlp38.1 s37-2)
10. **Dictyotriletes bireticulatus** (Ibrahim) Smith and Butterworth 1967 (09jlp41.3 r24-2)
11. **Dictyotriletes muricatus** (Kosanke) Smith and Butterworth 1967 (09jlp76.1 t31-2)
12. **Reticulitriletes clatriformis** (Artüz) Ravn 1986 (09jlp2.4 d30)
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2. *Cordylosporites papillatus* (Naumova) Playford and Satterthwait 1985 (09jlp87.2 o41-4)
3. *Secarispites remotus* Neves 1961 (09jlp126.1 x32)
4. *Secarispites remotus* Neves 1961 (09jlp125.2 m42-3)
5. *Ahrensisporites guerickei* (Horst) Potonié and Kremp 1954 (09jlp74.3 l45-2)
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7. *Tripartites vetustus* Schemel 1950 (09jlp6.3ox r41)
8. *Triquitrites cf. additus* Wilson and Hoffmeister 1956 (09jlp77.4 o47-3)
9. *Triquitrites bransonii* Wilson and Hoffmeister 1956 (09jlp77.4 o41)
10. *Triquitrites sculptilis* (Balme) Smith and Butterworth 1967 (09jlp17.1 f29-3)
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4. *Savitrisporites majus* Bharadwaj 1957 (09jlp87.3 n28-4)
5. *Savitrisporites nux* (Butterworth and Williams) Smith and Butterworth 1967 (09jlp2.3 d30-3)
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7. cf. *Savitrisporites nux* (Butterworth and Williams) Smith and Butterworth (09jlp13.4 032) proximal oblique
8. cf. *Savitrisporites nux* (Butterworth and Williams) Smith and Butterworth (09jlp21.3 y48)
9. *Reticulatisporites reticulatus* (Ibrahim) Ibrahim 1933 (09jlp76.1 o37-2)
10. *Crassispora kosankei* (Potonié and Kremp) Smith and Butterworth 1967 (09jlpf46-3ox v42)
11. *Crassispora kosankei* (Potonié and Kremp) Smith and Butterworth 1967 (BGS2782.1 v29-2)
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8. *Cristatisporites indignabundus* (Loose) Staplin and Jansonius 1964 (09jlp125.3 j46-1)
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3. *Endosporites globiformis* (Ibrahim) Schopf et al., 1944 (09jlp60.1ox o52)
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7. *Rugospora polyptycha* Neves and Ioannides 1974 (09jlp12.4 t49)
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4. *Kraeuselisporites ornatus* (Neves) Owens *et al.* 1976 (09jlp7.4 t35-4)
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1. *Pteroretis primum* (Felix and Burbridge) McLean *et al.* 2006 (09jlp5.2 l28)
2. *Florinites florini* Imgrund 1960 (09jlp17.1 s45)
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4. *Florinites mediapudens* (Loose) Potonié and Kremp 1956 (09jlp28.3 d41-3)
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6. *Florinites pumicosus* (Ibrahim) Schopf *et al.*, 1944 (09jlp129 p51-4)
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1. *Florinites visendus* (Ibrahim) Schopf et al., 1944 (09jlp125.2 m49-4)
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4. *Cordaitina uralensis* (Luber) Samoilovich 1953 (09jlp48.1ox f40-2) trilette
5. *Cordaitina uralensis* (Luber) Samoilovich 1953 (09jlp122.1ox m42-4)
6. *Plicatipollenites cf. malabarensis* (Potonié and Sah) Foster 1975 (10jlp1.1 m45-4)
7. *Wilsonites delicatus* Kosanke 1950 (09jlp77.2 t31)
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3. *Illinites unicatus* (Kosanke) Helby 1966 (09jlp76.4 k42-2)
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6. (09jlp1.2 r44)
7. (09jlp1.2 z55)
8. (09jlp1.1 q54)
9. (09jlp1.1 y50)
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2. “*Granulate spore*” spp. (10jlp1.1oc w43-2)
3. *Lophozonotriletes* sp. 1 (10jlp1.1ox u54)
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5. *Spelaeotriletes obtusus* 10jlp1.1 n37)
6. "*Acanthomorph*" sp. 1 (09jlp7.1 w28)
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8. "*Sputnik*" sp. 1 (09jlp20.1 M54-3)
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10 Appendices
**Appendix 1- Matrix detailing all samples collected, prepared and analysed**

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<tr>
<th>Stratigraphical units</th>
<th>Description</th>
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<tbody>
<tr>
<td>WF</td>
<td>Winterbourne Formation</td>
</tr>
<tr>
<td>PSF</td>
<td>Pennant Sandstone Formation</td>
</tr>
<tr>
<td>PSF (DM)</td>
<td>Pennant Sandstone Formation (Downend Member)</td>
</tr>
<tr>
<td>PSF (DM) - PSF (MM)</td>
<td>Pennant Sandstone Formation (Downend Member-Mangotsfield Member boundary)</td>
</tr>
<tr>
<td>PSF (MM)</td>
<td>Pennant Sandstone Formation (Mangotsfield Member)</td>
</tr>
<tr>
<td>GF (FM)</td>
<td>Grovesend Formation (Farrington Member)</td>
</tr>
<tr>
<td>GF (BRM)</td>
<td>Grovesend Formation (Barren Red Member)</td>
</tr>
<tr>
<td>GF (RM)</td>
<td>Grovesend Formation (Radstock Member)</td>
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<tr>
<td>GF (PM)</td>
<td>Grovesend Formation (Publow Member)</td>
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Data key

- Semi-quantitative counts (200 specimens)
- Presence - absence data
- Barren
- Not used

Repository key

- BGS: British Geological Survey, Keyworth
- BCMAG: Bristol City Museum and Art Gallery
- BU: Bristol University
- MBB: MB Biostratigraphy Ltd., Sheffield
- NWGW: National Museum and Galleries, Wales
- USPRF: University of Sheffield Palynological Research Facility

Collector key

- JLP: Janine L. Pendleton
- CHW: Charles H. Wellman
- NC: Nick Chidlaw
- DH: David Hardwick
- LRM: Leslie R. Moore
- BGS: Borehole core material supplied by British Geological Survey
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<td>Dingle leaf bed quarry</td>
<td>East</td>
<td>Bottom, 5cm</td>
<td>PSF (MM)</td>
<td>092p69</td>
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<td>Dingle leaf bed quarry</td>
<td>West</td>
<td>Top, 85cm</td>
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<td>Dingle leaf bed quarry</td>
<td>West</td>
<td>Top, 85cm</td>
<td>PSF (MM)</td>
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<td>10</td>
<td>All The Dingle</td>
<td>Grey black coal from west side of face</td>
<td>PSF (MM)</td>
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<td>11</td>
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<td>South</td>
<td>Lowest siltstone, bottom, 5cm</td>
<td>PSF (MM)</td>
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<td>South</td>
<td>Lowest siltstone, middle, 15cm</td>
<td>PSF (MM)</td>
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<td>South</td>
<td>Lowest siltstone (south), top, 25cm</td>
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<td>North</td>
<td>Middle siltstone</td>
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<td>North west</td>
<td>Upper siltstone, bottom, 5cm</td>
<td>PSF (MM)</td>
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<td>Upper siltstone, middle, 15cm</td>
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<td>Serpentine drainage add</td>
<td>Base of accessible section of High Vein just below water level (~50cm water)</td>
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<td>High Coal</td>
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<td>40cm from base</td>
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<td>Coal lumps in scribe at 5.8 chains (211m south of bridge)</td>
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<td>A4174 cutting, Shortwood</td>
<td>Great Coal?</td>
<td>164m north of bridge, coal fragments in scribe, likely Great Coal</td>
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<td>A4174 cutting, Shortwood</td>
<td>Hollybush Coal?</td>
<td>161m, coal fragments in soil near tree, likely Holbush Coal</td>
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<td>A4174 cutting, Shortwood</td>
<td>Top Vein?</td>
<td>164m, small coal fragments in soil tip near reported location of Top Coal</td>
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<td>A4174 cutting, Shortwood</td>
<td>194m, mudstone spoil tip near reported location of Top Coal</td>
<td>GF (FM)</td>
<td>09p104</td>
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<td>12f</td>
<td>A4174 cutting, Shortwood</td>
<td>224m, siltstone below coal</td>
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<td>GF (FM)</td>
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<td>A4174 cutting, Shortwood</td>
<td>Hard Coal?</td>
<td>225m, visible coal seam near reported location of Hard Coal</td>
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<td>A4174 cutting, Shortwood</td>
<td>227m, siltstone bed</td>
<td>a few cm above siltstone with plant parts</td>
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<td>A4174 cutting, Shortwood</td>
<td>231m, siltstone beds</td>
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<td>A4174 cutting, Shortwood</td>
<td>Siltstone in scribe at 5.8 chains (161m south of bridge)</td>
<td>GF (FM)</td>
<td>09p109</td>
<td>JLP</td>
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<td>12f</td>
<td>Westleigh railway cutting</td>
<td>Grey clay, 30cm from floor</td>
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<td>GF (FM)</td>
<td>09p112</td>
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<td>Westleigh railway cutting</td>
<td>Purple clay, 150cm from floor</td>
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<td>Laminated siltstone, 215cm from floor</td>
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<td>Westleigh railway cutting</td>
<td>Purple clay, 315cm from floor</td>
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<td>Westleigh railway cutting</td>
<td>Coal clast from coarse sandstones and contorted beds, 4m above ledge</td>
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<td>Westleigh railway cutting</td>
<td>Sandy siltstone just above Hard Vein in east face of quarry</td>
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<td>10p37</td>
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<td>12f</td>
<td>Westleigh railway cutting</td>
<td>Stream, below main outcrop. Baren, not used in study</td>
<td>GF (FM)</td>
<td>11p13</td>
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<td>Stream, below main outcrop. Baren, not used in study</td>
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<td>Golden valley, Bitton</td>
<td>Ventilation shaft spoil tp. mudstones</td>
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<td>A4174, Stonehill</td>
<td>A4174 unmannped shear coal</td>
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<td>Bickei Wood A west</td>
<td>Bottom, 15cm</td>
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<td>PSF (DM)</td>
<td>09p76</td>
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<td>Bickei Wood A west</td>
<td>Middle, 40cm</td>
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<td>Bickei Wood A west</td>
<td>Top, 39cm</td>
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<td>Bottom, 22cm</td>
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<td>Bickei Wood A south</td>
<td>Middle, 95cm</td>
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<td>Top, 51cm</td>
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<td>Bickei Wood B</td>
<td>Bottom, 4cm</td>
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<td>Middle, 70cm</td>
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<td>Bickei Wood B</td>
<td>Fine grained palae siltstone clast, 1m</td>
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<td>Bickei Wood B</td>
<td>Top, 105cm</td>
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<td>PSF (DM)</td>
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<td>Salridge Vein near Keysham</td>
<td>Main mudstone, 23cm</td>
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<td>Salridge Vein near Keysham</td>
<td>Main mudstone, 2.4m</td>
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<td>Salridge Vein near Keysham</td>
<td>Main mudstone, 3.5m</td>
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<td>Salridge Vein near Keysham</td>
<td>Main mudstone, 4.4m</td>
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<td>Sainidine Vein near Keynsham</td>
<td>Main muscovite, 6.1m</td>
<td>Sainidine Vein near Keynsham</td>
<td>PSF (DM) - PSF (MM)</td>
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<td>Sainidine Vein near Keynsham</td>
<td>Main muscovite, first thin coal (2cm), 7.3m</td>
<td>Sainidine Vein near Keynsham</td>
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<td>Sainidine Vein near Keynsham</td>
<td>Main muscovite, second thin coal (1.5cm), 7.7m</td>
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<td>Sainidine Vein near Keynsham</td>
<td>Main muscovite, seat clay of second thin coal. Looks coaly when dried in lab</td>
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<td>Main muscovite, 9cm shiny coal, 7.75m</td>
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<td>First (lowest siltstone)</td>
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<td>Fourth (below main siltstone) siltstone</td>
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<td>Sainidine Vein near Keynsham in A4174 road cutting</td>
<td>Slate, 0.5m above Sainidine coal</td>
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<td>Base of hard dark mudstone (8.5m)</td>
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<td>Sainidine Vein near Keynsham</td>
<td>15cm coal (8.8m)</td>
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<td>Middle of 85cm Sainidine coal</td>
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<td>Fine sandstone, in road cutting, opposite lay-by</td>
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Appendix 2 - *StrataBugs* charts of miospore assemblages from the Coalpit Heath Basin (north)
Appendix 3 - *StrataBugs* charts of miospore assemblages from the southern limb of the Kingswood Anticline
Appendix 4 - StrataBugs charts of reworked taxa from the Coalpit Heath Basin (north)
Appendix 5 - StrataBugs charts of reworked taxa from the southern limb of the Kingswood Anticline
Appendix 6 - Miospore generic counts by parent plant affinity (north)
<table>
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<th>Locality</th>
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**Fern - Tree**

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**TOTAL FERNS**

|          | 28.0    | 19.0  | 27.0  | 21.0    | 20.0  | 21.0  | 35.0  |

**Gymnosperm - Unknown monosaccate**

|          | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |
|          | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |

**Gymnosperm - Monocolpate**

|          | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |
|          | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |

**Gymnosperm - Coniferale**

|          | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |
|          | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |
| Cordaffina | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |
| Ilinites   | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |
| Pitycaspites | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |
| Poloniaspites | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |

**Gymnosperm - Cordaitae**

|          | 57.0    | 34.0  | 44.0  | 48.0    | 75.0  | 111.0 | 24.0  |
| Florilites | 57.0    | 34.0  | 44.0  | 48.0    | 75.0  | 111.0 | 24.0  |

**TOTAL GYMNOSPERM**

|          | 57.0    | 34.0  | 44.0  | 48.0    | 75.0  | 111.0 | 24.0  |
| Cardale   | 57.0    | 34.0  | 44.0  | 48.0    | 75.0  | 111.0 | 24.0  |
| Non-cardale | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |

**Lycopsid - Herbaceous**

|          | 2.0     | 3.0   | 2.0   | 10.0    | 1.0   | 0.0   | 0.0   |
| Cetraradiales | 2.0     | 3.0   | 2.0   | 10.0    | 1.0   | 0.0   | 0.0   |
| Lundbladiaspore | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |

**Lycopsid - Arborescent**

<p>|          | 58.0    | 68.0  | 60.0  | 46.0    | 70.0  | 46.0  | 115.0 |
| Cordiapor | 0.0     | 0.0   | 0.0   | 0.0     | 0.0   | 0.0   | 0.0   |
| Sigillariaceae (Crassispore) | 49.0    | 57.0  | 52.0  | 1.0     | 25.0  | 31.0  | 87.0  |</p>
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Appendix 8 – Published paper: Pendleton and Wellman (2012)
Pennsylvanian (mid-Bolsovian to Asturian) megaspores and large pollen of the Bristol Coalfield, UK

JANINE L. PENDLETON* & CHARLES H. WELLMAN
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ABSTRACT – A detailed account of assemblages of megaspores and large pollen grains from the mid-Bolsovian to late Asturian Warwickshire Group (Winterbourne, Pennant Sandstone and Grovesend formations) of the Bristol Coalfield is presented. The megaspore assemblages show certain similarities to those from the well-documented, and partly coeval, sequence in the nearby Forest of Dean Coalfield. However, the Bristol Coalfield megaspore assemblages are generally less diverse. We consider the palaeoecological implications of the megaspore assemblages and conclude that differing depositional settings had different vegetational successions (including differences in the composition and diversity of megaspore-producing plants). A consideration of megaspore biostratigraphy suggests that the uppermost Pennant Sandstone Formation may be of early Asturian age, suggesting that the postulated gap between the Pennant Sandstone Formation and overlying Grovesend Formation is smaller than previously suggested. We also report the first European occurrence of the large enigmatic pteridosperm pollen grain Parasporites maccabei Schopf, 1938.


KEYWORDS: Carboniferous, Pennsylvanian, megaspores, pollen grains, lycopsids, pteridosperms, palaeoecology

INTRODUCTION
The Coal Measures Supergroup of the Bristol Coalfield has been little studied in comparison to other British Coalfields, such as the nearby Forest of Dean Coalfield (e.g. Arber, 1912; Spinner, 1965; Cleal, 1991) and South Wales Coalfield (e.g. Dix, 1934; Dimitrova et al., 2005; Cleal, 2007). As part of a multidisciplinary investigation of this neglected coalfield, part of the sequence (the Warwickshire Group) has been re-evaluated in terms of its stratigraphy/sedimentology, palaeobotany and palynology, and this new information utilized in a reinterpretation of its palaeoenvironments and palaeoecology. This paper is the latest contribution to a series of papers reporting on a detailed analysis of the megafloral assemblages (Pendleton et al., 2011; 2012), including permineralized material (Falcon-Lang et al., 2011; 2012), and palynology (Pendleton, personal data). This paper focuses on a series of assemblages of megaspores and large pollen grains recovered from numerous horizons spread throughout the Warwickshire Group that range from mid-Bolsovian to late Asturian (Moscovian) in age. These assemblages have interesting palaeoecological implications, particularly when specific comparisons are made with previous detailed studies on the nearby Forest of Dean Coalfield (Spinner, 1965).

MEGASPORES AND LARGE POLLEN GRAINS: A PALAEOBOTANICAL PERSPECTIVE
Megaspores are common in the Carboniferous Coal Measures where they are found in situ (e.g. Chaloner, 1953a, b, c; 1956) and dispersed (e.g. Spinner, 1965). They derive from heterosporous plants that, at this time, included certain lycopsids, sphenopsids and possibly also ferns and progymnosperms (Bateman & DiMichele, 1994). However, the vast majority of megaspores from the Carboniferous Coal Measures derive from lycopsids. This morphologically varied group ranged from herbaceous forms to the 40 m tall arborescent forms (Lepidocarpaceae and Sigilliariaceae) that dominated the tropical coal measure swamps for much of their existence.

Carboniferous Coal Measures megaspore preparations occasionally also contain large pollen grains and large seeds that derive from pteridosperms. Three main groups of pteridosperm are common in the Carboniferous Coal Measures: the hydrasperman, medullosan and callistophytalean pteridosperms. In situ pollen is known from all of these groups and their pollen wall ultrastructure is also well understood through detailed transmission electron microscopy (TEM) analyses (summarized in Osborn & Taylor, 1994; Wellman, 2009).

The hydrasperman pteridosperms were a group of relatively small plants that included shrubs and scrambling and climbing plants. In situ pollen reported from hydrasperman seed-ferns is usually small and simple pollen that is accommodated in such dispersed spore genera as Cyclogranisporites and Punctatisporites (Balme, 1995). The pollen is generally small (40–70 μm), spheri-
cal, monolet or trilette, with an ornamented exospore. Wall ultrastructure has been examined in a number of investigations (Millary et al., 1978; Stidd, 1978; Taylor, 1982; Meyer-Berthaud & Galtier, 1986). Hydrosperman pollen does not feature in megaspore preparations as it is too small.

The medullosan pteridosperms were a diverse group that developed a variety of growth habits, dominated by trees and shrubs, but also including scrambling plants and lianas. They bore foliage referred to various genera, including Neuropteris, Linopteris, Macronuopteris, Alethopteris and Odontopteris. Pollen organs are referred to several genera, including Potoniea and Paraspororheca. The pollen is more complicated than that seen in the hydrasperman pteridosperms. Essentially it falls into two categories: those with Zonalisporites (Monoletes)-type pollen and those with Parasporites-type pollen (Balme, 1995). Zonalisporites is a simple monolet pollen grain with a bilayered exine consisting of an inner, laminate, endexine and an outer, alveolate, ectexine (e.g. Taylor, 1982). Parasporites is a bi-pseudosaccate monolet pollen grain with a bilayered exine consisting of an inner laminated endexine and an outer alveolate ectexine (Millyay...
et al., 1978; Taylor, 1982). There is considerable size variation (100–600 μm) in the pollen of this group, with some very large forms. Consequently, medullosan pollen regularly occurs in megaspore preparations.

The callistophytalean pteridosperms were a group of scrambling plants. The pollen is monosaccate and can be accommodated in the dispersed pollen taxon *Vesicaspora* (Balme, 1995). They are demonstrably pollen grains in that Rothwell (1972) recovered grains with emerging pollen tubes trapped within seeds. Ultrastructure of these pollen grains has been reported by Millay & Taylor (1974; 1976). Callistophytalean pollen is generally too small to feature in megaspore preparations.

**GEOLOGICAL SETTING**

Using the revised lithostratigraphic-based framework of Waters et al. (2009; 2011), the Upper Coal Measures are now referred to as the Warwickshire Group. The Warwickshire Group of the Bristol Coalfield comprises from base to top: the Winterbourne, Pennant Sandstone and Grovesend formations. The broadly comparable lithological succession from the Forest of Dean comprises from base to top: the Trenchard, Pennant Sandstone and Grovesend formations. The base of the Warwickshire Group is defined at the *Cambriense* Marine Band; locally known as the Winterbourne Marine Band in Bristol and Upper Cwmgorse Marine Band in South Wales. Where this marine band has not been proved, the first thick (>3 m) sandstone of Pennant-type (lithic arenite) is taken as the lower boundary of the Warwickshire Group.

*Fig. 1. Pennsylvanian outcrop in the British Isles highlighting the location of the Bristol Coalfield (box).*

The Coal Measures Supergroup of the Bristol Coalfield lies to the east and NE of Bristol in the SW of Britain (Fig. 1) where it forms a north–south-orientated rhombic-shaped outcrop of ~90 km². The Warwickshire Group consists of two distinct outcrops: the Coalpit Heath Syncline in the north is separated from the southern outcrop by a wedge of South Wales Coal Measures Group in the core of the east–west-trending Kingswood Anticline (Fig. 2). For a more detailed review of the stratigraphy of the Bristol Coalfield see Pendleton et al. (2012).

The 120–180 m thick argillaceous measures with subordinate coals of the Winterbourne Formation lie between the Winterbourne Marine Band and the base of the Pennant Sandstone. The red measures within the upper portion of the Winterbourne Formation are postulated to reflect enhanced drainage associated with uplift along the Usk Anticline and Lower Severn Axis, which may have also provided a source for the conglomeratic bands (Waters & Davies, 2006; Waters et al., 2009). The Winterbourne Marine Band has not been recognized in the southern portion of the coalfield. Kellaway & Welch (1993) state that the marine band lies somewhere between the New Smith’s and Parrot coals. Falcon-Lang et al. (2011) interpreted the Winterbourne Formation as a poorly drained coastal plain, overlain by a periodically well-drained alluvial plain which was subjected to a seasonal (subhumid) climate. Tectonic-driven water-table fluctuations have been recorded in coal measures across Britain and NW Europe at this time; which almost certainly contributed to red-bed formation in Bristol (Besly & Turner, 1983; Besly & Fielding, 1989; Glover et al., 1993; Pagnier & van der Tongeren, 1996; Pierce et al., 2005; Bertier et al., 2008).

The Pennant Sandstone Formation lies stratigraphically above the Winterbourne Formation and consists of ~600–1000 m of thick lithic arenite beds with subordinate mudstones, coals and conglomeratic horizons. The basal Downend Member reaches its maximum thickness of ~600 m in the south, and diminishes gradually towards the north and NE, where it reaches ~150 m. The top of this member is taken at the lowermost part of the Mangotsfield coals in the Coalpit Heath Basin and the Saltridge Coal in the southern limb of the Kingswood Anticline (see Pendleton et al., 2012 for discussion of the correlation between the basinal components). Conglomeratic beds at the base of the Downend Member generally diminish towards the SSW, along with average clast size, suggesting a source region to the NNE (Pringle, 1921). The ~600 m Mangotsfield Member, which lies above the Downend Member, features a distinct reduction in mudstone horizons and a lack of economically exploitable coal seams. Palaeocurrent indicators for the Mangotsfield Member suggest a source region to the south or SE (Cleal & Thomas, 1996; Pendleton, field observations). The Pennant Sandstone Formation is interpreted as representing channels and floodplains within a broad braided-alluvial
Pennsylvanian of the Bristol Coalfield, UK

The first pulses of Variscan-related uplift are thought to have occurred in the Bolsovian. This probably heralded a switch in sediment type and palaeocurrent direction associated with the arrival of the diachronous Pennant Sandstone Formation from the south of the basin, along with the northerly attenuation of the Downend Member.

The Grovesend Formation is the uppermost unit of the Warwickshire Group. In the Bristol Coalfield the <70 m Farrington Member is an argillaceous sequence with several economically important coal seams. Four coal seams occur at Parkfield Colliery: the Great, Hollybush, Top and Hard coals. Three coal seams occur in Coalpit Heath Colliery: the High (representing merging of the Great and Hollybush coals at Parkfield Colliery), Hollybush and Hard coals. This northern merging of the coal seams suggests that subsidence rates were higher in the south. Up to 200 m of red mottled mudstones lay at the top of the local sequence, representing the Barren Red Member. This unit is interpreted as representing deposition of overbank lacustrine deposits on fluvial floodplains, with periods of increased drainage producing red measures (Waters et al., 2009). The Hursley Hill borehole was drilled just beyond the southern limit of the Bristol Coalfield outcrop (Fig. 2, locality 9), and penetrated the uppermost –600 m of the Grovesend Formation; the Radstock and Publow members.

The Forest of Dean Coalfield lies approximately 20 km to the NW of the Bristol Coalfield (Fig. 1). In contrast with the Bristol Coalfield, the Forest of Dean coal measures are well exposed and the Forest of Dean Free Miners still mine coal in the area to this day. The stratigraphy of the Forest of Dean Coalfield is broadly comparable with that of the Bristol Coalfield (Fig. 3). The lowermost unit, the Trenchard Formation, consists of a quartzose sandstone with conglomerate at the base sourced from the ENE (Jones, 1972) and is restricted to the northern part of the basin (maximum thickness 120 m). It is overlain by the Pennant Sandstone Formation that is represented by the Coleford Member consisting of 180–300 m of sandstone with subordinate mudstones and coals, which continue up to the Brazilly Coal. This unit thickens to the south, where it completely replaces the Trenchard Formation. Unlike the Trenchard Formation, the Coleford Member was sourced from the south (Jones, 1972). The Cinderford Member at the top of the sequence features ~105 m of argillaceous strata with coals (historically termed the Household Coals) which are topped by 230 m of sandstones or interbedded sandstone and shales (historically termed the Serridge Sandstones). Another 25 m of argillaceous strata and the Worgreen coals lie at the top of the sequence. Red beds occur within the Cinderford Member.

The South Wales Middle and Lower Coal Measures formations are absent in the Forest of Dean and the Trenchard Formation unconformably overlies Viséan and older lithologies (Cleal & Thomas, 1996). This angular unconformity probably represents the deformation which occurred in the late Bolsovian and Asturian during the first pulses of the Variscan uplift. It is probably contemporaneous with the Winterbourne Formation red measures that represent a switch in sediment source and the arrival of the Pennant Sandstone Formation in the Bristol Coalfield.

Biostratigraphy and correlation

Pendleton et al. (2012) demonstrated the presence of the following floral assemblages in the Bristol Coalfield: (i) those from the Winterbourne and Pennant Sandstone formations belong to the *Laveineopteris rarinervis* Subzone of the *Paripteris linguefolia* floral zone, indicating a mid-late Bolsovian age; (ii) those of the Farrington Member (Grovesend Formation) belong to the *Dicksonites pluknetii* subzone of the *Lobatopteris vestita* floral biozone, indicating a late Asturian age; (iii) those of the uppermost...
Publow Member (Grovesend Formation), from the Hursley Hill borehole beyond the southern outcrop limit of the coalfield, belong to the *Odontopteris cantabrica* Subzone, indicating a Cantabrian age. This suggests a stratigraphical gap between the Pennant Sandstone Formation and the Grovesend Formation that is probably related to a tectonic-induced hiatus referred to as the Leonian Phase of the Variscan Orogeny (*sensu* Wagner, 1966). This tectonic event also manifests itself as a hiatus in eastern South Wales (and marks the onset of coal-bearing deposition in the Forest of Dean, Severn, Newport and Oxfordshire coalfields (Cleal, 1986; 1987; 1997).

The Winterbourne Marine Band, which forms the basal limit of the Warwickshire Group, correlates with the *Cambriense* Marine Band which is roughly mid-Bolsovian in age and confirms the lower age constraint for this succession (Waters *et al*., 2009). Non-marine bivalves (Moore & Trueman, 1937) and miospore biozones (Pendleton, personal data) also provide biostratigraphical ages confirming those derived from the megafossil record. For a more detailed review of the biostratigraphy and correlation of the Bristol Coalfield, see Falcon-Lang *et al.* (2011) and Pendleton *et al.* (2012).

It is important to note that although the stratigraphical units can be correlated using lithostratigraphy this cannot be extrapolated in any way to imply coeval ages. The base of the Pennant Sandstone Formation, for example, is markedly diachronous and youngs northward. In the southerly Somerset Coalfield the first Pennant lithologies occur below the *Cambriense* Marine Band and are of early Bolsovian age (Stubblefield & Trotter, 1957; Green & Welch, 1965). In the northerly Bristol Coalfield the base of the Pennant Sandstone is dated as mid- to late Bolsovian using palaeobotanical (Pendleton *et al*., 2012) and palynological (Pendleton, personal data) biozones. In the Forest of Dean, roof shale megafloras from the Coleford High Delf Coal, which roughly equates to the base of the Pennant Sandstone Formation, suggests a late Asturian age in this northermost area (Wagner & Spinner, 1972; Cleal, 1991; 1997). The red beds at the top of the Winterbourne Formation in Bristol probably correlate with the Deri Beds of South Wales (mid-late Bolsovian), but despite their similar lithostratigraphic position, are older than the red beds at the top of the Trenchard Formation (late Asturian) in the Forest of Dean.

**MATERIAL AND LOCALITIES**

Forty-two coal samples were obtained from twenty coal seams, of which eight are considered stratigraphically important. These include named coal seams that were either commercially exploited in the past, or those that are mentioned by name in the Geological Survey Memoir and the accompanying map (1: 63 360-scale geological special sheet, British Geological Survey, 1972). These were the Hen Coal of the northern limb, one specimen from the Mangotsfield coal of Church Lane Colliery, Salridge Coal of the southern limb, the four main Parkfield Colliery seams and the High Coal of Coalpit Heath Colliery. These were sampled from *in situ* outcrops or localized spoil tips near historical exposures. Two unmapped coal seams were exposed during the widening of the A4174 Ring Road in c. 2007, which were collected and kindly donated by Nick Chidlaw.

Three of the lenticular coal seams, which occur sporadically in the Pennant Sandstone, were sampled; two from a disused quarry in the garden of Grove Cottage in Frome, and one from an outcrop in the garden of the cottage at 65, The Dingle in Winterbourne Down (see Fig. 2 and descriptions below for more field location details).

Six coal samples were obtained from Harry Stoke B borehole; one taken from material at British Geological Survey in Keyworth, and five from National Coal Board residues now housed at MB Biostatigraphie Ltd in Sheffield. A seam which Kellaway & Welch (1993) correlated to the Hen Coal was included in these samples.

**Highly productive localities**

The Dingle, Winterbourne Down (Pennant Sandstone Formation, Mangotsfield Member). Well-preserved and abundant mega-spores were recovered from a lenticular coal seam exposed at the top of a disused quarry wall in the back garden of number 65 on The Dingle in Winterbourne Down (Locality 4 [ST 656 794]). The coal seam is ~45 cm thick and ~ 4 m wide, extending for the full width of the exposure. The coal seam is on top of a 3 m thick bed of cross-bedded Pennant Sandstone, with an 80 cm bed of identical lithology resting atop it. A 15 cm thick sandstone parting occurs in the bottom quarter of the seam on the western side of the exposure, which dips to the east and merges with the top of the basal sandstone at the eastern limit of the exposure. This coal is interpreted as a localized area of peat generation on the margins of a channel, in a point bar-type setting, similar to that at Grove Cottage (see below). It is also possible this peat was infilling a large abandoned channel, whose dimensions cannot be appreciated based on the limited exposure.
Table 1. Quantitative counts of megaspore taxa.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Member</th>
<th>Facies</th>
<th>Clastic</th>
<th>Peat mire</th>
<th>Short-lived</th>
<th>Peat mire</th>
<th>Megaspores</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grovesend</td>
<td>Member</td>
<td></td>
<td>n = 250</td>
<td>9.0%</td>
<td>3.6%</td>
<td>6.1%</td>
<td>1.5%</td>
</tr>
<tr>
<td>Radstock</td>
<td>Member</td>
<td></td>
<td>n = 12</td>
<td>1.5%</td>
<td>1.5%</td>
<td>0.8%</td>
<td>5.0%</td>
</tr>
<tr>
<td>Locality 5</td>
<td>Farrington</td>
<td>Member</td>
<td>n = 276</td>
<td>3.0%</td>
<td>3.0%</td>
<td>1.1%</td>
<td>1.8%</td>
</tr>
<tr>
<td>Locality 6</td>
<td>Winterbourne</td>
<td>Member</td>
<td>n = 3</td>
<td>1.5%</td>
<td>1.1%</td>
<td>0.4%</td>
<td>74.3%</td>
</tr>
</tbody>
</table>

Farrington coals of Parkfield Colliery, Shortwood (Grovesend Formation; Farrington Member). Parkfield Colliery [ST 690 777], to the NW of Shortwood, worked the four economical coals of the Farrington Formation in this area between 1853 and 1936. These seams range from 0.5–1.5m in thickness, and extend across 60–70m of stratigraphy, and are also worked at Coalpit Heath nearly 5km to the NW. In the past these coal seams were exposed in a now disused railway cutting (Locality 5 [ST 674 762]) that is now part of the Darnaway cycle path. Original measurements along this section were made by Green & Kellaway in 1948 and reported in Kellaway & Welch (1993). These were all made using the northern side of the bridge, which now carries the B4465 over the A4174 at Shortwood, as a marker. Using these measurements, it was possible to measure out the section and locate the four Farrington Member coals: the Great, Hollybush, Top and Hard coals. These coals represent widespread and well-developed mire communities.

The outcrop of the Hard Coal was the only in situ coal found, but, more recently, even this seam has been completely obscured by overgrowth. At this locality the Hard Coal was found to be devoid of megaspores. Fragments of coal were found associated with a localized patch of landslipped material at the reported location of the Great Coal, which yielded poorly preserved megaspores (Locality 5a in Table 1).

Fragments of coal were also found in similar localized landslippages at the reported locations of the Hollybush and Top Coals. Although the fragments of the Hollybush Coal were devoid of megaspores, those from the Top Coal yielded abundant megaspores (Locality 5b in Table 1). No trace was found of the two Rag Coals and the Stinking Coal, which occur stratigraphically above the four major seams.

Crookall’s mudstones from Coalpit Heath Colliery (Grovesend Formation; Farrington Member). Crookall (1925a, b) catalogued the roof shale floras from major collieries, such as Coalpit Heath, Parkfield and Hanham. He mentions recovery of ‘Lycopod megaspores’ from five roof shale samples from Coalpit Heath Colliery (Locality 6 [ST 697 815]). Three of these samples now reside in the Bristol City Museum (registration number CG1573–1575), with the final specimen located in the Natural History Museum in London (registration number v16047). Small sub-samples of this material were acquired from each of these collections (CG1675 and v16047). Roof shales are traditionally interpreted as representing clastic swamps that fringed and infiltrated the peat mires, or alternatively as parautochthonous assemblages deposited during the final stages of peat mire drowning (Gastaldo et al., 1995).

Locations with limited megaspore recovery

Harry Stoke B borehole (Winterbourne Formation). The Harry Stoke B borehole (Locality 1 [ST 6321 7816]) was drilled in 1950 at a location near Hambrook, between the University of the West of England campus and Junction 1 of the M32. The lowermost formation of the Warwickshire Group, the Winterbourne Formation, is exposed through 145m of the borehole section. Although this borehole reportedly penetrated several coal seams, only fragmentary remains of one coaly shale at 59.03m depth were found in the surviving borehole material. From the drilling records this layer represents one of several thin
coaly layers, in a dark shaley mudstone, that rests on a 0.6 m thick grey fireclay. This coal, therefore, occurs in the upper portions of the Winterbourne Formation, 46.5 m below a coal thought to represent the Hen Coal, and 30 m below the point where persistent red mudstones become dominant. The sedimentology suggests that the sample represents a poorly drained clastic swamp, where short-lived and laterally restricted peat mires developed periodically. Unfortunately, the pre-prepared National Coal Board residues contained no megaspores, possibly due to differing preparation or sampling techniques.

_Grove Cottage (Pennant Sandstone Formation; Downend Member)._ Two small (<5 cm thick, ~1 m wide) lenticular coal seams occur in the Downend Member in a disused quarry surrounding the garden of Grove Cottage (Locality 2 [ST 640 772]) in Frencheay. The sedimentology of the outcrop is typical of the Pennant Sandstone Formation with a series of channel scours with patchy channel-lag conglomerates at the bases of metre-scale cross-bedded fluvial-deposited sandstones. Lateral accretion surfaces, festoon bedding and convolute bedding are also common, and are seen at the base or near the top of the larger sandstone beds. A bright coal caps one of the lateral accretion surfaces, and a dull coal appears to be filling a small conglomerate-filled scour, forming a lenticular bed with opposing inflexes (‘S’-shaped). This small scour appears at the base of the same lateral accretion surface packet as the previous coal. A limited megaspore assemblage was recovered from the dull coal. The bright coal contained abundant cuticle fragments, but no megaspores. These thin lenticular coals probably represent short-lived and localized peat-generating environments in close proximity to the braided fluvial system, possibly in a point-bar-type setting.

_High Coal of Coalpit Heath (Grovesend Formation; Farrington Member)._ Single specimens of _Lagenosporites rugosus_ and _Lagenicula verrurugosa_ were obtained from the High Coal of Coalpit Heath (Grovesend Formation; Farrington Member). The High Coal of Coalpit Heath was accessed via a drainage adit (Locality 7 [ST 668 796]), locally referred to as the Serridge Adit, beneath the Kendleshire golf course, with entrance to the adit via a manhole cover in a nearby field. This adit drains westward and enters the River Frome south of Huckford Quarry. At this partially flooded exposure the High Coal was measured as 1.7 m thick, with a red-stained roof shale almost certainly of secondary origin. This limited roof exposure was devoid of any visible plant fossils. The High Coal of Coalpit Heath represents a merging of two Parkfield coals: the Hollybush and Great coals. At this exposure, the High Coal clearly consists of 1.1 m of a more fissile coal that easily breaks into ~5 mm angular to sub-angular fragments, with 60 cm of more massive and hard coal above. Like the Farrington Member coals at Parkfield 3.8 km away, these coals represent widespread and well-developed mire communities. A sparse assemblage of megaspores was recovered from the very top of the coal seam, where the coal features widely dispersed brown and red streaks probably due to oxidation of pyrite. The same coal seam was also accessed 1.25 km to the NE, where it was briefly exposed during the summer of 2011 during building work in the basement of the Old Vicarage in Frampton Cotterell (Locality 8 [ST 673 807]). Here 50 cm of a soft black coal was exposed, which contained relatively high levels of pyrite compared to other Bristol coals. The visual appearance of the coal combined with high pyrite levels are similar to the coal exposed in the Serridge Adit, suggesting that the coal represents the upper portion of the High Coal and is equivalent to the Hollybush Coal of Parkfield.

_Salridge Coal (Pennant Sandstone Formation; division between Downend and Mangotsfield members)._ Megaspores were recovered from three horizons associated with the Salridge Coal exposure at Locality 3 [ST 642 599]. The 0.85 m thick Salridge Coal overlies 1.75 m of alternating coal and mudstones layers, on top of a 7.3 m thick seat earth. Two megaspore assemblages were obtained from the interbedded coal and mudstones, and one assemblage recovered from the top of the Salridge Coal proper (85 cm thick at this locality). The outcrop of the Salridge can be traced for nearly 2 km, and is probably an extension of the Mangotsfield coals of the Coalpit Heath basin 6 km to the north. Due to the thickness and extent of this coal seam, these megaspore assemblages are interpreted as being derived from a well-developed peat mire community. A fossil plant assemblage was recovered from the beige roof shale above the Salridge Coal and is discussed in Pendleton et al. (2012).

_Hursley Hill borehole (Grovesend Formation; Radstock Member)._ A single mudstone sample with megaspores was obtained from the Radstock Member of the Hursley Hill borehole (Locality 9 [ST 618 657]) at 328.65 m depth. This is ~49 m below the Asturian–Cantabrian boundary indicated by the megaflora (Pendleton et al., 2012). This mudstone is dark with several coaly layers, and is situated directly above a coal seam, according to the drillers logs. This sample, therefore, probably originated in a poorly drained clastic swamp. Although the sub-sample from this specimen yielded abundant and well-preserved miospores, only megaspore fragments were extracted after processing. Visual inspection of the megaspores on the original core material suggests _Laevigatosporites glabratus_, based on their size, laevigate exine and non-gulate contact areas. The miospore preparation is dominated by the corresponding microspore (Crassispora kosankei (Potonié & Kremp) Bharadwaj, 1957a, b), which supports this identification.

**METHODS**

All coal samples were processed using standard palynological preparation techniques for extracting megaspores from coal. Schulze solution (65% nitric acid supersaturated with potassium chloride) was used as the oxidation agent. Oxidation of 20–90 minutes in Schulze solution, followed by a brief wash in 2% potassium hydroxide, was found to yield megaspores sufficient for examination and photography under the light microscope. Samples from fresh exposure and borehole were found to require 60–90 minutes of oxidation to yield translucent megaspores, whereas weathered coals from spoil tips and exposed outcrop reacted rapidly and required only 20 minutes of oxidation. Some weathered coal samples reacted so vigorously that diluted Schulze solution, in some cases in conjunction with cold water jetting of the reaction beaker, was required to prevent almost explosive reactions. This phenomenon was also encountered by Schopf (1938) and Spinner (1965). It was noted by Spinner (unpublished thesis, University of Sheffield, 1964) that some megaspores shrank by up to 20% when allowed to dry. All measurements in this paper were made under a...
light microscope on specimens in water. It was found that pipetting megaspores with water on to a slide and covering with a cover slip provided optimal optics, and enabled specimens to then be mounted on stubs for scanning electron microscope (SEM) analysis.

Traditionally, miospores are separated arbitrarily from megaspores at a size boundary of 200 μm in palynological studies. Megaspores for this study were extracted from the processed organic residue using a 180 μm sieve. This size fraction included megaspores and large pteridosperm pollen (namely Zonalosporites and Parasporites). Miospore data from the samples discussed here are in preparation for publication (Pendleton, personal data). All processing was undertaken at the Palynological Research Facility at the University of Sheffield, UK.

SYSTEMATIC PALAEONTOLOGY

All taxa are adequately described in Spinner’s (1965) work on the Forest of Dean; therefore, only comparisons, comments and illustration of the Bristol specimens will be dealt with in this section. Descriptive terms for megaspore morphology broadly follow those in Spinner (1965), which is based on recommendations made by the Commission Internationale Microlite Paléozoïque (Couper & Grebe, 1961). All terms used can also be found in Punt et al. (2007). Due to the limited diversity, taxa will be listed alphabetically with no suprageneric classification system beyond differentiation of the Bristol specimens will be dealt with in this section.

Megasporites

Genus Laevigatisporites (Ibrahim) Potonié & Kremp, 1954

Type species. Laevigatisporites primus (Wicher) Potonié & Kremp, 1954

Affinity. Lycopsida; Sigillariaceae. The genus Laevigatisporites has been extracted from several cone species attributed to Sigillariaceae: Mazocarpon oedipternum Schopf, Sigillariostrobus gothani Bode (1928) and S. czarnockii Bochetski (1936) (reviewed in Spinner, 1965 and Balme, 1995). Studies of wall ultrastructure also support such an affinity (e.g. Hemsley & Scott, 1991).

Laevigatisporites glabatus (Zernndt) Potonié & Kremp, 1955

(Pl. 1, fig. 1; Pl. 2, figs 1, 2)

Affinity. Lycopsida; Sigillariaceae. L. glabatus has been extracted from the cone taxa Sigillariostrobus (Potonié, 1967; Balme, 1995) and Mazocarpon bensoni Pigg (Pigg, 1983).

Description. 10 specimens. Trilete megaspores, 1552(1593)1602 μm in diameter, with a circular to oval outline. Found in proximal-distal orientation. Laesurae 174(277)389 μm; around two-fifths to three-fifths of the spore radius. Laesurae straight and may be open at the pole. Curvatureae present, but only faintly developed. Exospore laevigate.


Occurrence. Winterbourne Formation (Harry Stoke B borehole) to Publow Member (Hursley Hill borehole).

Remarks. Laesurae considerably shorter than reported in Spinner (1965); in these specimens the laesurae extended between a half and two-thirds of the spore radius. The foveolate exospore (Pl. 1, fig. 1) mentioned in Spinner (1965) was also seen under SEM.

Genus Tuberculatisporites (Ibrahim) Potonié & Kremp, 1954

Type species. Tuberculatisporites tuberosus Ibrahim, 1933.

Affinity. Lycopsida; Sigillariaceae. The genus Tuberculatisporites has been recovered from many different Sigillariostrobus strobili (Potonié, 1967; Balme, 1995) and Mazocarpon (Balme, 1995).

Tuberculatisporites brevispicus (Schopf) Potonié & Kremp, 1955

(Pl. 1, fig. 2; Pl. 2, figs 3, 4)

Description. 3 specimens. Trilete megaspores, 1713(1795)1824 μm in diameter. Found in proximal distal compression. Laesurae 267(301)385 μm; marginally less than a third of the spore radius. Laesurae straight, often found torn open along their entire length. Curvatureae not present, but contact area is marked by a thinning of the exospore in some specimens. Exospore ornamented; with 2(4)6 μm coni and slightly pointed verrucae which appear to be of more or less uniform size. Coni are spaced at intervals roughly equally or slightly exceeding their basal diameters. Larger ornament occurs outside of the contact area; consisting of a disc-like verrucae the basal component of which is circular in plan view and broadly rounded in profile view. These verrucae are 12(26)53 μm broad at the base, and less than 8 μm in height. At the centre of the verrucae is a cumulic structure (Schopf, 1938). These projections are fragile and, when well preserved, they appear to be conate to spinate in shape, originally around 8–10 μm tall. They are more typically found compressed flat against the basal verrucae, or broken off so only small rounded discs remain. As with the ornament of the contact area, these verrucae with cumulic structures are evenly distributed, and spaced at intervals roughly equal to or exceeding their basal diameters. The exospore between the ornament appears foveolate.

Stratigraphic distribution. Asturian to Stephanian in paralic basins of the UK (Spinner, 1965; 1966; Wagner & Spinner, 1972), the Ruhr (Bharadwaj & Kremp, 1955; Bharadwaj, 1957a, b) and North America (Schopf, 1938). In the limnic basins of northern France (Saar Lorraine) this species also occurs in the Langsettian/Duckmantian (Soyez, 1967; Loboziaik, 1971; 1972). Reported range Trenchard to Worgreen coals in the Forest of Dean by Spinner (1965).

Occurrence. Upper Mangotsfield Member (65, The Dingle).

Remarks. Our specimens match the descriptions of the Forest of Dean species, the only difference being that the proximal coni and verrucae appear to be evenly spaced and do not decrease in size towards the pole. The species described as T. brevispicus by
Horst (1955) featured larger ornament (40–65 μm diameter) which is not consistent with this species and is typical of T. mamilliarius. Horst (1955) provided no figures of these specimens. Dijkstra (1946) also included all Tuberculatisporites-type megaspores in ‘Triletes’ mamilliarius’ Barlett, maintaining that large size variations in ornament suggested designation of only one species and that Tuberculatisporites brevispiculus was, therefore, a synonym. Although some support for this large variation in ornament size has been provided by investigations of megaspores from sigillarian cones (Bocheński, 1936; Chaloner, 1953b), specimens exhibiting the relatively fine ornament of T. brevispiculus were not recovered. Re-investigation of the type material suggests that the type specimen of T. mamilliarius is distinct from T. brevispiculus (Arnold, 1961).

Genus Lagenoisporites Potonié & Kremp, 1954

Type species. Lagenoisporites rugosus (Loose) Potonié & Kremp, 1954.

Affinity. Lycopsida; Lepidocarpaceae. The genus Lagenoisporites has been reported in situ from a number of species of the cone Flemingites (Brack-Hanes & Thomas, 1983; Balme, 1995). It has also been reported from the Permian bispores and taxon Asianidiondrom (Rayner, 1986).

Lagenoisporites rugosus (Schopf) Potonié & Kremp, 1954

(Pl. 1, fig. 3; Pl. 2, figs 5–7)

Affinity. Lycopsida; Lepidocarpaceae. L. rugosus has been reported from Flemingites cones (Brack-Hanes & Thomas, 1983; Balme, 1995).

Description. 20 specimens, Trilete megaspores. 435(911)1223 μm in diameter including apical prominence, with a circular to oval equatorial outline. Typically found in lateral compressions, where the gula gives the spore a distinctly flask shape. Laesurae often open and 239(431)645 μm long; roughly half of the spore radius. The contact areas are typically thickened in the region of the proximal pole. The gula is broader than it is tall; its width usually extending for two-thirds to almost the full width of the contact area. Curvatures almost always form low arcuate ridges, rarely more than 20 μm wide. Exospore is laevigate under the light microscope, with faint roughening of the contact areas. Under SEM the exospore is clearly foveolate, and the proximal roughness can be seen to be due to many irregular and closely spaced granula.

Occurrence. Downend Member to Farrington Member (Grove Cottage, Salridge Coal, 65, The Dingle, Top and Great Coal at Parkfield Colliery and High Coal of Coalpit Heath).

Remarks. It is likely that the thickening of contact areas near the proximal pole is partly due to these closely packed and irregular granula, which are only visible under SEM. As noted in Spinner (1965), the differences between the ornamented Lagenicula and unornamented Lagenoisporites are rarely satisfactory and may be an effect of differing laboratory preparation techniques. Specimens with a granulate contact area were retained within this species due to the fact that previous authors had noted the thickening of the contact area; but as an SEM was not used in these early works it is likely that the granula were not noticed previously. Therefore, for the purposes of this study, Lagenoisporites rugosus is taken to include spores where grana occur in restricted areas near the proximal pole. In the Forest of Dean, Spinner (1965) differentiated Cystosporites based on the apical prominence being less pronounced, but the exospore being thicker in this region and featuring fine-scale ornament (‘finely vermiculate to granulate’). In the Bristol specimens a complete spectrum was seen between obviously gulate megaspores, and those with a more subtle apical prominence which is slightly thickened in comparison to the rest of the exospore. For the purposes of this study, all this variation will be encompassed within L. rugosus. This seems logical as the forms grade into each other, and have both been found in cones affiliated with Lepidocarpaceae.

Lagenoisporites sp. 1

(Pl. 1, fig. 4; Pl. 2, fig. 8)

Description. 4 specimens. Trilete megaspores, 630(747)840 μm in diameter including apical prominence, with a circular to oval equatorial outline. Typically found in lateral and oblique compressions. Laesurae typically closed and 174(203)236 μm long; roughly
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half of the spore radius. The contact areas are typically thickened in the region of the proximal pole. The gula is poorly developed, projecting only due to the undulate lips either side of the laesurae. Curvaturae almost always form low arcuate ridges, rarely more than 20 μm wide. Exospore is laevigate under light microscope, with faint roughening of the contact areas. Under SEM the exospore is clearly foveolate, and the proximal roughness can be seen to be due to many irregular and closely spaced grana.

**Occurrence.** Mangotsfield Member to Farrington Member (65, The Dingle; Top Coal at Parkfield Colliery).

**Remarks.** Morphologically similar to *Lagenoisporites rugosus*; differing only in the generally smaller dimensions, poorly developed gula and convolute lips associated with the laesurae. One poorly preserved specimen shows subtle thickenings which may indicate the remains of ornament similar to *Lagenicula verrurugosa*.

Genus *Lagenicula* (Bennie & Kidston) Potonié & Kremp, 1954

**Type species.** *Lagenicula horrida* Zerndt, 1934.

**Affinity.** Lycopsida; Lepidocarpaceae. The genus *Lagenicula* has been reported in *situ* from a number of species of the cone *Flemingites* (Balme, 1995). Studies of megaspore wall ultrastructure also support such an affinity (e.g. Glasspool et al., 2000).

*Lagenicula verrurugosa* Spinner, 1965

(Pl. 1, fig. 5; Pl. 2, figs 9, 10)

**Affinity.** Lycopsida; Lepidocarpaceae. Reported in cones with *Lagenoisporites rugosus* by Dijkstra (1946) as reviewed in *Lagenicula irregularis* Spinner, 1965

Description. 11 specimens. Trilete megaspores, 820(953)1150 μm in diameter including apical prominence, with a circular to oval equatorial outline. Typically found in lateral compressions, where the gula gives the spore a distinctly flask shape. Laesurae often open, and 230(282)470 μm long; roughly half of the spore radius. The gula is domed or conical in lateral compression, and collapses to form folds in polar compression so it may not project beyond the spore outline. Contact areas indistinct, and curvaturae are only partially discernible and are not marked by a clear ridge. Exospore ornamented with variably spaced verrucae; with round to oval outlines in plan view and well-rounded apices in profile. Verrucae are biggest at the distal pole where they are 15(64)84 μm in basal diameter and 3(6)10 μm in height. Verrucae gradually diminish in size towards the proximal pole, and attain a relatively consistent basal diameter of 5(12)28 μm in the contact areas. Spacing between the verrucae varies with ornament size, being more or less equal to the basal diameter of the ornament in any given area.

**Stratigraphic distribution.** The only previous reports are from the Trenchard and Brazilly coals of the Forest of Dean by Spinner (1965).

**Occurrence.** Mangotsfield Member to Farrington Member (Salridge, 65, The Dingle and Top Coal at Parkfield Colliery).

Explanation of Plate 2.

*figs 1, 2, Lagenoisporites glabratius* (Zerndt) Potonié & Kremp, 1955. Harry Stoke B borehole (Winterbourne Formation): 1, SEM stub JLPBC-MEGAG, USPRF; 2, laevigate exospore. SEM stub JLPBC-MEGA, BCMAG. *figs 3, 4, Taberculatisporites brevispiculatus* (Schopf) Potonié & Kremp, 1955. The Dingle, Winterbourne Down (Pennant Sandstone Formation; Mangotsfield Member). SEM stub JLPBC-MEGAG2, USPRF: 3, illustrating restricted ornament in contact area; 4, illustrating verrucate ornament with central columellar structure. *figs 5–7, Lagenoisporites rugosus* (Schopf) Potonié & Kremp, 1955. The Dingle, Winterbourne Down (Pennant Sandstone Formation; Mangotsfield Member): 5, SEM stub JLPBC-MEGAG3, USPRF; 6, gula ornament. SEM stub JLPBC-MEGAG3, USPRF; 7, punctate exospore. SEM stub JLPBC-MEGAG4, USPRF: 8, Lagenoisporites sp. 1. The Dingle, Winterbourne Down (Pennant Sandstone Formation; Mangotsfield Member). SEM stub JLPBC-MEGAG3, USPRF: 9, 10, Lagenicula verrurugosa Spinner, 1965. Farrington coals of Parkfield Colliery, Shortwood (Grovesend Formation; Farrington Member). SEM stub JLPBC-MEGAG5, USPRF: 9, gula; 10, illustrating dense verrucate exospore. *figs 11, 12, Lagenicula irregularis* Spinner, 1965. Farrington coals of Parkfield Colliery, Shortwood (Grovesend Formation; Farrington Member). SEM stub JLPBC-MEGAG5, USPRF: 11, gula; 12, punctate exospore. *figs 13, 14, Lagenicula* sp. 1. Farrington coals of Parkfield Colliery, Shortwood (Grovesend Formation; Farrington Member). SEM stub JLPBC-MEGAG5, USPRF: 13, illustrating small and dense verrucae associated with the curvaturae; 14, gula. Scale bars 200 μm for whole megaspores (figs 1, 4, 5, 8, 9, 11, 14). Scale bars 20 μm for images of exospore detail (figs 2, 3, 6, 7, 10, 12, 13). USPRF, University of Sheffield Palynological Research Facility. 97
Remarks. Spinner (1965) also noted indistinct contact areas lacking curvaturae, as well as the uniform nature of the reduced ornament in the contact area. This ornament is notable for its consistent size when compared to the gradation of size from the distal pole to the edge of the contact areas.

*Lagenicula* sp. 1

(Pl. 1, fig. 7; Pl. 2, figs 13, 14)

**Description.** 6 specimens. Trilete megaspores, 940 (1070)1145 μm in diameter including apical prominence, with a circular to oval equatorial outline. Typically found in lateral compressions, where the gula gives the spore a distinctly flask shape. Laesurae often open and 230(282)470 μm long; roughly half of the spore radius. The gula is domed or conical in lateral compression, and collapses to form folds in polar compression so it may not project beyond the spore outline. Contact area delimited by clear curvaturae, which is marked by a ridge 10–15 m wide. Small baculae and verrucae 3(8)8 μm tall are developed on the curvaturae ridge and scattered verrucae may occur up to halfway towards the distal pole of the spore.

**Stratigraphic distribution.** Reported range Trenchard to Mangotsfield Member (Top Coal at Parkfield Colliery).

**Occurrence.** Mangotsfield Member to Farrington Member (Salridge, 65, The Dingle and Top Coal at Parkfield Colliery).


Genus *Setosisporites* (Ibrahim) Potonié & Kremp, 1954

**Type species.** *Setosisporites hirsutus* (Loose) Ibrahim, 1933.

**Affinity.** Lycopsida; *Porostrobus*-producing Selaginellaceae lycopsids (Balme, 1995; Bek & Leary, 2012). Megaspores of *Setosisporites hirsutus* have been recovered from *Porostrobus* cones along with *Demosporites* (Scott & King, 1981; Leary & Mickle, 1989). Studies of wall ultrastructure also support a lycopsid affinity (e.g. Hemsley & Scott, 1991; Glasspool et al., 2000).

*Setosisporites* sp. 1

(Pl. 3, figs 1, 2)

**Description.** 2 specimens. Trilete megaspores, 602(691)781 μm in diameter including apical prominence, with a circular to oval equatorial outline. Typically found in lateral compressions, where the gula gives the spore a distinctly flask shape. Laesurae often open. Contact area delimited by the absence of ornament. Baculae 5(18)25 μm in length and 3(4)6 μm in basal width occur on the curvaturae, reducing in density towards the distal pole where they may be scattered or absent.

**Occurrence.** Farrington Member (Top Coal at Parkfield Colliery).

**Remarks.** Ornament of *Lagenicula* sp. 1 is restricted to the area around the curvaturae, and is verrucate but also features rare and very small baculae which are not comparable in size. *Setosisporites pilatus* Spinner, 1965 from the Forest of Dean is a similar size, has a *Lagenicula*-style gula and the baculate ornament that is smaller and denser on the curvaturae and that becomes larger and scattered distally. Due to the limited number and poor preservation of the Bristol species, no true pilate ornament was seen (baculae with clearly laterally expanded apices) so it does not appear to be the same species as Spinner reported. *S. pilatus* also has smaller ornament (<15 μm)

Genus *Triangulatisporites* Potonié & Kremp, 1954

**Type species.** *Triangulatisporites triangulatus* (Zerndt) Potonié & Kremp, 1954.

**Affinity.** Lycopsida; Selaginellaceae. Megaspores similar to *Triangulatisporites triangulatus* were extracted from cones of *Sellaginellites suissei* Zeiller by Zeiller (1886) and Chaloner (1954). This species has also been recovered from *Selaginella gutbieri* (Göppert) Thomas by Rößler & Buschmann (1994). Studies of wall ultrastructure also support such an affinity (e.g. Cottman et al., 2000).

*Triangulatisporites regalis* (Ibrahim) Potonié & Kremp, 1955

(Pl. 1, figs 8, 9; Pl. 3, figs 3–6)

**Affinity.** Lycopsida; Selaginellaceae (Zeiller, 1906; Chaloner, 1954; Bek et al. 2001; 2009).

**Description.** 9 specimens. Trilete, zonate megaspores 642 (714)846 μm in diameter. Inner body circular 408(469)549 μm in diameter, occupying 64(66)67% of the total spore radius. Equatorial zone discordant with inner body shape, giving the megaspore a convexly triangular outline in polar view. Zona widest at the apices 133(148)172 μm, and narrowest in the interradial regions 80(97)120 μm. Megaspores typically preserved in proximal–distal orientation. Prominent ridge accompanies the laesurae, up to 15 μm tall with an undulating crest. Ridge tallest where the laesurae reach
at the proximal pole, and diminish in height radially. Ridges extend to the equatorial outline defined by the zona. Contact areas ornamented with a reticulum; which is typically only preserved in localized patches at the junctions where muri fuse. Muri ~ 2 μm and polygonal lumina ~10–15 μm in the centre of the contact face, and become radially elongate towards the laesae and edge of the inner body. At the edge of the inner body the muri become partially anastomosing verminiculae which extend on to the zona. Distally the polygonal lumina are bigger, 37(65) 85 μm, and muri more robust, 5(6)12 μm, and therefore the distal reticulum is generally better preserved than the proximal reticulum. Distal lumina are also of a fairly consistent size over the inner body; but may become slightly radially elongate as they extend on to the zone. Between the reticulum, the exospore is laevigate.


**Occurrence.** Farrington Member (Crookall’s mudstone specimens from Coalpit Heath).

**Remarks.** Triangulatisporites triangularis (Zerndt) Potonié & Kremp, 1954 is smaller, 560(600)960 μm, with more robust muri from Coalpit Heath). Type species. Zonalosporites ellipsoides (Ibrahim, 1933)

**Type species.** Zonalosporites vitatus Ibrahim, 1933

**Affinity.** Medullosan pteridosperm: Parasporites has been recovered in situ from the medullosan pteridosperm pollen organ Parasporotherca (reviewed in Taylor et al., 2009).

**Parasporites maccabei** Schopf, 1938

**Type species.** Parasporites maccabei Schopf, 1938


**Description.** 13 specimens. Bi-pseudosaccate pollen with a circular to oval body 179(209)246 μm by 180(205)220 μm occupying 67(74)80% of the spore width along the long axis of the grain. Generally haploxylonoid, but may be slightly diploxylonoid; long axis 243(282)310 μm. Proximal suture variable; monolete with median deflection and incipient reticulate conditions are seen on 9 specimens. Suture 103(120)139 μm long, 50(57)66% of body long axis. Proximal ornament of pollen body consists of a network of interconnecting, convolute rugulae 2(6)10 μm wide. These rugulae may almost abut against each other, or be separated by up to 4 μm. Two generally crescentic pseudosacci, lacking endoreticulation, are attached to the distal side of the equator. Pseudosacci dimensions 163(176)192 μm by 64(83)107 μm.

**Stratigraphic distribution.** Rock Island (base of Desmoinesian) to Calhoun Coal ( upperrmost Missourian) of Illinois (Millay et al., 1978). This suggests an Asturian to Barruelian range. This pollen has not been reported previously in Europe.

**Occurrence.** Mangotsfield Member (65, The Dingle, Winterbourne Down).

**Remarks.** Millay et al. (1978) suggest that the nature of the proximal sutures is evidence for a preformed line of weakness, which is to be expected if proximal rupture occurs during germination.

**BIOSTRATIGRAPHY**

A limited biostratigraphy for the Bristol Coalfield can be drawn up using the ranges of the megaspores and large pollen grains (Fig. 4). Tuberculatisporites brevistipulus is restricted to the Asturian in the paralic basins of Western Europe and equivalent Desmoinesian strata in Illinois (Schopf, 1938; Potonié & Kremp, 1956; Bharadwaj, 1957a, b; Spinner, 1965; 1966). This taxon occurs approximately in the middle of the Mangotsfield Member. This suggests that the Bolsovian–Asturian Boundary lies within the Mangotsfield Member. Parasporites maccabei is known to range from the lower Desmoinesian (Asturian) to the latest Missourian (Barruelian) in NE North America (Millay et al., 1978).
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Fig. 4. Megaspore composite stratigraphic ranges for the Warwickshire Group of Bristol. Position of the Bolsovian–Asturian boundary using the new megaspore biostratigraphy and megafossil biostratigraphy from Pendleton et al. (2012). Locality numbers (as in Fig. 2) to left of lithostratigraphic columns.
The presence of high numbers of this pteridosperm pollen in the middle of the Mangotsfield Member also supports an Asturian age for this horizon.

The only productive plant fossil horizon from the Mangotsfield Member examined by Pendleton et al. (2012) featured no bionstratigraphically useful taxa and thus provided no evidence for Asturian-aged rocks at the top of the Pennant Sandstone. Assemblages from the Mangotsfield coals and Salridge Coal contain the following plant species which do not extend beyond the Laveineopteris rar-rinervis Subzone: Laveineopteris tenuifolia (Sternberg) Cleal et al., 1990, Lobatopteris miltonii (Artis) Wagner, 1958 and Laveineopteris dussartii (Laveine) Laveine, 2005 and, therefore, indicate a Bolsovian age. Several stratigraphically significant miospore species have their first occurrence near the base of Mangotsfield Member in the Coalpit Heath Basin: Cadiospora magna Kosanke, 1950, Mooreispites inustiatus (Kosanke) Nevés, 1958 and Savitisporites compositus (Alpem) Venkatachala & Bharadwaj, 1964 accompanied by a general increase in Thymospora spp. These taxa are indicative of the OT biozone of Clayton et al. (1977), the base of which just pre-dates the Bolsovian–Asturian boundary. Taking together evidence from megaflora, miospore and miospore biozonation, it seems likely that the base of the Asturian is within the lower portion of the Mangotsfield Member.

**PALAEOECOLOGY**

**Palaeeocological considerations**

Quantitative miospore data for each locality are given in Table 1. The assemblage from the poorly drained coastal plains of the Winterbourne Formation features few miospores, with only those of a sigillarian affinity (Laevigatosporites glabratus) reported. Pteridosperm pollen (Zonalospites) is also common. Sigillarian dominance in these types of coastal plain is typical of the Westphalian of Euramerica (DiMichele & Phillips, 1994). Miospore assemblages from the same horizon (Pendleton, personal data) are co-dominated by cordaites pollen (31%) and lepidodendrid spores (27%), with low numbers of sigillarian spores (3.5%). The absence of lepidodendrid megaspores in the assemblage, therefore, seems unusual. However, the diverse and well-preserved miospore assemblage suggests that a simple preservation bias between more robust sigillarian megaspores and relatively less robust lepidodendrid megaspores is unlikely in this case. A taphonomic bias manifested as low sigillarian miospore abundance in coastal plain assemblages despite dominance among plant megafossils has been reported for the Joggins Formation of Nova Scotia (Hower et al., 2000; Falcon-Lang et al., 2006) and may be more broadly comparable.

Miospore assemblages from the localized and short-lived point-bar peat mires of the Pennant Sandstone Formation are dominated by lepidodendrid megaspores (Lageniosporites and Lagenicula) with high levels of pteridosperm pollen (Parasporites and Zonalospites). Miospore assemblages from the Downend Member coal at Grove Cottage (Pendleton, personal data) are dominated by lepidodendrid spores (50%), with subordinate tree-fern spores (21%) and calamitalean spores (16%). The Mangotsfield Member coal (The Dingle) assemblage is dominated by tree-fern spores (30.5%) with subordinate calamitalean spores (20.5%) and fern spores (18%), with only 8.5% lepidodendrid spores. Differences between dominance patterns in the miospore counts are likely to be at least partially due to subtle differences in depositional setting and, therefore, corresponding vegetational composition. However, the temporal differences between these Bolsovian (Downend Member) and early Asturian (uppermost Mangotsfield Member) will almost certainly play a crucial role with the differences reflecting tectonic- and/or climatic-driven reductions in species diversity near the end of the Bolsovian (Cleal, 2007; Opluštil & Cleal, 2007).

Megaspore assemblages from the late Asturian Farrington Member peat mires feature only lepidodendrid megaspores (Lageniosporites and Lagenicula) and pteridosperm pollen (Zonalospites), which are abundant and well-preserved in the Top Coal at Parkfield Colliery. Miospore assemblages (Pendleton, personal data) feature typical Asturian dominance of small fern spores (22%), tree-fern spores (18.5%) and calamitalean spores (15.5%). Lepidodendrid spores make up only 10.5% of the palynomorphs. The assemblage from the roof shale of a Farrington Member coal seam, reflecting the flora from clastic swamps fringing the peat mires, is dominated by sigillarian megaspores (Laevigatosporites glabratus), with megaspores from herbaceous selaginellids (Triangulatisporites regalis) and pteridosperm pollen (Zonalospites ellipsoides). The miospore assemblage (Pendleton, personal data) is also dominated by sigillarian megaspores (Crassispora kosankei, 79.5%). However, no selaginellid megaspores (Cirratridentites) were found in the preparations. Sigillarian dominance in the megaspore preparations is also seen in the clastic swamps of the Radstock Member, and in the poorly drained coastal plain of the Winterbourne Formation.

Pteridosperms, specifically those which produce Zonalospites-type pollen, occur in all of the megaspore-bearing horizons of the Warwickshire Group. Miospore preparations of both coals and siliciclastics (Pendleton, personal data) show that pteridosperm pollen (Zonalospites and Wilsonites) ranges throughout the Warwickshire Group occurring in almost every miospore-yielding horizon investigated. This suggests that these plants were widespread across both the peat mire and clastic environments. Pteridosperm anatomy and distribution support the suggestion that these plants colonized a wide variety of wetland habitats with mineral-rich substrates, from clastic floodplains and saturated stream sides to comparatively well-drained levees, but are rarely found in peat-generating areas (DiMichele et al., 2006). Although ecologically widespread, pteridosperm pollen rarely accounts for more than 1% of the total miospore preparations and is always subordinate in the megaspore fraction. Several factors have been proposed for this dearth of pollen grains compared to the abundance of their fossilized foliage. These generally involve analogies with the infrrequent reproduction of their nearest living relatives, the cycads, and their limited dispersal potential in water based on modelling studies (Schwendemann et al., 2007).

*Parasporites* has prominent pseudosacci and is likely to have been wind dispersed. Its presence in the thin coal bed of the upper Mangotsfield Member is the first record of this taxon in the British Isles. Although this species has been extracted from pollen organs, it has not been possible to link these with the parent plant. Thus, we know that this pollen derives from a pteridosperm, but we do not know the nature of the parent plant. The concentration of *Parasporites* in this point bar was probably derived from pteridosperms living on the margins of this localized peat-generating area, with the wind-dispersed pollen being blown into the mire.
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Comparison with the Forest of Dean – shedding more light on palaeoecological signals

Spinner (1965) documented megaspore assemblages from the Forest of Dean coal seams, and several corresponding roof shales. Most of the coal seams show a dominance of lepidodendrid megaspores (Lagenosporites and Lagenicula) similar to that seen in the coals of the Bristol Coalfield. In the Forest of Dean the coals preserve a much more diverse megaspore assemblage, including Valvissporites (reported in situ from a Polyopsoria con- assigned to the Chaloneriaceae (Pigg & Rothwell, 1983)), Zonalesporites (reported in situ from Sporangiostrobis, a cone also assigned to the Chaloneriaceae (Pigg & Rothwell, 1983)), Cystosporites (lepidodendrid) and Triangulatisporites (selaginellid). Triangulatisporites (selaginellid) are often subordinate to lepidodendrid megaspores (Lagenosporites and Lagenicula) (Spinner, 1965). However, in Bristol the only accessory mega- spore seen in the coals is rare Tuberculatisporites brevispiculus at the top of the Mangotsfield Member.

Peat mires generally follow a predictable pattern of hydrological evolution; from initial topogenous (planar) through to ombrogenous (domed) mire. This drives a corresponding evolution in the vegetation signal that can be seen in both the fossil plant assemblages (DiMichele & Phillips, 1994) and the corre- sponding palynological assemblages (Smith, 1957). Initially lepi- dodendrids are dominant in the flooded planar mire (‘Lycospore Phase’; Smith, 1957), with peat accumulation eventually leading to a better-drained domed mire that is dominated by stunted veget- ation and sub-arborescent lycopsids (‘Denispore Phase’; Smith, 1957). This model can be used to explain a lot of the differ- ences between the Forest of Dean and Bristol assemblages. The Forest of Dean assemblages were obtained from thick coal seams that are laterally extensive and traceable over the entire coalfield. The plant communities that formed these would have been well established and, therefore, probably more diverse, than those in the disturbed floodplains of the Winterbourne Formation and the short-lived point-bar ecosystems of the Pennant Sandstone Formation.

The Top Coal of Bristol, along with the restricted assemblage from the Salridge Coal, represents the only laterally extensive peat mire megaspore assemblages derived from the Bristol Coalfield. Like the Forest of Dean seams these are dominated by lepidodendrid megaspores (Lagenosporites and Lagenicula). However, like the Pennant Sandstone point-bar coals they do not feature the array of herbaceous and sub-arborescent lycopsid accessory taxa present in the Forest of Dean. The Top Coal mio- spore preparations show dominance of ferns and tree-ferns (Pendleton, personal data). Forest of Dean seams, which are fern and tree-fern dominated – the Brazilly to Starkey seams – also have similar megaspore assemblages where sub-arborescent and herbaceous lycopsid megaspores are not present in the assemblage (Spinner, 1965). This is presumably due to better-drained condi- tions in the mires favouring ferns and tree-ferns over lycopsids.

Clastic mires (roof shales) on the fringes of a laterally persist- ent mire, which produced the roof shales of the Yorkley Coal in the Forest of Dean, have megaspore assemblages dominated by a sub-arborescent lycopsid (Zonalesporites) (Spinner, 1965). Miopore preparations from this horizon are dominated by the corresponding microspores: Denispores (data from Spinner, unpublished thesis, University of Sheffield, 1964). The roof

shales of the Brazilly and Twenty Inch contained a similar lepi- dodendrid-dominated assemblage as the associated coal seams (Spinner, 1965). The Bristol roof shale indicates that the clastic fringes of one of the Farrington Member peat mires was domi- nated by sigillarian (Laevigatisporites) megaspores, with subordi- nate herbaceous lycopsid megaspores (Triangulatisporites). Unfortunately, it is not known which coal seam Crookall acquired this specimen from so further comparison is not possible.

CONCLUSIONS

1. Abundant and well-preserved megaspore assemblages were obtained from the Warwickshire Group of the Bristol Coalfield, representing four distinct depositional settings: poorly drained and disturbed coastal plain; periodically established point-bar mires associated with active braidplains; temporally and laterally persistent peat mires; and clastic swamps on the fringes of the well-developed peat mires.

2. Sigillarian megaspores dominate the better-drained and disturbed settings of the coastal plains and clastic mire fringing peat mires. Selaginellid megaspores are also found in the clastic swamps.

3. Lepidodendrid megaspores dominate both the well- developed peat mire, and the relatively short-lived point-bar mire assemblages.

4. The biostratigraphically important taxa, Tuberculatispo- rites brevispiculus and Parasporites maccabei, suggest that the upper Mangotsfield Member is Asturian in age. This diminishes the duration of the stratigraphic gap reported in Pendleton et al., (2012).

5. Megaspore assemblages reported from the Forest of Dean Coalfield generally feature a more diverse col- lection of taxa compared to those reported here from the Bristol Coalfield. These differences are probably driven by the difference in the depositional environ- ments sampled in the Forest of Dean (thick and later- ally extensive economic coal seams reflect widespread and well-developed mire communities) and those avail- able for sampling in the Bristol Coalfield (dominated by clastic swamps and small-scale and short-lived peat mires, with little available material from well-developed mires).

6. Parasporites maccabei is recorded here for the first time in Europe. Here this species is associated with the periodically established point-bar mires.

ACKNOWLEDGEMENTS

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REFERENCES


Pennsylvanian of the Bristol Coalfield, UK

Formation of Bristol, southern Britain: Further evidence for taphonomic megabias.


Appendix 9 – Published paper: Falcon-Lang et al. (2011)
Dryland plant communities in the Pennsylvanian (mid- to late Bolsovian) Winterbourne Formation of Bristol, southern Britain: Further evidence for taphonomic megabias

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Abstract

Pennsylvanian dryland plant communities are poorly known compared to those of coeval wetlands – a function of taphonomic megabias. Here we describe a new example from the mid- to late Bolsovian Winterbourne Formation of Staplehill, Bristol, southern Britain based on a re-examination of historical fossil material. These fossils, collected by Herbert Bolton in 1905/6, initially studied by Dennis Lillie in 1908/9, and later re-assessed by Robert Crookall in 1926/7, were thought to have been lost until their recent discovery in an unaccessioned repository at the British Geological Survey. The calcified assemblage, which we describe and fully illustrate for the first time, is dominated by cordaitalean remains (Dadoxylon trunks, Amyelon roots and Mesoxylon aerial axes), together with a single medullosan pteridosperm (Sutcliffia illinoi) and an indeterminate lycopsid (possibly sigillarian). Locality and facies data collected at the time of the original discovery, combined with new facies data from boreholes, limited outcrops, and sediments adhering to the fossils, demonstrate that this assemblage was deposited in a well-drained alluvial plain environment. Three independent lines of evidence indicate a seasonal subhumid tropical climate: (1) the breccia-conglomerate unit that hosts the fossil assemblage is interpreted as the deposits of a somewhat flashy alluvial drainage, (2) carbonate rhizoconcretions reworked into the conglomerate with the water-worn fossils are interpreted as remains of caliche paleosols that develop only under conditions of seasonal water deficit, and (3) erratic growth interruptions in the fossil woods indicate the plants grew under aperiodic water-stressed conditions. These findings provide further evidence that gymnosperm-dominated dryland ecosystems were more abundant and widespread in the Pennsylvanian tropics than previously recognized.

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1. Introduction

The ‘Coal Forests’ that characterize the Pennsylvanian Subsystem are some of the best-understood terrestrial ecosystems in the entire Phanerozoic Eon (DiMichele and Phillips, 1994; DiMichele et al., 2001, 2007). This is partly due to the fact that fossil trees are commonly preserved in growth position, allowing unrivalled insights into forest structure and function (DiMichele and Falcon-Lang, 2010). However, another reason is their close association with coal-bearing strata. Coal deposits originated in permanently waterlogged environments where the preservation of plant material was maximized (Behrensmeyer et al., 2000; Gastaldo and Demko, 2010), and have been extensively mined, giving geologists the opportunity to inspect fossils and strata in an unusual level of detail (DiMichele et al., 2007).

Far less well documented are the ecosystems that colonized Pennsylvanian tropical drylands (Falcon-Lang, 2003a). The United Nations Environment Program defines ‘drylands’ as regions where the ratio between mean evapotranspiration exceeds mean annual rainfall, and there is seasonal water-deficit for ecosystems (Anon, 1997). Such regions comprise arid, semi-arid and dry subhumid zones and are extremely widespread, covering ~40–50% of the global land surface (Anon, 1997). The deposits of alluvial drylands are recognized in the Pennsylvanian record by the presence of primary red beds (Besley and Turner, 1983; Besley and Fielding, 1989), well-drained paleosols such as vertisols and calcisols (Tandon and Gibling, 1994; Feldman et al., 2005), playa carbonates, evaporites, badland topography (Falcon-Lang et al., 2010b), and the coarse-grained deposits of flashy drainages (Rygel and Gibling, 2006; Fielding et al., 2009), amongst other criteria.

Studies of paleosols in a sequence stratigraphic context strongly suggest that Pennsylvanian drylands were most widespread during glacial phases when sea level was lowered, continentality enhanced, and the moisture carrying-capacity of the atmosphere reduced.
(Tandon and Gibling, 1994; Feldman et al., 2005). However, even during humid interglacial phases, when wetland Coal Forests were dominant (Falcon-Lang, 2004; Falcon-Lang and DiMichele, 2010), drylands existed at the periphery of the tropics (Falcon-Lang et al., 2011b), and are also inferred to have existed in many upland (extra-basinal) terrains (Stopes, 1914). Thus, our knowledge of Pennsylvanian dryland vegetation has to be pieced together from fragmentary remains, often poorly preserved and allochthonous, derived from upland, well-drained lowland, and subtropical sources (DiMichele et al., 2010; Bashforth et al., 2010).

Those limited (but widespread) data suggest that Pennsylvanian drylands were dominated by gymnosperms, including pteridosperms, cordaitaleans, conifers, and plants of uncertain affinity, in contrast to the mostly pteridophyte-dominated swamps (DiMichele et al., 2010). However, the variability of plant assemblages points to considerable landscape heterogeneity in dryland environments (Stopes, 1914; Havlena, 1953; Chaloner, 1958; Remy and Remy, 1975; Leary and Pfefferkorn, 1977; Galtier et al., 1992; Rössler and Barthel, 1998; Falcon-Lang and Bashforth, 2004, 2005; Dolby et al., 2011; Falcon-Lang et al., 2011a,b), probably reflecting local differences in climate, elevation, gradient, aspect, and bedrock.

For example, some Pennsylvanian dryland plants show mesophytic (Lesleya, Megasporites) (DiMichele et al., 2010) or perhaps even xerophytic (conifers) adaptive traits (Falcon-Lang et al., 2011b), suggestive of growth under conditions of pronounced seasonality. However, other assemblages are dominated by broad-leaved cordaitaleans (Falcon-Lang, 2003a,b,c; Falcon-Lang, 2004), which show very wide tracheids (Falcon-Lang and Scott, 2000a,b), and if present at all, only very weakly developed growth interruptions in their wood (Falcon-Lang, 2007); these traits are suggestive of dry subhumid settings consistent with independent facies data from host alluvial strata (Rygel and Gibling, 2006).

In this paper, we document probable subhumid plant communities from Pennsylvanian (mid- to late Bolsovian) dryland facies in the Winterbourne Formation of Staplehill, Bristol, southern Britain (Fig. 1). The fossil material that we describe has been known for over a century but its significance has only now come to light following studies of its geological context. In the following, we (1) describe the history of discovery of the Staplehill plant assemblage, (2) use historical maps and borehole sections to fix its precise location and stratigraphic position, (3) re-examine boreholes, limited outcrops, and sediments adhering to the fossils to understand their sedimentary context, (4) re-examine historic slide collections to fully illustrate material for the first time, and (5) synthesize data to understand its unusual palaeoecology.

2. History of discovery

The earliest record of the discovery of the Staplehill fossils is found in correspondence between Herbert Bolton (1863–1936), curator of the Bristol Museum and Art Gallery (Wallis, 1936) and palaeobotanist, Marie Stopes (1880–1958), accessioned in the British Library (BL58476–BL58477). Bolton had hoped that Stopes, an expert on the origin of Pennsylvanian coal balls (Falcon-Lang, 2008a), might examine the plant assemblage herself. However, as she was about to depart on an 18-month long fieldtrip to Japan from July 1907 to January 1909 (Falcon-Lang, 2008b), she turned down the opportunity to collaborate with him.

On 3 June 1907, Bolton wrote to Stopes: “It will interest you to know that some little while ago whilst examining the Pennant Grit in Fig. 1. Stratigraphic distribution of well-studied Pennsylvanian dryland plant assemblages in Euramerica (note that many Late Pennsylvanian assemblages are not shown because such floras are common by this time interval). Sites as follows: Joggins, Nova Scotia, Canada (Falcon-Lang, 2003a,b); Tynemouth Creek, New Brunswick, Canada (Falcon-Lang et al., 2010); Rock Island, Illinois, USA (Leary and Pfefferkorn, 1977); Errurra Formation, northern Britain (Galiker et al., 1992; Clouter et al., 1993); Sydney Mines, Nova Scotia, Canada (Falcon-Lang, 2004; Dolby et al., 2011); Cottage Grove, Illinois, USA (Falcon-Lang et al., 2009); 7–11 Mine, Ohio, USA (McComas, 1988; Falcon-Lang et al., 2011a); Socorro, New Mexico, USA (Falcon-Lang et al., 2011b); Hamilton, Kansas, USA (Rothwell and Mapes, 1988); Garnett, Kansas, USA (Cridland and Morris, 1963).
the vicinity of Bristol, I found that some of the large masses of material were really calcified plants showing structure. I extracted several, one of which I cut down to show the structure, and sent to Dr. Scott [D. H. Scott (1854–1934), the well-known palaeobotanist at Kew Gardens]. It was of the cordaitan type. He suggested I send them to Mr. Arber [E. A. N. Arber (1870–1918), curator of the Sedgwick Museum, Cambridge] for examination, but our local lecturer in Botany, Mr. J.H. Priestley, desired to work at the specimens, and I accordingly gave them to him. I am afraid however, that he has not done anything yet. I have visited the place since and obtained more specimens that Priestley now has*. (BL58476: 52).

J. H. Priestley (1883–1944) was lecturer in Botany at the University of Bristol from September 1905–1911 (Anon, 1944). This fixes the date of discovery to late 1905/1906 because Bolton’s phrase “some little while ago” and his evident exasperation with Priestley’s lack of progress implies that an interval of time had passed since the fossils were first extracted.

The next mention of the Staplehill material that we have been able to track down is in correspondence between E.A.N. Arber at the Sedgwick Museum and Dennis Gascoigne Lillie (1884–1963), a...
Cambridge-based biologist, undertaking general studies of the Pennsylvanian plant assemblages of the Bristol Coalfield (Lillie, 1910a). In a letter dated 23 September 1907, Arber wrote to Lillie, “These petrifactions at Bristol promise well for the future & you're just the right man to do it. Bolton’s letter struck me as very satisfactory & you must see him next year” (accessioned in the Welcome Library, London; MS5254.17). The implication of Arber’s letter is that Bolton’s patience with Priestley had finally run out and he was looking to get others interested in the material.

This is confirmed in a later letter, dated 22 July 1908, between Bolton and Stopes (now in Japan), informing her of the following development: “I had Mr. Lillie of St. Johns, Cambridge, in Bristol the other day in order to examine the Pennant Grit containing plant remains. He carried off a fair amount of the material and seemed very well satisfied with his visit. I am sorry to say that the coal mining venture has not succeeded and the shaft [at Staplehill] has been disabled so that no more material will be obtained. There is a fair quantity still lying on the pit heap and it seems a pity that it should not be made use of, but I know of no one who will really take it up” (BL58477: 46).

Unfortunately, although Lillie made more progress than Priestley, he was only able to publish a brief note on the Staplehill material (Lillie, 1910b), as a result of mental illness (Crookall, 1927a); he was delusional, and is also believed to have been a manic depressive (Griffiths, 2007). In addition, in August 1910, he departed for Antarctica on Robert Falcon Scott’s fateful Terra Nova Expedition (1910–1913), serving as marine biologist and acquiring the nickname “Ooze” because of his interest in deep-sea ooze.

Consequently, the Staplehill specimens were not further studied until palaeobotanist, Robert Crookall (1890–1981) undertook a brief re-description (Crookall, 1927a). Crookall had completed his Ph.D. on the Bristol Coalfield fossil plants at the University of Bristol in 1924.
3. Location and stratigraphy

Despite being collected over a century ago, the location and stratigraphic position of Herbert Bolton's fossil site can be precisely determined. Lillie (1910a,b) noted that the fossils were collected from Staplehill, a district of northeast Bristol (Fig. 2A), at the bottom of a newly sunk shallow shaft. Although Lillie (1910a,b) did not give further location details, comparison of historic Ordnance Survey maps for 1903 and 1916 (County Series, 1: 2500, Grid ST67) fixes the position of the shaft precisely. There was only one excavation in this area between these dates, and the later map indicates that it was abandoned by 1916 matching Lillie’s description exactly. This excavation was positioned at the northwest corner of present day Riviera Crescent, Staplehill (postcode BS16 4SF, 51°28′42.58″N, 2°30′14.72″W; Fig. 3).

This site lies on the northern limb of the Kingswood Anticline of the Bristol Coalfield, near the steeply dipping (40–50°) boundary of the Middle Pennsylvanian Winterbourne Formation and the overlying Pennant Sandstone Formation in the lower part of the Warwickshire Group (Green, 1992; Kellaway and Welch, 1993; Waters et al., 2009). Lillie (1910a, p. 60) further remarked that the shallow shaft, in which Bolton’s fossils were found, was abandoned somewhat below “the Pennant Grit” (= Pennant Sandstone Formation). Our inferred location for the shaft is 35 m south of the boundary between the Pennant Sandstone Formation and underlying Winterbourne Formation (marked by the Hen = Parrot Coal), within the surface crop of uppermost Winterbourne Formation (Fig. 3), again closely matching Lillie’s description.

The Winterbourne Formation is a 120–180 m thick unit whose distribution is restricted to the Kingswood Anticline and Coalpit Heath Syncline regions of the northern part of the Bristol Coalfield (Green, 1992; Kellaway and Welch, 1993; Waters et al., 2009). Although minimal surface outcrop currently exists, it is intersected by at least seven British Geological Survey (BGS) boreholes including Harry Stoke B and C, Yate Deep, Stoke Gifford 1 and 2, Winterbourne and Westerleigh 1, demonstrating its distribution over about 20 km² (Fig. 2B). The Winterbourne Marine Band (also known as the Cambriense Marine Band) is the base of the Winterbourne Formation in the Coalpit Heath Syncline region, although this marine marker bed has not been found in the adjacent Kingswood Anticline region (Waters et al., 2009). The top of the Winterbourne Formation is taken to be the base of the first major, coarse-grained sandstone bed of the Pennant Sandstone Formation (Waters et al., 2009).

The base of the Winterbourne Formation is of mid-Bolsovian age given the occurrence the nautilioid index fossil, Anthracoceras philippisi in several horizons of dark grey shale near the base and top of the Winterbourne Formation, and throughout most of the overlying Pennant Sandstone Formation (Moore and Trueman, 1937). The near surface occurrence of this conodont, in the Winterbourne Marine Band (Stubblefield and Trotter, 1957) is consistent with reports of the non-marine bivalve Anthracoceras philippisi in several horizons of dark grey shale near the base and top of the Winterbourne Formation, and throughout most of the overlying Pennant Sandstone Formation (Moore and Trueman, 1937). The near surface occurrence of this conodont, in the Winterbourne Marine Band (Stubblefield and Trotter, 1957) is consistent with reports of the non-marine bivalve Anthracoceras philippisi in several horizons of dark grey shale near the base and top of the Winterbourne Formation, and throughout most of the overlying Pennant Sandstone Formation (Moore and Trueman, 1937), suggestive of a late Bolsovian age for these strata (Waters et al., 2009). Palynological assemblages from Harry Stoke B borehole further imply a mid-Bolsovian (TS subzone) age for the Winterbourne Formation, consistent with ongoing studies of megafossil remains (Cleal, 1997; J. Pendleton, unpublished data). Thus, we infer that the Winterbourne Formation is of mid- to late Bolsovian age (Fig. 4).

4. Sedimentary facies

The Winterbourne Formation comprises a mudstone-dominated succession, which is dominantly grey and coal-bearing in its lower part, but mostly red with distinctive quartz-conglomerate beds in its upper part (Moore and Trueman, 1937, Fig. 4). As discussed above, the Staplehill fossil plant assemblage that forms the focus of this paper originated from the upper (red) part of the formation, and as Lillie (1910a) noted, the host lithology was “a peculiar breccia-conglomerate, containing numerous angular and rounded pebbles, set in a sandstone matrix” (p. 60).

4.1. Harry Stoke C borehole

In the absence of any current extensive outcrops, the most detailed record of the sedimentary facies of the Winterbourne Formation is found in Harry Stoke C, the British Geological Survey borehole located in nearby Downend (Grid Reference ST65047677), 900 m NNW of the fossil site (Fig. 4). In this borehole, the uppermost 40 m of the Winterbourne Formation is dominated by red mudstone beds or red/grey/green mottled mudstone beds showing common rootlet, slicken-sides and localized mud cracks (63% of stratal thickness). Hosted within these primary red bed units, at three separate intervals (depths 337–341 m, 353–356 m, and 390–393 m in the Harry Stoke C borehole), are conglomeratic beds comprising poorly-sorted rounded, sub-angular or angular pebbles of quartz, lithic fragments and mudstone rip-up clasts. The conglomerate beds are up to 2–3 m thick, fine-upwards into coarse-grained sandstone, and may show rooted upper surfaces.

4.2. Disused railway cutting near Staplehill

Another source of facies data is a very poor outcrop on the south side of a disused railway cutting (now used as a cycle track; 51°28′44.69″N, 2°30′46.91″W), located approximately 800 m east and along-strike of the Staplehill site. Here strata belong to the upper part of the Winterbourne Formation at a horizon approximating to the Staplehill fossil layer. Large angular blocks of rock scattered over this area comprise breccia-conglomerate containing abundant, sub-rounded (water-worn) clasts of permineralised wood, up to 0.18 m long (Fig. 5), which exactly match Lillie’s description the lithology at Staplehill. The conglomerate contains subangular to subrounded pebbles of quartz, subangular feldspar, and lithic fragments pebbles in a coarse-grained, red to green sandstone matrix. Red to brown mudstone intraclasts are also common.

4.3. Sediments adhering to Bolton’s fossil specimens


![Fig. 5. Hand specimen of a green/red conglomerate containing dark grey, rounded clasts of permineralised wood (arrows), found at the side of a disused railway line, 800 m alongside strike from the source of Bolton’s material (51°28′44.69″N, 2°30′46.91″W).](image-url)
lithic fragments that show distinctly reddened rims (Fig. 6A); sub-angular red mudstone rip-ups, locally containing small carbonate glaebules (Fig. 6B); large carbonate nodules showing fluffy, nodular, brecciated and laminar textures suggestive of an amalgamated caliche layer (Fig. 6D); cylindrical rhizoconcretions with root hairs that are composed of red silty carbonate (Fig. 6C, E-F); and haematite nodules, up to 12 mm diameter.

4.4. Palaeoenvironmental synthesis

Drawing together these disparate observations, the uppermost part of the Winterbourne Formation is interpreted as the product of a well-drained alluvial plain. Conglomeratic beds represent the deposits of alluvial drainages, and clast angularity and poor sorting implies somewhat flashy seasonal discharge. The most likely source for the coarse conglomeratic detritus was the Usk Anticline (Waters et al., 2009), an elevated area with a few hundred metres of topography, positioned 40 km west of Bristol (George, 1956). Thick, rooted mudstone successions within some upward-fining alluvial channel deposits possibly represent abandonment facies, consistent with recent facies models for dryland rivers (Fielding et al., 2009). Primary red colouration, combined with evidence of reworked caliche soils (carbonate glaebules, nodules, rhizoconcretions) within conglomeratic channel facies, and lithic clasts with oxidized rims, provide additional support for seasonal dryness (Tandon and Gibling, 1994). Such sediments are characteristic of dry subhumid alluvial plains of...
in his papers (Crookall, 1927a, 1931), he neither cited Sedgwick and prepared additional slides of his own (Crookall, 1927b, 1931). Yet, borrowed all of Lillie’s material, including his original thin sections the curator of the Sedgwick Museum (Arber had died in 1918), and degrading interpermineralised plant axes suggests material from transported from Sinha et al., 2006). The rounded, water-worn character of the was unknown, and it was feared that these important specimens had later study, Crookall (1927a) noted that he contacted Mr. H. Woods, Cambridge, he did not publish specimen numbers. At the time of his ordered the hand specimens to be discarded after they were cut. we can ascertain); only the thin sections have been located. In fact, Crookall’s notes on some thin sections suggest that he may have prepared additional slides of his own (Crookall, 1927b, 1931). Yet, in his papers (Crookall, 1927a, 1931), he neither cited Sedgwick specimen numbers, nor gave BGS numbers, although he made cryptic reference to specimens with the pre-fix R.C. (presumably standing for Robert Crookall).

5.1. Rediscovery

In 2010/11, one of us (HFL) attempted to re-locate the Staplehill specimens. However, no trace of them was found at the Sedgwick Museum (according to curator, Matt Riley), and perplexingly, they were not numbered in the formal registry (despite the fact that Lillie’s other specimens from the Bristol Coalfield, collected at the same time, were on the register). Neither were the specimens found during an exhaustive search of collections at the Natural History Museum, London (by curator, Dr. Tim Ewin), where Crookall (1927a, 1931) had reposited other specimens from his Bristol papers. A search of the Bristol City Museum (by curator, Roger Vaughan), where Bolton had been director, also proved fruitless and it was feared that the specimens had been destroyed in Nazi bombing raids, which had badly damaged the museum in 1940.

Finally, on the suggestion of Cedric Shute (retired curator, Natural History Museum, London), a search was made of the holdings of the British Geological Survey (BGS), Keyworth, Nottingham (by curator, Paul Shepherd), and a small number of slides bearing the name “Lillie” came to light. On February 3, 2011, one of us (HFL) spent a day checking through all the BGS’s thin sections. Additional thin sections bearing the word “Lillie” were found and these led back to an old register that had belonged to Crookall (simply labeled “Slides”). Cross-checking with this document eventually turned up the whole Staplehill collection scattered through seven BGS drawers.

5.2. Surviving material

None of the original hand specimens of the fossils, or samples of the lithology in which they occurred, have been preserved (as far as we can ascertain); only the thin sections have been located. In fact, Crookall’s notes on some thin sections suggest that he may have ordered the hand specimens to be discarded after they were cut. According to Crookall’s notes in his ‘Slides’ register, Lillie’s material comprised 18 specimens lettered A, B, C, D, E, F, H, L, M, N, O, P, Q, R, S, T, U, and Z (though we might infer that there were specimens lettered G, I, J, K, V, W, X and Y, which never came into Crookall’s possession for

### Table 1

**Summary of Lillie’s fossil collection from Staplehill giving a list of the thin sections preserved at the British Geological Survey, Keyworth, UK.**

<table>
<thead>
<tr>
<th>Lillie code</th>
<th>BGS number(s)</th>
<th>Number of slides</th>
<th>Slide maker</th>
<th>Identity</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>R.C. 9–19</td>
<td>12</td>
<td>Crookall</td>
<td>cf. <em>Mesoxylon</em></td>
</tr>
<tr>
<td>B</td>
<td>P.B. 257–268</td>
<td>12</td>
<td>Hemingway</td>
<td><em>Sutclifia lilliei</em></td>
</tr>
<tr>
<td>C</td>
<td>P.B. 209–280, R.C. 60–61</td>
<td>14</td>
<td>Lomax, Crookall</td>
<td><em>Mesoxylon</em></td>
</tr>
<tr>
<td>D</td>
<td>P.B. 281–284, R.C. 64</td>
<td>5</td>
<td>Lomax, Crookall</td>
<td><em>Amylon</em></td>
</tr>
<tr>
<td>E</td>
<td>R.C. 62</td>
<td>1</td>
<td>Crookall</td>
<td><em>Dadoxylon</em></td>
</tr>
<tr>
<td>F</td>
<td>P.B. 288–290</td>
<td>3</td>
<td>Lomax</td>
<td>cf. <em>Amylon</em></td>
</tr>
<tr>
<td>G</td>
<td>P.B. 294–296</td>
<td>3</td>
<td>Lomax</td>
<td><em>Dadoxylon</em></td>
</tr>
<tr>
<td>H</td>
<td>P.B. 244–246</td>
<td>3</td>
<td>Lomax</td>
<td><em>Lycospid wood</em></td>
</tr>
<tr>
<td>I</td>
<td>P.B. 291–292</td>
<td>2</td>
<td>Lomax</td>
<td><em>Dadoxylon</em></td>
</tr>
<tr>
<td>J</td>
<td>P.B. 297–299</td>
<td>3</td>
<td>Lomax</td>
<td><em>Dadoxylon</em></td>
</tr>
<tr>
<td>K</td>
<td>P.B. 285–287</td>
<td>3</td>
<td>Lomax</td>
<td><em>Amylon</em></td>
</tr>
<tr>
<td>L</td>
<td>P.B. 300–302</td>
<td>3</td>
<td>Lomax</td>
<td><em>Dadoxylon</em></td>
</tr>
<tr>
<td>M</td>
<td>P.B. 303–304</td>
<td>2</td>
<td>Lomax</td>
<td><em>Amylon</em></td>
</tr>
<tr>
<td>N</td>
<td>P.B. 305</td>
<td>1</td>
<td>Lomax</td>
<td>indeterminate</td>
</tr>
<tr>
<td>O</td>
<td>P.B. 306–308</td>
<td>3</td>
<td>Lomax</td>
<td><em>Dadoxylon</em></td>
</tr>
<tr>
<td>P</td>
<td>P.B. 247–255</td>
<td>9</td>
<td>Lomax</td>
<td><em>Mesoxylon</em></td>
</tr>
<tr>
<td>Q</td>
<td>P.B. 288</td>
<td>1</td>
<td>Lomax</td>
<td>Not a fossil</td>
</tr>
<tr>
<td>R</td>
<td>P.B. 293</td>
<td>1</td>
<td>Lomax</td>
<td><em>Mesoxylon</em></td>
</tr>
<tr>
<td>S</td>
<td>P.B. 319–320b</td>
<td>3</td>
<td>Hemingway</td>
<td><em>Dadoxylon</em></td>
</tr>
</tbody>
</table>

The modern Gavetic Plain, where caliche develops on interfluves, and is reworked into drainages under a strongly seasonal rainfall regime of 800–1000 mm, or up to 1500 mm per year (Gibling et al., 2005; Sinha et al., 2006). The rounded, water-worn character of the permineralised plant axes suggests material from transported from the degrading interfluves on which caliche soils were forming.

## Plate I

*Mesoxylon* cf. *sutclifia*, Lillie’s specimens A, C, and T (Table 1).

1. Axis comprising pith, primary vasculature and secondary xylem only, TS, scale 2.5 mm, P.B. 277, specimen C.
2. Axis comprising pith, primary vasculature and secondary xylem only, TS, scale 3 mm, P.B. 249, specimen T.
3. Septate pith, RLS, scale 3 mm, P.B. 279, specimen C.
4. Cauline bundles embedded near to the outer edge of pith (arrows), departing at steep angle, RLS, scale 1 mm, P.B. 270, specimen C.
5. Vascular traces departing through the secondary xylem at a shallow angle, TS, scale 2 mm, P.B. 247.
6. Growth interruptions (arrow), TS, scale 1 mm, P.B. 249, specimen T.
7. Septate pith bordered by rectangular cells with dark contents, RLS, scale 750 μm, P.B. 274, specimen T.
8. Mesarch cauline bundle (arrow), TS, scale 200 μm, P.B. 277, specimen C.
9. Tracheid pits, 1-2-seriate, alternate, contiguous, and rays, RLS, scale 100 μm, P.B. 274, specimen C.
10. Cross-fields with 2-4-equisetoid pits, RLS, scale 75 μm, P.B. 274, specimen C.
11. Uneiserate rays, typically 1-5 cells high, RLS, scale 175 μm, P.B. 272, specimen C.

## Plate II

*Amylon* sp., Lillie’s specimens D, F, G, and Q (Table 1). (see on page 276)

1. Axis showing strongly unequal radial growth (arrow), TS, scale 3 mm, P.B. 285, specimen O.
2. Part of axis lacking pith, TS, scale 3 mm, P.B. 283, specimen D.
3. Growth interruptions partly defined by axial parenchyma with dark contents, TS, scale 500 μm, P.B. 283, specimen D.
4. ?Axial parenchyma (?) with dark contents, RLS, scale 250 μm, P.B. 282, specimen D.
5. ?Axial parenchyma (?) with dark contents, RLS, scale 250 μm, P.B. 282, specimen D.
6. Axis showing pitting, RLS, scale 75 μm, P.B. 288, specimen D.
7. Inflated tracheids or (?) axial parenchyma, TS, scale 100 μm, P.B. 285, specimen O.
8. Tracheid pitting, alternate, contiguous, 2-4-seriate, RLS, scale 100 μm, P.B. 286, specimen O.
9. Axial parenchyma with dark contents, within growth interruption zones, RLS, scale 250 μm, P.B. 288, specimen F.
10. Rays, uniseriate with short biseriate portions, up to 23 cells high, RLS, scale 150 μm, P.B. 303, specimen Q.
11. Contorted tracheids, RLS, scale 300 μm, P.B. 282, specimen D.
12. Circular holes with ragged margins, TS, scale 250 μm, P.B. 290, specimen F.

The rounded, water-worn character of the was unknown, and it was feared that these important specimens had been lost. Although Lillie (1910b) indicated that he had accessioned his fossils and associated thin sections in the Sedgwick Museum, Cambridge, he did not publish specimen numbers. At the time of his further study, Crookall (1927a) noted that he contacted Mr. H. Woods, the curator of the Sedgwick Museum (Arber had died in 1918), and borrowed all of Lillie’s material, including his original thin sections and prepared additional slides of his own (Crookall, 1927b, 1931). Yet, in his papers (Crookall, 1927a, 1931), he neither cited Sedgwick
Plate II (caption on page 274).
some unknown reason). The thin sections of Lillie's 18 specimens can be ordered into three groups, based on their quality of preparation and the printed labels affixed to the slides.

Most of the thin sections (n = 53) bear the label “Lomax Bolton Lancashire, Petrographic and Palaeo-botanical laboratories (Lancashire and Cheshire Coal Research Association)”. These represent most of the thin sections on which Lillie (1910b) based his original study. James Lomax (1857–1934), who prepared thin sections for the palaeobotanical community on a commercial basis (Howell, 2005), cut the material around 1908/9. These Lomax thin sections are of excellent quality, though the balsam has contracted somewhat over the past century, creating creases and undulations in the fossil material. The Lomax thin sections bear letters that correspond to each of Lillie's specimens, although thin sections for specimens A, B, E, M, and Z are missing. Crookall (1951) indicates that palaeobotanist, Prof. W.T. Gordon (1884–1950) of King's College, London, assisted Lillie in the preparation of some of his material, but the nature of his assistance is not clear.

A few thin sections (n = 15) bear the label of another commercial thin section manufacturer, “W. Hemingway, Derby”. Twelve of these thin sections are labeled 1–32, and notes in Crookall's 'Slides' register show they represent Lillie's specimen B. Three others are unlabeled, but these represent Lillie's specimen Z according to Crookall’s 'Slides' register. As Crookall obtained thin sections of his other Bristol material from Hemingway in 1926/7, we infer that the thin sections for specimens B and Z were also cut at that time. This raises a problem, however, because we know that Lillie (1910b) obtained sections for specimen B himself (presumably from Lomax). What happened to the Lomax thin sections for specimen B is unknown.

Finally, a few other thin sections (n = 18) bear the label of the British Geological Survey and must represent the slides that Crookall prepared, around 1926/7, from the surviving off-cuts of Lillie’s material, brought back from the Sedgwick Museum. The slides are very poorly made. Eleven are labeled “Lillie's A”, two are labeled “Lillie's M”, and five are variously labeled Lillie's XA, XC, XD, XE; we infer that latter labels indicate extra material from Lillie's specimens A, C, D, E and F. If this inference is correct, then sections from each of Lillie’s 18 specimens have survived. Table 1 summarizes this thin section collection, giving current BGs accession numbers.

6. Description of plant assemblage

To date, no detailed systematic study has been made of Lillie’s 18 calcified plant fossils from Staplehill, nor has the material been adequately illustrated. Lillie (1910b) variously assigned his specimens to Cordaites and Myeloxylon, while Crookall (1927a) reassigned them to Mesoxylon sp. and Sutcliffia lilliei, respectively, morphogenera of cordaitaleans and medullosan pteridosperms. Here we show that, of the 16 determinable specimens, cordaitaleans are dominant, including roots (Amyelon sp., n = 4), mature axes (Dadoxylon sp., n = 7) and juvenile aerial axes (Mesoxylon cf. sutcliffia, n = 3), while medullosan pteridosperms (Sutcliffia lilliei) and lycopsids are each represented by a single specimen. In the following descriptions, specimens are described in transverse (TS), radial longitudinal (RLS) and tangential longitudinal (TLS) sections.

Class CONIFEROPSIDA

Order CORDAITALES

Mesoxylon cf. sutcliffia (Plate I)

Material: British Geological Survey, Lillie's specimens A7, C, and T (Table 1). Thin sections: P.B. 247–255, 269–280; R.C. 9–19, 60–61. Notes on material: Specimen A is poorly preserved and referred to Mesoxylon with uncertainty (R.C. 9–19); it is not used in the following description. Specimen C has been cut into two transverse segments (C, P.B. 277; Ca, P.B. 278). Six serial longitudinal sections have been cut for C (P.B. 269–270, 272–273, 279–280) and four for Ca (P.B. 271, 274–276) and their relative position is marked on each transverse section (P.B. 277–278) by means of numbered black lines (Plate I, 1). Specimen T has been cut into six serial transverse sections (P.B. 247–252), whose relative order is indicated by numbers 1–6 annotated on the labels, together with two radial (P.B. 254–255) and two tangential sections (P.B. 253, 256). Thin section P.B. 269 is badly broken and missing its cover slip.

Description: Small axes comprising pith, primary vasculature, and secondary xylem cylinder, but lacking extraxylary tissue (Plate I, 1, 2). Of the two well-preserved specimens, specimen C is up to 22 mm diameter with a 8 mm diameter pit (Plate I, 1) and specimen T is up to 34 mm diameter with a 11 mm diameter pit (Plate I, 2). In both cases, the pith is parenchymatous, septate (Plate I, 3), and bordered by up to 9 rows of vertically arranged, rectangular cells (35 μm high × 110 μm wide), with dark contents (Plate I, 7, 8).

Primary vasculature is non-symподial (Plate I, 4) with typically 32–34 mesarch cauline bundles arranged around the pith circumference (Plate I, 8) in specimen C. Cauline bundles, 300–350 μm diameter, are composed of scalariform- to reticulate-thickened tracheids, 20–25 μm diameter, and surrounded by a parenchymatous sheath. They originate within the outermost pith (up to 300 μm from the edge of the pith), departing initially at an angle of about 80° (Plate I, 4), before passing out through xylem cylinder at an angle of 20–25° (Plate I, 5). Unfortunately cauline bundles are rarely seen in the larger specimen T (the only specimen for which serial transverse sections exist) so further details of the vasculature cannot be established.

Secondary xylem comprises tracheids, 34–68 μm diameter, showing typically 1–2-seriate (rarely 3–4-seriate), circular to oval, contiguous, alternate bordered pits (Plate I, 9), and uniseriate rays, 1–8 cells high (typically 1–5) showing 2–3 oval cupressoid pits per cross-field (Plate I, 10, 11). Secondary xylem shows common, irregular growth interruptions, defined by rhythmic fluctuations in tracheid diameter (Plate I, 6). Interruptions fade around the cambium as they locally wedge out by merging with adjacent interruptions (Plate I, 3).

Identity: Based on their mesarch cauline bundles and non-symподial primary vasculature, specimens are placed in the genus, Mesoxylon (Scott and Maslen, 1910; Trivett and Rothwell, 1985). Similar specimens have been described from marine maximum flooding surfaces in the Langsettian of northern Britain (Maslen, 1911; Scott et al., 1997) and from red beds in the Langsettian of Canada (Falcon-Lang, 2003c) under the name Mesoxylon sutcliffia. In the absence of extraxylary tissue, which forms part of the diagnosis for this species, we refer our specimens to Mesoxylon cf. sutcliffia. Cordaitaleans are generally considered to have been the parent plant of Mesoxylon-type axes (Trivett and Rothwell, 1991). However, a recent study raises the possibility that some younger Kasimovian specimens of Mesoxylon may have belonged to conifers, based on their co-occurrence with Walchia-dominated assemblages, marked tree-rings, and evidence for a deciduous phenology (Falcon-Lang et al., 2011b). Nonetheless, in the absence of these indicators, our Staplehill specimens are considered most probably to be cordaitaleans.

Amyelon sp. (Plate II)

Material: British Geological Survey, Lillie's specimens D, F7, O, and Q (Table 1). Thin sections: P.B. 281–290, 303–304; R.C. 64.

Description: Small protostelic axes (Plate II, 1, 2, 3) whose primary anatomy is not intersected in the longitudinal sections available. The inferred diameter for the incomplete specimen D is 34 mm while specimen O is 22 mm in diameter. Secondary xylem comprises tracheids, 51–73 μm diameter, showing typically 2–4-seriate, circular, contiguous, alternate bordered pits (Plate II, 9), and uniseriate rays (some with short biseriate portions), 1–23 cells high (typically 1–10) showing 2–7 oval cupressoid/araucarioid pits per cross-field (Plate II, 9, 11). Individual tracheids, and localized zones of secondary xylem, maybe contorted along their length (Plate II, 13). Growth interruptions are present and show strongly unequal radial growth around the circumference (Plate II, 1). Interruptions are defined by a decline in
tracheid diameter and the occurrence of axial parenchyma containing dark contents (Plate II, 4, 8). Axial parenchyma cells are typically arranged in vertical series (Plate II, 5, 6, 10) and may show small pits (Plate II, 7). Circular holes, 200 μm diameter, showing ragged margins, are seen in some specimens.

**Identity and functional morphology:** The secondary xylem is similar to the facies-associated *Mesoxylon* axes and probably derived from the same parent plant. However, rather than representing aerial axes as in *Mesoxylon*, the specimens probably comprise roots given the protostelic organization, the occurrence of strongly unequal radial growth, and the presence of somewhat contorted tracheids. Carboniferous axes with these features are placed in the genus *Amyelon* (Barnard, 1962), and represent the roots of cordaitaleans (Scott, 1900).

The secondary xylem of *Amyelon* differs from that of *Mesoxylon* in three ways. It shows (1) larger diameter tracheids showing more numerous rows of tracheid pits; (2) taller, wider rays, and (3) prominent axial parenchyma, locally resin-filled, distributed along growth interruptions. These differences are characteristic of root wood (compared to trunk wood) in modern conifers (Manwillar, 1972; Metcalfe and Chalk, 1983; Falcon-Lang, 2005; Denne and Gasson, 2006; Denne and Turner, 2009). Tracheids are wider with more numerous pits in roots, and rays wider and taller (compared to aerial axes) because rootwood is not involved in mechanical support and therefore can maximize conductivity (Sperry et al., 2006). Axial parenchyma cells are common in conifer roots because they are rich in phenols and act as barrier to decay-causing organisms (Tippett and Shigo, 1981), and a similar function is likely in our cordaitalean roots. Circular holes in some of our root may represent arthropod borings (cf. Cichan and Taylor, 1982).

**Dadoxylon sp. (Plate III)**

**Material:** British Geological Survey, Lillie’s specimens E, H, M, N, P, S and Z (Table 1). Thin sections: P.B. 257–268. Notes: The material comprises three serial transverse sections (P.B. 257, 265–266; labeled 1–3) and nine longitudinal sections (P.B. 257–258, 260–264, 267–268; labeled L1–L9). Thin sections P.B. 267–268 are badly broken and missing cover slips.

**Description:** Specimen B comprises a fragment of a petiole, measuring 27 × 18 mm diameter, whose original diameter would have been around 50–60 mm when complete. Less than half of one side of the petiole is preserved, and the central area is missing. The inner part of the petiole fragment shows at least 14 vascular bundles embedded within parenchymatous tissue (Plate IV, 1). A small area comprising the largest specimen Z (Plate III, 1). Secondary xylem comprises tracheids, 35–67 μm diameter, showing circular to oval, contiguous, alternate bordered pits, which range from 1(2)-seriate in specimen N to 2–3(4)-seriate in specimen P (Plate III, 4, 6, 8), and 2–4 oval to slit-like cupressoid pits per cross-field (Plate III, 5). Rays are uniseriate with heights ranging from 1–5 cells (typically 1–3 cells) in specimen N to 1–15 cells (typical <10 cells) in specimen P (Plate III, 3, 7). Specimen N with its very low rays and uniseriate tracheid pits probably represents tissue close to the pith because it shows two vascular traces in TLS, while specimen P, which is more typical of the specimen suite, probably represents relatively mature wood. Growth interruptions are entirely lacking in all specimens (Plate III, 1).

**Identity:** Wood of this type is placed in the genus, *Dadoxylon*. Many species of *Dadoxylon*-type wood have been described from the Carboniferous and Permian, primarily sub-divided on the basis of ray dimensions and tracheid pitting (Doubinger and Marguerier, 1975). In Euramerica, they represent the wood of either cordaitaleans or conifers, but at present there is no satisfactory way of distinguishing one group from the other based solely on secondary xylem (Falcon-Lang et al., 2011b). As we infer that facies-associated *Mesoxylon* and *Amyelon* axes are cordaitalean (see above), the *Dadoxylon* material is best placed in this group as well.

**Class CYCADOPSIDA**

**Order MEDULLOSALES**

**Sutcliffia lilliei Crookall (Plate IV)**

**Type material:** British Geological Survey, Lillie’s specimen B (Table 1). Thin sections: P.B. 257–268.

**Description:** Specimen B comprises a fragment of a petiole, measuring 27 × 18 mm diameter, whose original diameter would have been around 50–60 mm when complete. Less than half of one side of the petiole is preserved, and the central area is missing. The inner part of the petiole fragment shows at least 14 vascular bundles embedded within parenchymatous tissue (Plate IV, 1). A small area comprising...
Plate III.
Plate IV (caption on page 278).
Plate V (caption on page 278).
part of the outer sclerenchymatous rind of the petiole shows numerous fibre bundles, interspersed with a few vascular bundles (Plate IV, 1, 9, 10). Except for those in the outer rind, vascular bundles are arranged in arcs, curving toward the inferred centre of the petiole (Plate IV, 1). Vascular bundles are up to 1 mm diameter and surrounded by a continuous or discontinuous ring of fibre strands (Plate IV, 2). These are more numerous on the side of the bundle opposite the protoxylem (Plate IV, 2). In some cases, groups of vascular bundles may be entirely surrounded by fibre strands (Plate IV, 4), implying that these bundles anastomose vertically – an inference that cannot be completely demonstrated in longitudinal section. Metaxylem tracheids are 140–220 μm diameter (Plate IV, 6) and show reticulate thickening (Plate IV, 5). A few ‘secretory cells’ containing with dark contents are scattered through the petiole, being especially common in the outer rind, but also associated with vascular strands (Plate IV, 6, 7, 8).

Identity: Lillie (1910b) assigned specimen B to Myeloxylon, but following consultation with D.H. Scott, Crookall (1927a) transferred it to a new species of medullosan pteridosperm petiole, Sutcliffea (Scott, 1906; de Fraine, 1912). Because Crookall (1927a) published in a somewhat obscure periodical, and given that the type material was believed to have been lost, subsequent studies of Sutcliffea (Taylor et al., 2009) have not considered S. lilliei. The key character seen in specimen B, which allow it to be referred to Sutcliffea, and distinguishes it from the related taxa, Medullosa and Myeloxylon is the occurrence of vascular bundles enclosed by fibre rings, arranged in arcs towards the centre of the petiole, or embedded in the outer sclerenchyma zone (Phillips and Andrews, 1963; Stidd et al., 1975). Another key diagnostic feature for Sutcliffea, the occurrence of a large central vascular bundle, cannot be confirmed because only part of the petiole is preserved.

Class Lycopida

Indeterminate secondary xylem (Plate V).

Material: British Geological Survey, Lillie’s specimen L (Table 1). Thin sections: P.B. 244–246.

Description: The single specimen, 16 mm long, comprises secondary xylem only (Plate V, 1). Files of tracheids are parallel, with a pronounced wedging on one side (Plate V, 2). Tracheids, 125–140 μm diameter × 7–10 mm long with tapering ends, show exclusively scalariform-thickening on both radial and tangential walls (Plate V, 6). Scalariform bars, 4–5 μm thick, show some bifurcations (Plate V, 7), but vertical threads connecting adjacent bars (fimbriis) are seen only very rarely. Rays are uniseriate, 1–13 cells high (Plate V, 6, 7). Oval leaf traces are present in TLS (Plate V, 4), but they are too few in number (n = 6) to determine arrangement; they may imply helical arrangement but this is uncertain (Plate V, 4, arrows). Traces comprise tracheids, 20–25 μm diameter, and > 150 μm long and show scalariform thickening (Plate V, 8).

Identity: The exclusively scalariform thickened tracheids seen in this fragment of secondary xylem, combined with the great length of tracheids (> 10 mm) and small, uniseriate rays, is strongly suggestive of arborescent lycopsids (Cichan, 1985). Many lepidodendrids (e.g., Lepidodendron, Lepidophloios, Paralycopodites) produced only small amounts of secondary xylem, with radii up to 9.5 mm thick recorded (Andrews and Murdy, 1958). However, a nuanced assessment of the development of secondary xylem is hindered by ontogenetic variation (Egger, 1961). Nonetheless, secondary xylem with a radius as large as in our specimens has not been recorded for lepidodendrids. In addition, our samples do not show fimbriis connecting scalariform bars as in Sigillaria (Jennings, 1977) and Lepidophloios (Cichan et al., 1981).

Sigillarians, by contrast, show more extensive secondary xylem development (Brongniart, 1828–1838; Arber and Thomas, 1908), although relatively few anatomically preserved taxa have been described (Delevoryas, 1957). The radius of the secondary xylem of some sigillarians can be as great as 24 mm (Dawson, 1877) to 30 mm (Baker and DiMichele, 1997), comparable to our specimen. It is possible that our material represents sigillarian rather than lepidodendrid wood, although criteria to distinguish the two types based on secondary xylem alone are weak. However, if helical arrangement of vascular traces can be confirmed, then affinity with stigmarian or lepidodendrid axes is more likely, although some sigillarians (e.g., Sigillaria bradii) show a leaf cushion arrangement, which superficially appears to be helical. Overall, the limited anatomical data and dryland context support a sigillarian affinity.

7. Growth interruptions

Cyclical growth interruptions are seen in all specimens of Mesoxylon and Amyelon, but are lacking in Dadoxylon. Interruptions are subtle, defined by radial fluctuations in tracheid diameter, which are symmetrical across the feature. In addition, interruptions may fade around the circumference, locally merging with adjacent interruptions. These phenomena contrast with temperate tree-rings where fluctuations in tracheid diameter shows a distinct asymmetry such that diameter gradually declines through the latewood, before abruptly increasing at the start of the earlywood.

Growth interruptions similar to those observed in our woods have been previously reported in cordaitalean roots of Amyelon-type from coal balls at several other localities in the Midcontinent and Illinois basins of the USA (Cridland, 1964; Costanza, 1985). Significantly, such interruptions are only found in Amyelon roots that lack aerenchyma (Phillips, 1982), implying that the trees in question were ill-equipped to deal with waterlogged soil conditions and must have grown during times when the water-table was lowered and the peat substrate was in the process of being oxidized.

The type of growth interruptions observed in our woods is very characteristic of wood formation in seasonal tropical climates (Falcon-Lang, 2003d). In such settings, the endogenous rhythm of trees is most strongly controlled by seasonal fluctuations in rainfall (Jacoby, 1989). Seasonal tropical climates may have one, two, or rarely several distinct dry/wet seasons (Rumney, 1968), such that multiple interruptions can be produced in a single year. Thus, the rings seen in our woods are not necessarily annual rings but may reflect the vagaries of a somewhat erratic seasonal tropical rainfall. The occurrence of growth interruptions in juvenile tissue (Mesoxylon, Amyelon) and their absence in mature tissue (Dadoxylon) is a phenomenon observed in modern and ancient trees (Chapman, 1994; Henderson et al., in press), merely reflecting the relative proximity of juvenile tissue to the meristems, rather than any climatological phenomena.

The growth interruption patterns are consistent with sedimentary evidence (reworked caliche soils, red beds) for a seasonally dry, subhumid environment. As plant fossils found in alluvial channels commonly represent riparian vegetation, trees probably grew along channel margins, where groundwater would have been elevated (Gilbinger et al., 1998), and trees somewhat buffered against seasonality, as seen in modern dryland alluvial plains (Falcon-Lang et al., 2004).

Well-drained alluvial plain deposits of late Bolsovian age have been found very extensively across the British Isles, from Bristol in the south (this paper), to the English Midlands (Glover et al., 1993), and as far north as Scotland (Jones et al., 2011), suggesting that red beds mark a regional shift to drier climates rather than the effects of local topography that enhanced alluvial plain drainage.

8. Discussion

The Bristol coalfield has played an important role in the historical development of Pennsylvanian palaeobotany, with many prominent palaeobotanists publishing classic monographs on its plant assemblages (Sternberg, 1820–1838; Brongniart, 1828–1838; Kidston, 1887; Lillie, 1910a; Arber, 1922; Crookall, 1925a,b; Moore and Trueman, 1937; Jongmans, 1940; Moore, 1940). However, these
workers have focused nearly exclusively on adpression floras from wetland facies, and no dryland floras have been documented to date.

In this paper, we have described probable subhumid dryland plant communities, for the first time from mid- to late Bolsovian alluvial strata in the Bristol Coalfield. This is only the second well-documented example of Pennsylvanian dryland ecosystems from Britain. The other example is from the late Bolsovian deposits of the Etruria Formation (British Midlands), which have been similarly interpreted as the deposits of alluvial drylands (Waters and Davies, 2008). Small, calcified axes, apparently preserved in growth position, were rooted in well-drained palaeosols, and buried by volcanic tuffs (Glover et al., 1993) may represent early conifers (Galtier et al., 1992).

In contrast, our Staplehill assemblage is dominated by cordaitaleans together with a single medullosan pteridosperm and a lycopsid. In terms of composition, the assemblage is somewhat similar to those seen in Namurian-early Westphalian roof-shales from northern Britain, which contain Mesoxylon, Succiflora and lycopsid wood (Stopes and Watson, 1908; de Fraine, 1912; Scott et al., 1997). The roof taxa are of kinds not seen in associated ‘coal ball’ assemblages and are thus thought to represent well-drained hinterland floras (Stopes and Watson, 1908; Falcon-Lang, 2008a). It is also similar in composition to early Westphalian alluvial dryland assemblages from the Joggins (Falcon-Lang, 2003a,b;c; Falcon-Lang et al., 2004) and Tynemouth Creek (Falcon-Lang, 2006; Falcon-Lang et al., 2010), which are dominated by cordaitaleans (including Mesoxylon) with subordinate medullosan pteridosperms. In younger strata in the USA (late Westphalian-early Stephanian equivalent), Mesoxylon and Succiflora occur in coal ball assemblages, consistent with DiMichele and Aronson’s (1992) model of dryland innovation followed by wetland infiltration.

The occurrence of a single lycopsid in the Staplehill assemblage is especially interesting. Arboreal lycopsids were hygrophilic plants, but they occur in coal balls assemblages, consistent with DiMichele and Aronson’s (1992) model of dryland innovation followed by wetland infiltration.

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References


Appendix 10 – Published paper: Falcon-Lang et al. (2012)
Research papers

Pennsylvanian (mid/late Bolsovian–Asturian) permineralised plant assemblages of the Pennant Sandstone Formation of southern Britain: Systematics and palaeoecology

Howard J. Falcon-Lang a,b,c, Christopher J. Cleal c, Janine L. Pendleton d, Charles H. Wellman d

1. Introduction

Permineralised plant assemblages are abundant in the Pennsylvanian of Britain, but restricted to a limited number of localities and stratigraphic intervals, mostly within the Lower Pennsylvanian strata of central and northern England (Falcon-Lang and Scott, 2000; Galtier, 1997; Scott et al., 1997). Although somewhat rare, these fossils have nonetheless played a major historical role in transforming our understanding of the anatomy, architecture, physiology, and ecology of Pennsylvanian plant communities, not just in Britain, but also for the Euramerican palaeotropics as a whole. Broadly speaking, the permineralised fossils occur in one of three facies associations (Types I–III) as described below:

‘Type I’ assemblages are low diversity accumulations of allochthonous permineralised tree-trunks found in fluvial sandstone bodies, described beginning in the early nineteenth century (Arber, 1913; Black, 1837; Crokall, 1931, 1934; Dawes, 1845; Johnson, 1999; Lindley and Hutton, 1832; Scott, 1902; Walton, 1926; Winch, 1817). These assemblages are mostly confined to early to mid-Westphalian strata in England and Wales and are dominated by Dadoxylon trunks, up to tens of metres in length, in some rare cases, showing a septate pith and Mesosylon-type primary vasculature (Crokall, 1931; Falcon-Lang and Scott, 2000). Remains are thought to be of large cordaitalean trees that either occupied well-drained areas outside the coal swamp basins (Dimitrova et al., 2011; Falcon-Lang and Bashforth, 2005) or represent the cryptic floras of drier climatic intervals when sea level was lowered (Falcon-Lang and DiMichele, 2010; Falcon-Lang et al., 2009).

‘Type II’ assemblages are allochthonous accumulations associated with goniatite-bearing carbonate nodules in marine ‘roof shales’ overlying coal seams, first described in the mid-nineteenth century (Hooper, 1848a,b,c). These assemblages are confined to late Namurian to earliest Westphalian (Langsettian) strata in north-west and central England and comprise assemblages of variable...
composition (Stopes and Watson, 1909). Some assemblages are rich in lycopsid axes and strobili (Hooker, 1848a,b,c) while others contain a medium diversity mixture of tree-ferns, pteridosperms, calamiteans, cordaitaleans, and lycopsids (Scott et al., 1997; Stopes and Watson, 1909). They probably represent the remains of late-stage Coal Forests flooded by marine transgression, mixed with some of the surviving plants that grew on elevated, better-drained ground (Falcon-Lang, 2009).

‘Type III’ assemblages – best known of all of the Pennsylvanian permineralised assemblages in Britain – comprise coal ball floras (Galtier, 1997). These assemblages were first encountered by Hooker and Binney (1854), and initially described in two classic series of papers by Binney (1865, 1868–1875, 4 part monograph) and Williamson (1871–1893, 19 part monograph). Interest in British coal balls peaked in the earliest twentieth century when the most productive mine at Shore, Lancashire was worked specifically for such fossils (Andrews, 1980; Scott, 1906), and the material was showcased in leading textbooks (Seward, 1898–1919, 4 volumes; Scott, 1900, 1920, 1923). The British coal ball assemblages are restricted to three (or perhaps, four) latest Namurian sites for which thin sections were prepared; grey, sites for which unsectioned hand specimens are known). Sites are as follows: Bristol area, 1, Conham Quarry; 2, Bickley Wood; 3, Hanham Quarry; 4, Near Swansea, South Wales (Grid Reference SS 7394), it attains a maximum thickness of ~1350 m, but thins to ~275 m towards the eastern edge of the South Wales Coalfield (SO 2503). In southwest England, the Pennant Sandstone Formation is ~950 m in Somerset, thinning northwards to ~600–800 m in the Bristol coalfield, and eastward to ~350 m in Oxfordshire. In the English Midlands, the Pennant Sandstone Formation correlates lithostratigraphically with the Halesowen Formation (Besly, 1988), which contains somewhat similar anatomically preserved assemblages to those described here (Arber, 1913; Kay, 1913). The Pennant Sandstone Formation is characterised by very thickly bedded, mostly grey, feldspathic, micaceous, lithic arenites, locally pebbly, interbedded with thin mudstone successions containing a few economic coal seams (Waters et al., 2007, 2009).

2. Geological context

The Pennant Sandstone Formation is a mid/late Bolsovian–Asturian unit developed in a ~220-km wide, E–W oriented belt, extending from Oxfordshire in the east (concealed) through Bristol and South Wales, as far as west as Pembrokeshire, southern Britain (Fig. 1A). Near Swansea, South Wales (Grid Reference SS 7394), it attains a maximum thickness of ~1350 m, but thins to ~275 m towards the eastern edge of the South Wales Coalfield (SO 2503). In southwest England, the Pennant Sandstone Formation is ~950 m in Somerset, thinning northwards to ~600–800 m in the Bristol coalfield, and eastward to ~350 m in Oxfordshire. In the English Midlands, the Pennant Sandstone Formation correlates lithostratigraphically with the Halesowen Formation (Besly, 1988), which contains somewhat similar anatomically preserved assemblages to those described here (Arber, 1913; Kay, 1913). The Pennant Sandstone Formation is characterised by very thickly bedded, mostly grey, feldspathic, micaceous, lithic arenites, locally pebbly, interbedded with thin mudstone successions containing a few economic coal seams (Waters et al., 2007, 2009).

2.1. Stratigraphy and age

The lithostratigraphic base of the Pennant Sandstone Formation is highly diachronous (Fig. 2), being formally defined at the level of the lowermost thick (>3 m) bed of ‘Pennant-type’ sandstone. In the Somerset Coalfield, the first sandstone of Pennant-type occurs up to 120 m below the mid-Bolsovian Cambriense Marine Band (Stubbfiled and Trotter, 1957). In the western region of the South Wales Coalfield the Pennant Sandstone Formation base is around 50 m above the marine band, whereas in the Bristol and the eastern South Wales Coalfield, it is up to 180 m or 200 m above the marine band, respectively. Thus, the base of the Pennant Sandstone Formation is of mid-Bolsovian age in Somerset and mid/late Bolsovian of Cardiff found the earliest recorded specimen in Caerphilly; Anon, 1867), but despite some superficial treatments (Lillie, 1910a,b; Crookall, 1925a,b,c, 1927a,b, 1931, 1934; Seyler and Williams, 1927), our paper is the first to fully describe and illustrate the material. In addition to investigating plant anatomy, we also discuss the palaeoecological and palaeoclimatological implications of the assemblage.
elsewhere, and the lower Pennant Sandstone Formation in South 
Wales and Somerset is, in part, time-equivalent to the Winterbourne 
Formation in Bristol (Falcon-Lang et al., 2011a; Waters et al., 2009).

Equally diachronous is the top of the formation. In the Somerset 
Coalfield it is defined at the Rudge Coal and in the Bristol Coal 
field, at either the Rock Coal on the southern limb of the Kingswood Anti 
cline or the High Vein Coal in the Coalpit Heath Syncline (e.g. 
Kellaway, 1970; Waters et al., 2009). The Rudge and Salridge coals 
have in the past been considered as time-equivalent (apparently 
based on similar megafloras obtained from their roof shales) implying 
that the formation has a near-isochronous top in these areas. 
However, more recent palaeobotanical (Pendleton et al., in press) 
and palynological (Pendleton and Wellman, in press) studies sug 
gests the Salridge has a lower stratigraphic position, equivalent to 
the Mangotsfield seams of the Coalpit Heath Syncline to the north 
(a correlation that we use in this paper). Ongoing work implies 
that the top of the Pennant Sandstone Formation lies close to the 
Bolsovian–Asturian boundary in this area. This is supported by oc 
currence of the non-marine bivalve Anthracosnaila phillipsii through 
ou the Pennant Sandstone Formation of Bristol, which is a late 
Bolsovian index fossil (Moore and Trueman, 1937).

In South Wales, the top of the Pennant Sandstone Formation is 
taken as the base of the Swansea Four-Feet Coal, and its correlative 
equivalents, the Mynyddiswynsh Coal, east of the Tafl valley, and the 
Llantwit No. 3 Coal in the Pontypridd district (Cleal, 1997, 2007; 
Waters et al., 2009). These units are of latest Asturian (possibly low 
ermost Cantabrian) age. However, a major disconformity occurs 
between these uppermost units in the eastern part of the South Wales 
Coalfield (Cleal, 1986; Fig. 3), with the early Asturian Birthdir 
Member being directly overlain by the latest Asturian–Cantabrian 
Grovesend Formation. A similar disconformity has now been recog 
nised at the same level in the Bristol Coalfield based on ongoing 
megafloral biostratigraphic work (Pendleton et al., in press).

In this paper, we focus on permineralised fossils from two areas: the South Wales Coalfield and the Bristol Coalfield. In the former re 

gion, where the formation is thickest, it is subdivided into five 
members: these are, from base to the top, the Llynfi, Rhondda, Brit 
third, Hughes and Swansea members, with the Bolsovian–Asturian boundary positioned within the upper Rhondda Member (Cleal, 1978). In the Bristol Coalfield, two members are recognised: these are, from base to the top, the Downend and Mangotsfield members, with the Bolsovian– 

2.2. Palaeoenvironment and tectonic context

The Pennant Sandstone Formation is interpreted as the deposit of large-scale braided rivers based on the dominance of very thick 
bedded, trough cross-bedded, pebbly sandstone, which fine-upward 
and show channel scours tens to hundreds of metres wide, and locally, 
large scale (>3–4 m high) tabular cross-stratification (Kelling, 1968, 
1974; Jones and Hartley, 1993; H.J. Falcon-Lang, unpublished observa 
tions). These braided rivers drained the rising Variscan Deformation 
Front to the south based on (1) palaeocurrent data and sediment 
petrology, which indicate predominantly northward patterns of
drainage and sediment dispersal, locally deflected by E–W structures (Hartley and Warr, 1990; Heard, 1922), and (2) the timing of the earliest incursion of coarse-grained detritus, which coincides with the first pulse of Variscan tectonism in mid-Bolsovian times (Green, 1992; Kombrink, 2008, Kombrink et al., 2007; Waters et al., 2009).

A second pulse of Variscan uplift (Leonian Phase) documented in the basins of central and northern Europe (Opluštil and Cleal, 2007), appears to have resulted in an early/mid Asturian hiatus in the eastern South Wales Coalfield extending into the Bristol Coalfield, whereas in the more rapidly subsiding central South Wales Coalfield, Pennant-type sandstones continued to accumulate throughout mid- to late Asturian times (Waters et al., 2009; Fig. 3). Analysis of subsidence patterns in this latter region is consistent with deposition in a foreland basin (Burgess and Gayer, 2000).

While there is consensus over the general braided river interpretation for the Pennant Sandstone Formation, the overall palaeoenvironmental context of these massive drainages is less well established. Interfluve deposits are infrequently preserved and poorly exposed, but comprise two general types. Some fine-grained intervals are composed of grey mudstone with <0.9 m thick coal seams and platy shales with nonmarine bivalves (Moore and Trueman, 1937), while a marine band occurs in the lowermost part of the formation in the Somerset Coalfield (Waters et al., 2009; Fig. 3). Analysis of subsidence patterns in this latter region is consistent with deposition in a foreland basin (Burgess and Gayer, 2000).

In contrast, some other fine-grained intervals are composed of red mudstone (Kellaway and Welch, 1993) and reworked calcrete and silcrete nodules have been locally observed in fluvial channel lags in the Bristol Coalfield (H.J. Falcon-Lang, unpublished observations) implying that, at different times, interfluves were comparatively well drained, supporting an alluvial plain context for these specific horizons. The significance of these alternations of grey and red interfluve fines is uncertain, but may represent the complex interplay of tectonics, eustasy, and sediment supply (cf. Gibling et al., 2004).

Fig. 3. Geological correlation of the key localities, from left to right, Swansea, Caerphilly, Severn, Bristol, north of the Kingswood Anticline, and Bristol, south of the Kingswood Anticline (modified from Cleal, 1986, 1997; Pendleton et al., in press). Position of the Bolsovian–Asturian boundary after Cleal (2007) and Pendleton and Wellman (in press). Stratigraphic position of key fossil collections (*), where known, labelled using the same numbering system as in Fig. 1 caption and in the text. Abbreviations: SWF is South Wales Middle Coal Measures Formation; F is Farrington Member; WF is Winterbourne Formation; Fm, Formation; Mb, Member; and SH is the Staplehill permineralised assemblage in the Winterbourne Formation (Falcon-Lang et al., 2011a).

Fig. 4. Rounded clasts of calcified fossil wood (right) and coal (left) in basal channel conglomerate facies, at Portishead, near Bristol. Coin 24 mm diameter.
3. Material and collectors

In this paper, we describe Type I permineralised plant assemblages from the Pennant Sandstone Formation based on museum collections and new field discoveries. All fossil assemblages comprise allochthonous accumulations within channel-lag conglomerate and coarse-grained sandstone facies of large, braided river channels. These assemblage include both large, isolated permineralised trunks up to 0.35 m diameter, and up to several metres long, locally showing branch scars, to water-worn rounded ‘cobble’ of fossil wood, which have evidently undergone extensive bedload transport. Permineralised material is commonly associated with channel bases containing rounded clasts of coal or coal chips (Fig. 4).

Drawing together this synthesis of the permineralised flora in the Pennant Sandstone Formation has been challenging because the material is widely dispersed through the collections of the Natural History Museum, London (BMNH), the National Museum Wales (NMGW), the University of Bristol Geology Museum (BRSGU), the Bristol City Museum and Art Gallery (BCMAG), the Glenside Hospital Museum, Fishponds, Bristol (GHM), the Sedgwick Museum, Cambridge (CAMSSM), and the British Geological Survey, Keyworth (BGS), often in old, uncatalogued collections. An inventory of permineralised fossils including thin sections (Table 1) and uncut hand specimens (Table 2) is provided.

The collections derive from at least 21 sites spread across the South Wales and Bristol coalfields (Fig. 1B, C). In many cases, locality data for the historic museum collections was poorly documented, so

### Table 1

<table>
<thead>
<tr>
<th>Locality and number on Fig. 1</th>
<th>Stratigraphy</th>
<th>Accession numbers of thin sections</th>
<th>Number of thin sections</th>
<th>Number of specimen</th>
<th>Collector Identity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bristol area</td>
<td></td>
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</tr>
</tbody>
</table>
| Penparc, near Newport         | Downend Member | BCMAG: Cc. 5194–5200            | 7                       | 2                 | Fry Messoxylon cf. sutclif Sutclif Mark 
|                               |              |                                   |                         |                   |                    |
| Hanham Quarry, Hanham, Bristol | Downend Member | BGS: M.P.K. 14123–14136; P.B. 312–318 | 20                      | 2                 | Crookall Messoxylon cf. sutclif Sutclif Mark 
|                               |              |                                   |                         |                   |                    |
| Oldbury Court, Fishponds, Bristol | Downend Member | BCMAG: Cc. 5205–5208            | 5                       | 3                 | Fry Paronius cf. blockier Blockier Mark 
|                               |              |                                   |                         |                   |                    |
| Hambrook, near Bristol (5)    | Downend Member | BCMAG: Cc. 5201–5203            | 3                       | 1                 | Fry Dadoxylon Dadoxylon Mark 
|                               |              |                                   |                         |                   |                    |
| Winterbourne Down, near Bristol | Mangotsfield Member | BMNH: V.673ab, V.674ab, V.51430, V.51543, V.5237E1–2; BGS: R.C. 41, R.C. 47 | 11                      | 6                 | Bryson Amyelon Amyelon Mark 
|                               |              |                                   |                         |                   |                    |
| Rock Quarry, near Brislington, Bristol (7) | Mangotsfield Member | BCMAG: Cc. 5194–5195 | 8                       | 1                 | Evens Paronius cf. mesoxylon mesoxylon sp. 2 
|                               |              |                                   |                         |                   |                    |
| Clevedon, Somerset (9)        | Penman Sandstone Fm | BGS: M.P.K. 14141–14144, 14154–14157 | 26                      | 77                | Evens Dadoxylon Dadoxylon Mark 
|                               |              |                                   |                         |                   |                    |
| Severn Tunnel, Bristol Channel (11) | Penman Sandstone Fm | BMNH: V.537, V.5873ab, V.9911–9912 | 6                       | 3                 | Starrie Dadoxylon Dadoxylon Mark 
|                               |              |                                   |                         |                   |                    |
| South Wales area              |              |                                   |                         |                   |                    |
| Caerphilly Common, South Wales (14) | Near boundary of Rhosidda and Brethir members | BMNH: V.8930 | 1                       | 1                 | Starrie Dadoxylon Dadoxylon Mark 
|                               |              |                                   |                         |                   |                    |
| Parrot Quarry, Caerphilly, South Wales (15) | Penman Sandstone Fm | BMNH: V.8930 | 1                       | 1                 | Starrie Dadoxylon Dadoxylon Mark 
|                               |              |                                   |                         |                   |                    |
| Treforest, near Caerphilly, South Wales (16) | Penman Sandstone Fm | BMNH: V.8930 | 6                       | 4                 | Starrie Dadoxylon Dadoxylon Mark 
|                               |              |                                   |                         |                   |                    |
| Six Bells, Abertillery, South Wales (17) | Penman Sandstone Fm | BMNH: V.8930 | 2                       | 2                 | Hemingway Dadoxylon Dadoxylon Mark 
|                               |              |                                   |                         |                   |                    |
| Buil Quarry, near Pwllhyfany, Caerphilly, South Wales (18) | Penman Sandstone Fm | BMNH: V.8930 | 1                       | 1                 | Starrie Amyelon Amyelon Mark 
|                               |              |                                   |                         |                   |                    |
| Gelligroes, Monmouthshire, South Wales (19) | Penman Sandstone Fm | BMNH: V.8930 | 10                      | 27                | Starrie Anthophyta Anthophyta Mark 
|                               |              |                                   |                         |                   |                    |
| Moesetown, Skewen, near Neath, South Wales (21) | Penman Sandstone Fm | BMNH: V.8930 | 2                       | 2                 | Starrie ‘Lepidodendron’ Lepidodendron Mark 
|                               |              |                                   |                         |                   |                    |

4. Bristol Coalfield localities

Within the Bristol Coalfield, permineralised plant material occurs in the Pennant Sandstone Formation at 11 localities, listed below from stratigraphically oldest to youngest. However, a few Bristol specimens are accessioned with insufficient locality data for accurate placement, so this must be a minimum estimate of localities (e.g., BMNH V. 674, V. 9911).

4.1. Conham Quarry, near St. Anne’s, Bristol (Locality 1)

This site was investigated by Thomas R. Fry (1902–1997), a long-time amateur collector (Fig. 5A), who intermittently worked for Bristol City Museum and Art Gallery and the University of Bristol in 1934 (Large, 1994), where it was deposited many years later in the teaching collection. Fry’s field notes allow the site to be identified as a small quarry, north of the horseshoe bend of the River Avon, near St. Anne’s, south west Bristol (51°26’50.94″N, 2°32’17.48″W). Historic maps show that the quarry had been disused as a small quarry, north of the horseshoe bend of the River Avon, near St. Anne’s, south west Bristol (51°26’50.94″N, 2°32’17.48″W). Historic maps show that the quarry had been disused for several decades by the time of Fry’s excursion (County Series 1:10560, 1921, ST66, Gloucestershire). The exposed interval lies below the Salridge Coal, on the southern limb of the Kingswood Formation. The Conham material, when aged 18, in May 1920, and sold it to the University of Bristol Geology Museum. See Fig. 1 for location details and numbers of the sites and Fig. 3 for their age and geological context.

Table 2

Inventory of hand specimens of permineralised plant fossils from the Pennant Sandstone Formation, southern Britain. Abbreviations: BGS, British Geological Survey, Keyworth, UK; BCMAG, Bristol City Museum and Art Gallery, Bristol, UK; BMNH, British Museum of Natural History, London, UK; NMGW, National Museum of Wales, Cardiff, UK; and BRSUG, University of Bristol Geology Museum. See Fig. 1 for location details and numbers of the sites and Fig. 3 for their age and geological context.

<table>
<thead>
<tr>
<th>Locality and number in Fig. 1</th>
<th>Stratigraphy</th>
<th>Number of specimens</th>
<th>Notes</th>
<th>Collector</th>
<th>Probable identity</th>
</tr>
</thead>
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<tr>
<td>Bristol area</td>
<td></td>
<td></td>
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<tr>
<td>Conham Quarry, St. Anne’s,</td>
<td>Downend Member</td>
<td>7</td>
<td>BRSUG: P30 collection; BCMAG: CMPL93</td>
<td>Fry</td>
<td>Dadoxylon</td>
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<tr>
<td>Bristol (1)</td>
<td></td>
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<tr>
<td>Bickley Wood, near Hanham,</td>
<td>Downend Member</td>
<td>3</td>
<td>Private collection</td>
<td>Falcon-Lang</td>
<td>Dadoxylon</td>
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<tr>
<td>Bristol (2)</td>
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<tr>
<td>Oldbury Court, Fishponds,</td>
<td>Downend Member</td>
<td>6</td>
<td>Private collection; Glesside Hospital</td>
<td>Falcon-Lang</td>
<td>Dadoxylon</td>
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<td>Bristol (4)</td>
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<tr>
<td>Clapton in Gordano, near Bristol (8)</td>
<td></td>
<td>3</td>
<td>Museum, Fishponds</td>
<td>Falcon-Lang, England</td>
<td>Messoxylon</td>
</tr>
<tr>
<td>Conygar Quarry, near Clevedon,</td>
<td>Pennant Sandstone Formation</td>
<td>5</td>
<td>BCMAG: 60/1967, several pieces of wood from MS cutting</td>
<td>Jeffrey</td>
<td>Dadoxylon</td>
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<tr>
<td>Somerset (9)</td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Norton Wood, near Clevedon,</td>
<td>Pennant Sandstone Formation</td>
<td>3</td>
<td>BCMAG: CMPL87, 0.3 m diameter trunk; SGM, unaccessioned collection</td>
<td>Hawkins</td>
<td>Dadoxylon</td>
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<tr>
<td>Somerset (10)</td>
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<tr>
<td>Caerphilly area</td>
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<tr>
<td>Black Vein Colliery, near Caerphilly,</td>
<td>Near boundary of Lymny and</td>
<td>1</td>
<td>NMGW: 86.60.G205</td>
<td>Storrie</td>
<td>Dadoxylon</td>
</tr>
<tr>
<td>South Wales (12)</td>
<td>Rhondda members and 7Rhondda Member</td>
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<td></td>
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<tr>
<td>Blackwood Colliery, near Caerphilly,</td>
<td>Several</td>
<td></td>
<td>Crookall (1931) mentions collecting fossil wood from this site but gives few details</td>
<td>Crookall</td>
<td>Dadoxylon</td>
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<tr>
<td>South Wales (13)</td>
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<tr>
<td>Caerphilly Common, South Wales (14)</td>
<td>Near boundary of Rhondda and Brithdr members</td>
<td>1</td>
<td>NMGW: 86.60.G273</td>
<td>Storrie</td>
<td>Dadoxylon</td>
</tr>
<tr>
<td>Parrot Quarry, Caerphilly South Wales (15)</td>
<td>Pennant Sandstone Formation</td>
<td>1</td>
<td>NMGW: 86.60.G272</td>
<td>Storrie</td>
<td>Dadoxylon</td>
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<tr>
<td>Swansea area</td>
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</tr>
<tr>
<td>Cockett and Town Hill quarry,</td>
<td>Pennant Sandstone Formation</td>
<td>many</td>
<td>Seyler and Williams (1927) collected abundant fossil wood</td>
<td>Seyler and Williams</td>
<td>Dadoxylon</td>
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<td>Swansea, South Wales (20)</td>
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Fig. 5. Portraits of principal historic fossil collectors about the time of their fossil discoveries. (A) Thomas R. Fry (1902–1997), seated in centre, on a fossil collecting trip in May 1922, courtesy of Bristol City Museum and Art Gallery, (B) Robert Crookall (1890–1981), in August 1923, courtesy of the Barry Thomas, (C) Eric Evens (1893–1971), in March 1919, courtesy of Bristol City Museum and Art Gallery, and (D) John Storrie (1844–1900), late in life, in the 1890s, courtesy of the National Museum Wales.
Anticline, in the upper part of the Downend Member (late Bolsovian). Fry's collections, including thin sections and uncut specimens, are accessioned in the Bristol City Museum and Art Gallery and the University of Bristol Geology teaching collection.

4.2. Bickley Wood, Hanham Abbots, Bristol (Locality 2)

This site was investigated by one of us (HFL) in 2011, following up earlier reports by Tom Fry in the 1920s. The material was obtained from a disused quarry in Bickley Wood, Hanham Abbots, south Bristol (51°25′52.62″N; 2°30′58.31″W), and comprises unaccessioned and unsectioned fossil wood specimens stored at Royal Holloway, University of London. This locality has been classified as a Site of Special Scientific Importance (SSSI) based on the rare occurrence of adpressed megafossil collected by Fry (Cleal and Thomas, 1996) and strata belong to the late Bolsovian Downend Member.

4.3. Hanham Quarry, Hanham, southwest Bristol (Locality 3)

This site was similarly investigated by Tom Fry and the material was collected in April 1922 (Fry, 1926). Fry's field notes indicate that the locality is near an old wharf on the River Avon at Hanham, and these and other data pinpoint it to a small quarry, long disused at the time of Fry's visit (County Series 1:10560, 1921, ST66, Gloucestershire), near the Chequer's Inn at the south end of Ferry Road (51°25′42.38″N; 2°30′26.05″W). Fry's collections are accessioned in the Bristol City Museum and Art Gallery and the University of Bristol Geology teaching collection.

Robert Crookall (1890–1981), the palaeobotanist (Thomas, 1981; Fig. 5B), apparently collected additional material from the same site around 1924 in the course of his Ph.D. work on the Bristol Coalfield at the University of Bristol. It is unknown whether he knew, or had contact with, Tom Fry. Crookall recorded his site only as "Hanham Quarry" but this name is used on old maps (County Series 1:10560, 1887, ST66, Gloucestershire) for Fry's locality. Crookall's material is accessioned in the collections of the British Geological Survey. This locality lies just below the Salridge Coal, on the southern limb of the Kingswood Anticline, in the uppermost Downend Member (late Bolsovian).

4.4. Oldbury Court, Fishponds, Bristol (Locality 4)

This site was investigated by one of us (HFL) between 2008 and 2011, with additional collections made by Steve England, an amateur collector, in 2011. It comprises a series of disused nineteenth century stone quarries along the River Frome from Eastville to Fendale, northeast Bristol. Permineralised material was obtained from several localities, but especially near Wickham Bridge (51°28′53.42″N; 2°33′04.30″W), Snuff Mills (51°29′12.22″N; 2°32′29.81″W), Ha'Penny Bridge (51°29′20.50″N; 2°31′52.71″W), and Oldbury Court (51°29′18.05″N; 2°31′55.28″W). Thin sections and uncut hand specimens are accessioned in the Bristol City Museum and Art Gallery, and other hand specimens are in the Glenside Hospital Museum, Fishponds, Bristol. All these sites lie within the middle to upper part of the Downend Member (mid/late Bolsovian) on the northern limb of the Kingswood Anticline.

4.5. Frome Valley quarries at Hambrook, near Bristol (Locality 5a–b)

This site, which consists of two adjacent localities, was investigated by two of us (JLP, CHW) in April 2009. They are located near the village of Hambrook, close to where the River Frome meets a small tributary locally known as The Stream. The first is an old quarry face (51°30′15.89″N; 2°30′46.38″W) on the eastern bank of the River Frome, almost adjacent to the tributary mouth. This quarry, complete with crane, was operational in the early 1900s according to the historical maps (County Series 1:10560, 1904, ST66, Gloucestershire). The second exposure is on the northern bank of the tributary, 100 m upstream of the tributary mouth and adjacent to where a small footbridge crosses The Stream (51°30′17.37″N; 2°30′51.14″W). This latter locality is mentioned in Kellaway and Welch (1993) as being adjacent to the crop of the Stinking Vein; it is estimated as being approximately 90 m below the Mangotsfield seams near the top of the Downend Member (late Bolsovian) in the Coalpit Heath Syncline area of the Bristol Coalfield. The material is accessioned in the National Museum Wales, Cardiff.

4.6. Winterbourne Down quarries, near Bristol (Locality 6)

This site was, investigated by two of us (JLP, CHW) over a thirty year period between 1979 and 2009; it comprises a spoil tip (51°30′49.27″N; 2°30′04.33″W) on the north bank of The Frome at Winterbourne Down between The Dingle and where the Frome Valley Footpath bridge crosses the river. This quarry dates back to at least the 1880s according to the historical maps (County Series 1:10560, 1887, ST66, Gloucestershire). A large (0.6 m) quarried block of Pennant Sandstone containing abundant permineralised wood fragments was found and sampled. This site lies near the base of the Mangotsfield Member (late Bolsovian) in the Coalpit Heath Syncline area of the Bristol Coalfield. The material is accessioned in the National Museum Wales, Cardiff.

4.7. Rock Quarry, near Brislington, Bristol (Locality 7)

This site was located in a quarry in Brislington, Bristol and investigated by Mr Alex Bryson, an amateur collector, in 1884 (Crookall, 1931; Tim Ewin, pers. comm., 2011). Although details are scarce, there is only one quarry in the late nineteenth century and early twentieth century whose location could be construed as Brislington. This lay in a tiny hamlet called Rock, just 500 m NNE of the centre of Brislington (51°26′23.11″N; 2°32′45.06″W), and we attribute our fossils to this locality (albeit with some uncertainty). Although the most recent British Geological Survey map erroneously places this site in the overlying Grovesend Formation, it is actually positioned above the Salridge Coal in the upper part of the Mangotsfield Member (late Bolsovian–earliest Asturian) of the Pennant Sandstone Formation. The specimens are accessioned in the Natural History Museum, London.

4.8. Clapton in Gordano, Bristol (Locality 8)

This site was investigated by Mr. T.C. Jeffrey, in 1967, following blasting of the Upper Sidelscut Cutting, near New Farm, Clapton in Gordano, during the construction of the M5 motorway (51°27′41.67″N; 2°45′30.09″W). Five uncut hand specimens are accessioned at the Bristol City Museum and Art Gallery. The stratigraphic placement of this section at the western edge of the Bristol Coalfield is uncertain, and these rocks are assigned to the undivided Pennant Sandstone Formation, which is of late Bolsovian–earliest Asturian age in this area.

4.9. Conygar Quarry, near Clevedon, Somerset (Locality 9)

This site was investigated over a 27 year period, from 1912 to 1939, by Mr. Eric D. Evens (1893–1971), a keen amateur geologist, microscopist and photographer (Fig. 5C). Evens held a B.Sc. in Chemistry from the University of Bristol and worked as a manager of a colour manufacturer in Keynsham and part-time Chemistry lecturer at the university (Roger Vaughan, pers. comm., 2011). His collecting site comprised a very large active quarry near Clevedon, Somerset (51°26′45.74″N; 2°50′04.32″W), which had commenced operation prior to 1885 and was only finally abandoned in the late 1950s. The
long period of collecting (from 1912 to 1939) likely reflects inter-
mittent discoveries as the active quarry face retreated. Evens pro-
duced his own thin sections of the Conwy Quarry material and
passed them onto Robert Crookall at the British Geological Survey
(Crookall, 1931), where they are accessioned. Some unsectioned
material is accessioned at the Bristol City Museum and Art Gallery.
The stratigraphic placement of this section at the western edge of
the Bristol Coalfield is uncertain, and these rocks are assigned to the
undivided Pennant Sandstone Formation, which is of late Bolsovian–
earliest Asturian age in this area.

4.10. Norton Wood Quarry, near Clevedon, Somerset (Locality 10)

This site was investigated by Mr. Hawkins in 1953 at a disused
quarry at Norton Woods, near Clevedon (51°28′14.85″N; 02°45′
12.43″W). One uncut hand specimen is accessioned at the Bristol City
Museum and Art Gallery. The stratigraphic placement of this section
at the western edge of the Bristol Coalfield is uncertain, and these
rocks are assigned to the undivided Pennant Sandstone Formation,
which is of late Bolsovian–earliest Asturian age in this area.

4.11. Severn Tunnel beneath the Bristol Channel (Locality 11)

Material from this site was investigated by John Storrie (1844–1901),
in 1882, during his second tenure as curator of the Cardiff Free Museum
and Art Gallery (later the National Museum Cardiff; Pardoe, 2007; Fig. 5D). The fossils were obtained from a stratum of Pennant Sandstone
intersected during the construction of the 7 km long Severn Tunnel
(completed 1885) between South Wales and Somerset, England. Al-
though the precise location of the discovery is not disclosed, megafossil
remains obtained from boreholes and localised outcrops indicate that
the Pennant Sandstone Formation in this region is of probable late
Asturian age, overlying the regional disconformity (Cleal, 1986; Fig. 3). The fossils are accessioned in the National Museum Wales, Cardiff.

5. South Wales Coalfield localities

Within the South Wales Coalfield, permineralised plant material
occurs in the Pennant Sandstone Formation at 10 localities, listed
below from stratigraphically oldest to youngest. However, a few
Welsh specimens are accessioned with insufficient locality data for
accurate placement, so this must be a minimum estimate of localities
(e.g., BMNH: J.P. 405–406, J. P. 827).

5.1. Black Vein Colliery, Caerphilly, South Wales (Locality 12)

This site was investigated by John Storrie in 1882. Black Vein
Colliery is located near Risca, Caerphilly, South Wales (51°37′03″
N; 03°07′39″W). It is recorded as having worked the Little Rock,
Big Rock, Bodwr, Lymog fach, Lymog fawr, Red, Big, Black, Forked
and Hard Vein coal seams. An uncut hand specimen from this site,
accessioned in the National Museum Wales, Cardiff, is labelled
“Pennant”, which if correct means it was probably obtained from
near the Little Rock Vein (correlative equivalent with the No. 2
Rhondda Seam), either in the upper Llynfi or lower Rhondda Mem-
ber (late Bolsovian).

5.2. Blackwood Colliery, near Caerphilly, South Wales (Locality 13)

This site was investigated by Crookall (1931) but few details were
recorded. Hand specimens were obtained from Blackwood Colliery,
near Caerphilly, South Wales (51°40′12″N; 03°12′14″W), probably
from a horizon in the late Bolsovian–early Asturian Rhondda Member.
The material has since been lost.

5.3. Caerphilly Common, South Wales (Locality 14)

This site was also investigated by John Storrie in 1882, and there are
several small quarries depicted near the eastern edge of Caerphilly
Common (1.5 km south of Caerphilly, South Wales) on maps dating
from shortly after the discoveries (County Series 1: 10560, 1885,
Monmouthshire) that could represent the source of the fossil material
(51°36′46.60″N; 3°13′03.47″W). The quarries straddle the boundary
between the Rhondda and Brithdir members indicating fossils are of
late Bolsovian–early Asturian age. Thin section and uncult material is
accessioned in the National Museum Wales, Cardiff.

5.4. Parrot Quarry, Caerphilly, South Wales (Locality 15)

This site was also investigated by John Storrie in 1882, but no
quarry of this name is known in the Caerphilly area or more widely
across South Wales. Thus, only a very general assignment to the late
Bolsovian–Asturian Pennant Sandstone Formation is possible. Thin
section and uncult specimen material is accessioned in the National
Museum Wales, Cardiff.

5.5. Treforest, South Wales (Locality 16)

This site was also investigated by John Storrie in 1882. Treforest is
a small town, near Pontypidd, South Wales (51°43′54.93″N; 3°18′
43.58″W). Unfortunately, there are insufficient details recorded to
pinpoint the locality or stratigraphic position apart from a general
assignment to the Pennant Sandstone Formation (which in this
region is of late Bolsovian–early Asturian age). Thin section material
is accessioned in the National Museum Wales, Cardiff.

5.6. Six Bells Colliery, Abertillery, South Wales (Locality 17)

It is unclear who investigated this site, but thin sections of fossil
wood were prepared by professional slide-maker Mr. W. Hemingway of
Derby (Howell, 2005), and given to Crookall at the British Geo-
logical Survey prior to 1931. The locality details given for the site
are Six Barrels Colliery, Abertillery, South Wales (51°43′50.57″N;
03°07′52.88″W) and Crookall (1931) indicates that specimens
were collected “from a thick-bedded sandstone cut through in
sinking the shaft of the colliery, many years ago” (p. 58). Although
there are no records of a mine of this name ever having existed in
Abertillery, there was a colliery called Six Bells, whose shaft was
sunk in 1891, and this seems to have been the most likely source.
Unfortunately it is impossible to determine from which level in
the mine the material was obtained and only a general Pennant
Sandstone Formation age (in this region, late Bolsovian–early Asturian)
can be inferred. Thin section material is accessioned in the National
Museum Wales, Cardiff and the British Geological Survey.

5.7. Bute Quarry, Pwllypant, near Caerphilly, South Wales (Locality 18)

This site was also investigated by John Storrie in 1882. There is some
confusion about the location of the site because the best-known
(and still active) Bute Quarry near Caerphilly quarries Mississippian
Limestone. However, Bute is a common name in this region because
vast estates are owned by the Marquis of Bute. Comparison with
historic maps (County Series 1: 10560, 1885, Monmouthshire) indi-
cates that Storrie’s ‘Bute Quarry’ (disused since the 1930s) was
positioned on the west side of present-day Llanbradach, near
Caerphilly (51°36′12.48″N; 3°14′04.80″W), an inference indepen-
dently confirmed by Cleal and Thomas (1996). This site lies below
the Mynydddyslyn Coal, but in a region where a major disconform-
ity has removed underlying beds (Fig. 2), such that exposed/quartered
strata comprise the Brithdir Member (early Asturian). Thin section
material is accessioned in the British Museum of Natural History and the National Museum Wales, Cardiff.

5.8. Gelligroes, Monmouthshire, South Wales (Locality 19)

This site was investigated by John Pringle (1878–1948), fossil collector to the British Geological Survey, in 1902 (Stubblefield, 1948). No further locality details are given on the label but Gelligroes is positioned c. 8 km north of Caerphilly. According to historic maps prepared at the time of the discovery (County Series 1: 2500, 1901, Monmouthshire, ST19), the Gelligroes Colliery was disused by that date, but there were a number of small disused quarries about 200 m south and west of Gelligroes. These were working grits in the uppermost Hu-ghes Member (early Asturian), just below the unconformable contact with the Grovesend Formation. Thin section material is accessioned at the British Geological Survey.

5.9. Cockett and Townhill Quarry, Swansea, South Wales (Locality 20)

This site was reported by Seyler and Williams (1927) and comprised a large quarry present about 100 m south of Cockett and 300 m west of Townhill, 1.5 km northwest of Swansea, South Wales (51°37′42″N; 03°57′39″W; County Series 1: 10560, 1921, Glamorganshire, S559). Although Seyler and Williams (1927) sectioned their material, they did not give repository details and we have been unable to locate these fossils. The quarry worked the early Asturian Hughes Member. Identity: In the first specimen, the helically arranged diamond-shaped structures containing elastic sediment are inferred to repre- sent the decayed leaf cushions of a lepidodendrid. This is consistent with the overall anatomy, and the occurrence of scalariform-thickened tracheids, which has been observed in the upper trace is more enigmatic, but could be related to the ligule, a feature common to all lycopsids. Although no parichnos were observed, this may be due to poor preservation and so this specimen is best referred to Lepidodendron sensu lato (DiMichele, 1985). The size of the leaf cushions and their proximity to the xylem cylinder may suggest a position within the crown or a deciduous lateral branch (W.A. DiMichele, pers. comm., 2011). The identity of the second specimen is uncertain, but scalariform-thickened secondary xylem of this type is most characteristic (though not indicative) of indeterminate lycopsids in Carboniferous times (Cichan, 1985).

Class Sphenopsida
Order Equisetales ex. Berchtold & Prest, 1820
Genus Arthropitys
Description: Specimen Y and Z (BMNH V. 8922 – V. 8924 and Specimen Z comprises V. 8925 – V. 8927abc and V. 8928, each represented by the full compliment of TS, RLS and TLS slides. A further three thin sections in the Storrie collection of the National Museum Wales, Cardiff (28.3.G24, 28.3.G55 – 28.3.G56) may have been cut from the same BMNH material, or perhaps a different specimen. The original hand specimens have not been preserved.

Locality: Bute Quarry, Pwllypant, near Caerphilly, South Wales (51°36′45.40″N; 03°51′12.18″W). Collector: John Storrie (in 1882).

Class Lycopsida
Order Lepidodendrales
‘Lepidodendron’ sp. Plate I, 1–3

Material: Total of two separate specimens in the National Museum Wales collection each comprising a single section as follows: 28.3.G20 and 28.3.G32
Locality: Bute Quarry, Pwllypant, near Caerphilly, South Wales (51°36′12.48″N; 3°14′04.86″W).
Collector: John Storrie (in 1882).

Description: One specimen (NMGW 28.3.G20), which is very difficult to study and image due to the variable thickness of the ground section and poor preservation, is a TLS showing helically arranged, diamond-shape structures each 4 mm wide by 6 mm high (Plate I, 1). The structures, are mostly filled with elastic sediment, but in some cases contain two vascular traces, sub-rectangular in cross-section, one near the lower/middle of the diamond, up to 1.7 mm high by 0.85 mm wide, and a second near the upper margin of the diamond, 0.7 mm high by 0.6 mm wide (Plate I, 2). The vascular traces comprise scalariform-thickened tracheids, 61–87 μm diameter. The tissue that wraps the diamond-shaped structures also comprises scalariform-thickened tracheids, 60–111 μm diameter (Plate I, 3). The second specimen (NMGW 28.3.G32) is a TS of a small fragment of secondary xylem comprising large diameter (76–142 μm) tracheids, arranged in parallel files, and showing scalariform-thickening, with hints of a few, very poorly preserved, uniseriate rays.

Identity: In the first specimen, the helically arranged diamond-shaped structures containing elastic sediment are inferred to represent the decayed leaf cushions of a lepidodendrid. This is consistent with the overall anatomy, and the occurrence of scalariform-thickened tracheids surrounding the leaf cushions indicates that the tangential section passes through the secondary xylem tissue cylinder. The middle vascular trace comprises the leaf scar while the upper trace is more enigmatic, but could be related to the ligule, a feature common to all lycopsids. Although no parichnos were observed, this may be due to poor preservation and so this specimen is best referred to ‘Lepidodendron’ sensu lato (DiMichele, 1985). The size of the leaf cushions and their proximity to the xylem cylinder may suggest a position within the crown or a deciduous lateral branch (W.A. DiMichele, pers. comm., 2011). The identity of the second specimen is uncertain, but scalariform-thickened secondary xylem of this type is most characteristic (though not indicative) of indeterminate lycopsids in Carboniferous times (Cichan, 1985).
Calamitea Cotta 1832 by Rößler and Noll, 2007) and Arthraxonylon Reed 1952. Of these, Arthropits, which is known from rocks of mid-Carboniferous to Late Permian age, is by far the most common and widespread type (Rößler and Noll, 2010), and our material is placed into this taxon based on its upright to isodiametric (rather brick-like) ray cells and tracheids of one type. Although many species of Arthropits have been erected, some based on details of the secondary xylem, the intra-taxon variability of these characters is poorly understood (Rößler and Noll, 2010), and we therefore do not assign our fragmentary material to a particular species.

Class Filicopsida
Order Marattiales Link 1833
Genus Psaronius Cotta 1832
Psaronius cf.blickleimorgan 1959, Plate II, 1–7

Material: Total of five (or six?) specimens. In the Bristol City Museum and Art Gallery, there are three specimens each represented by a TS (Cc. 5204–Cc. 5206) and, in the case of one specimen, a longitudinal section (Cc. 5208), as well as hand specimens. Sections from one further specimen are in the Natural History Museum, London, including a TS (V. 8917) and a longitudinal section (V. 8918). In the National Museum Wales, Cardiff, there are additional poorly preserved transverse (283.831) and longitudinal (283.847) sections, which are assigned to this taxon with considerable uncertainty as well as transverse (2011.19C.4a) and longitudinal (2011.19C.4b) sections from a different specimen.

Localities: Hanham Quarry, near Hanham, Bristol, UK (51°25'45.97"N; 2°30'55.55"W); Bute Quarry, Pwllypant, near Caerphilly, UK (51°36'12.48"N; 3°14'04.86"W); and Winterbourne Down quarries, near Bristol, UK (51°30'49.27"N; 2°30'04.33"W).

Collectors: John Storrie (in 1882), Tom Fry (in 1922), and Janine Pendleton (in 2000).

Description: The fossils are fragments of 14–22 mm radius, and up to 67 mm length, composed of prominent roots, 1–3 mm in diameter, embedded in parenchymatous interstitial tissue (Plate II, 1). In TS, each root comprises an actinostele, which is exarch and stellate, with typically 3–6 (dominantly 5) protoxylem poles (Plate II, 2). Xylem is composed of scalariform-thickened tracheids, 70–200 μm in diameter (Plate II, 2, 7). The actinostele, which is not preserved in some specimens, is surrounded by aerenchymatous cortical tissue and a dense outer layer of sclerenchyma. Lateral roots are locally seen at various stages of departure (Plate II, 5), including a proximal example where two lateral roots develop from adjacent protoxylem poles in the same root (Plate II, 6). Arthropod faecal pellets are very common in the roots, especially associated with aerenchymatous tissue (Plate II, 2, 4, 7), and will be fully described in a later paper.

Identification: Our specimens are characteristic of the marattian tree-fern Psaronius, and must represent part of the inner root mantle because the roots are embedded in parenchymatous interstitial tissue (Ehret and Phillips, 1977; Rothwell and Blickle, 1982). It is challenging to distinguish species of Psaronius based on details of the root mantle alone; however, our specimens show some similarities with the inner root mantle of P. blickleimorgan 1959, based on the typical size of the root actinostele and the number of protoxylem poles.

Palaeoecology: Although our fossils are highly fragmentary, they must have derived from trees of at least medium (>0.15 m) diameter, allowing for the stele and outer root mantle (Millay, 1997), and considering that most well preserved fossils (like ours) derive from the upper part of the stem (Millay, 1984). This is rather large compared with some tree-ferns known previously from this mid-late Bolsovian age (DiMichele and Phillips, 2002; Millay, 1997). It is also noteworthy that our specimens date from an interval when tree-ferns were still somewhat rare, prior to their rise to dominance beginning in mid-Asturian times (Perciflorkorn and Thomson, 1982).

Psaronius sp. 2, Plate II, 8

Material: In the Bristol City Museum and Art Gallery, there is a single specimen comprising one transverse section (Cc. 5209).

Localities: Oldbury Court, near Fishponds, Bristol, UK (51°29’18.05"N; 2°31’55.28"W).


Description: Specimen Cc. 5209 comprises a fragment of 23 mm radius, composed of prominent roots, 0.6–1.1 mm in diameter, embedded in parenchymatous interstitial tissue (Plate II, 8). Each root comprises an actinostele, which is exarch, with typically only 3 protoxylem poles. No surrounding cortical tissue is preserved (replaced by carbonate), but a dense outer layer of sclerenchyma encloses each stele.

Identity: The specimen represents a portion of inner root mantle of Psaronius (Ehret and Phillips, 1977); it is probably a different species to the one described above because of its much smaller roots with triarch steles, but it is not inconceivable that the differences could be ontogenetic.

Class Cycadopsida
Order Medullosales
Genus MyeloxylonBrongnarti 1849
Myeloxylon sp., Plate I, 9–10

Plate I. *Epidendrodon*, 1–3, Arthropteris sp., 4–8, and Myeloxylon, 9–10.

2. Detail of vascular traces visible in one well-preserved leaf cushion, showing the lower leaf scar and the upper ligule scar, scale 400 μm, TLS, NMGW28.3.G29.
3. Tissue between the leaf cushions comprises scalariform-thickened tracheids with some bifurcations, scale 100 μm, TLS, NMGW28.3.G29.
4. Ray comprising a mixture of square to upright rectangular cells, with one marginal row of slightly larger upright cells, scale 200 μm, TLS, BMNH V. 8923.
5. Putative cross-field pitting in ray comprises irregular, simple, circular pits, scale 50 μm, TLS, BMNH V. 8923.
6. Tracheids showing poorly preserved pitting, which may be scalariform to elongate, and locally, biseriate, oval and opposite, scale 50 μm, TLS, BMNH V. 8923.
7. Rays, mostly 1–2-seriate, and up to 15 cells high, scale 100 μm, TLS, BMNH V. 8924.
8. A zone of multiseriate rays, up to 7-seriate rays and up to 20 cells high, scale 100 μm, TLS, BMNH V. 8924.
10. General view of poorly preserved petiole showing several exarch vascular bundles within a compressed groundmass; secretory cells, scattered and empty, scale 750 μm, TS, NMGW28.3.G29.

Plate II. Psaronius cf. blickleimorgan, 1–7, and species 2, 8. (see on page 34)

1. General view of inner root mantle, scale 2 mm, TS, BCMAG Cc. 5206.
2. Scalariform-thickening of tracheids in the stele of rootlets. Note the arthropod faecal pellets (bottom right), scale 50 μm, LS, BCMAG Cc. 5208.
3. Close-up of a root comprising an exarch actinostele with 5 protoxylem poles surrounded by aerenchymatous cortical tissue (partially decayed) and a dense outer layer of sclerenchyma, embedded in parenchymatous interstitial tissue, scale 400 μm, TS, BCMAG Cc. 5206.
4. Close-up of a root similar to that in Plate II, 3, but note the abundant arthropod faecal pellets in the cortex (arrow), scale 500 μm, TS, BCMAG Cc. 5206.
5. Departing lateral root, scale 1 mm, LS, BCMAG Cc. 5208.
6. Lateral roots departing from central actinostele poles in the same root (arrow), scale 300 μm, TS, BCMAG Cc. 5206.
7. Root cortex has completed decay (or eaten) and the space contains scattered arthropod faecal pellets, scale 300 μm, LS, BCMAG Cc. 5208.
8. Small rootlets with triarch actinostele somewhat different from other specimens, scale 500 μm, LS, BCMAG Cc. 5209.
Plate I.
Plate II (caption on page 32).
Locality: Bute Quarry, Pwllypant, near Caerphilly, UK (51°36'12.48"N, 3°14'04.86"W).
Collector: John Storrie (in 1882).

Description: This poorly preserved transversely sectioned specimen is 7 mm by 16 mm. The section is of uneven thickness and difficult to study; however, it consists of at least 15 vascular bundles, randomly arranged, embedded in a highly crushed parenchymatous groundmass (Plate I, 9). Each bundle comprises 5–11 tracheids, up to 160 μm in diameter, which appear to show exarch maturation, and a small amount of phloem, somewhat poorly preserved (Plate I, 9). A few scattered, thick-walled secretory cells, 220 μm diameter, which are empty or contain dark contents are also present (Plate I, 10).

Identification: Although poorly preserved, this material is determinable as *Myeloxylon horni* (1849), the petiole of a medullaroxylon pteridosperm, and is somewhat similar to specimens described from the Middle Pennsylvanian of the USA (Arnold and Steidtmann, 1937).

Class Coniferopsida
Order Cordaitales
Genus *Mesoxylon* Scott & Maslen, 1910

*Mesoxylon cf. sutcliffi* (Maslen 1911) Plate III, 1–10

Material: Total of ten (or eleven?) specimens. In the British Geological Survey, one specimen has been cut into six serial transverse (M.P.K. 14123–14128) and six serial longitudinal sections (M.P.K. 14129–14134), by professional slide-maker, W. Hemingway, while a second specimen is represented by seven serial transverse sections only (P.B. 312–318), and a third by a single transverse section (P.B. 604=P.F. 7428). In the Bristol City Museum and Art Gallery, there are two specimens, each represented by TS, RLS, and TLS slides (Cc. 5194–5200). In the Natural History Museum, London, one specimen is represented by longitudinal (V. 8906, V. 8907ab) and TS (V. 800, V. 800ab) slides and a further specimen consists of TS material (Plate III, 9) of Mesoxylon sp. 2.

Description: Axes are mostly 11–19 mm in diameter (rarely up to 35 mm in diameter), with a pith, 63–82 mm in diameter, which may be partially infilled with coarse-grained clastic material in some specimens (Plate III, 1). The pith is septate, with septae spaced 0.26–0.86 mm apart (Plate III, 2, 3). composed of isodiametric parenchyma cells, 78–103 μm in diameter, often profusely pitted on all faces. In some specimens, parenchyma cells, often filled with dark contents, are arranged in up to 9 rows of vertically stacked, rectangular cells bordering the pith, whereas in other specimens, arrangement is somewhat irregular (Plate III, 3). Cauline bundles show mesarch maturation (Plate III, 4; although this is difficult to confirm for a few specimen because bundles are poorly preserved) and vasculature is secondary xylem in most specimens (Plate III, 1), and a small wound is seen on one side of two axes (Plate III, 10). In the absence of evidence for bundles dividing tangentially in TS. Despite the existence of specimens for which serial transverse sections have been cut, the infrequent preservation of cauline bundles precludes reliable determination of phloemata.

Primary xylem comprises tracheids, 41–52 μm diameter, showing spiral thickening (Plate III, 6). Later formed tracheids are 34–58 μm diameter, showing 1–2-seriate bordered pits, which are contiguous and alternate (Plate III, 7). Tracheid pits are typically circular, 14–17 μm diameter, with a circular aperture. Rays are exclusively uniseriate and 1–4 cells high (rarely up to 10 cells) near the pith (Plate I, 8) increasing to 1–19 cells high about 5 mm from the pith (Plate III, 9). Rays are composed of procumbent parenchyma cells, 52–61 μm wide by 29–34 μm high, with oblique end-walls; they are locally resin-filled (Plate III, 7) and show 2–5 acarauroid cross-field pits per field (not illustrated due to poor preservation). Prominent resin plugs, developed in and adjacent to rays, are visible in some tracheids, giving the misleading appearance of axial parenchyma (Plate III, 10). Weakly developed growth interruptions occur in the secondary xylem in most specimens (Plate III, 1), and a small wound is seen on one side of two axes (Plate III, 10). In the Natural History Museum, London, one specimen (NMCG 28.3.G31) is noteworthy because its pith appears to contain isolated roots, poorly preserved, but somewhat similar to those described above as *Prauniosia* — although only with the outer sclerenchymatous sheath of each root preserved; unfortunately the thin section of this specimen is so poorly prepared (too thick), as to be impossible to image.

Identification: Based on their mesarch cauline bundles and non-symodial vasculature, specimens are placed in the genus, *Mesoxylon* (Scott and Maslen, 1910; Trivett and Rothwell, 1985). Similar specimens have been described from marine flooding surface in the Bashkirian of central Britain (Maslen, 1911; Scott et al., 1997) and red beds in the Bashkirian of Canada (Falcon-Lang, 2003a,b) and southern Britain (Falcon-Lang et al., 2011a) under the name *Mesoxylon sutcliffi* and our material is compared with this species. Although the affinities of some Kasimovian specimens of *Mesoxylon* has been recently questioned (Falcon-Lang et al., 2011c), our specimens are probably cordaitaleans (Trivett and Rothwell, 1991).

Palaeoecology: The occurrence of one *Mesoxylon* axis containing probable *Prauniosia* roots in its pith implies that this cordaitalean may have intergrown with a tree-fern stem, perhaps climbing through its root mantles (cf. Rößler, 2000). However, it is unlikely that this taxon was an obligate climber because some specimens comprise septate trunks of up to 0.3 m in dia. (Table III, 10). In the absence of evidence for bundles dividing tangentially in TS. An alternative explanation is that *Prauniosia* was growing on top of a dead specimen of *Mesoxylon* (cf. Césari et al., 2010). The widespread occurrence of weakly developed growth interruptions may imply some seasonality of rainfall and a subhumid climate (cf. Falcon-Lang et al., 2011a).

*Mesoxylon* sp. 2 Plate IV, 1–11


Locality: Conygar Quarry, near Clevedon, Somerset, UK (51°26'45.74"N, 2°50'04.32"W).
Collector: Eric Evens (in 1921).

Description: This specimen comprises a solid (non-septate) parenchymatous pith, 2.3–5.5 mm diameter, surrounded by a woody cylinder, 9–12 mm radius (Plate IV, 1, 2). The pith consists of isodiametric cells, 30–111 μm diameter (Plate IV, 5), arranged in vertical rows. Cauline bundles show mesarch maturation (Plate IV, 3), but not one of the longitudinal sections intersect with departing leaf traces, it cannot be determined whether the vasculature is sympodial or non-sympodial (though the latter case is most likely based on the fact that in TS, there is no evidence of bundles dividing tangentially). Primary xylem comprises tracheids, 22–61 μm diameter, which shows uniserate, elongate to scalariform (Plate IV, 5), contiguous pits. Secondary xylem comprises tracheids, 61–89 μm diameter (Plate IV, 11), which show an unusual mixture of pit types on their radial walls as follows: uniserate, elongate (almost scalariform), contiguous pits, or oval, biserate, sub-opposite to alternate pits (Plate IV, 8), or 2–4-seriate, circular, alternate pits, especially in the vicinity of rays (Plate IV, 4, 7, 10). Rays are 1–9 cells high (typically 5; Plate IV, 6), uniseriate and comprise elongate parenchyma cells, up to 350 μm in length with oblique end-walls (Plate IV, 10). Cross-field pitting comprises up to 7–11 circular acarauroid pits.
with slit-like apertures per field (Plate IV, 9). Growth interruptions are marked at several points (Plate IV, 11).

Identification: Based on its mesarch cauleine bundles and probable non-sympodial vasculature, this specimen is assigned to Mesoxylon sp. (Scot and Maslen, 1910). It differs from M. sutcliffi in various aspects of the tracheid pittings. The occurrence of a solid (non-septate) pith is also unusual, suggesting that material may have derived from close to the shoot apex or root (Rothwell and Warner, 1984; Costanza, 1985; Trivett, 1992). Such axes are normally assigned to cordaitaleans.

Amyelon sp. Plate V, 1–4

Material: A total of seven specimens, in the Natural History Museum (V.673abc, V. 674ab, V.51543, V.5237E1–2) and the British Geological Survey (R.C.41, R.C.47).

Locality: Unnamed quarry at Rock, near Brislington, Bristol, UK (51°26′23.11″N; 2°32′45.06″W).

Collector: Alex Bryson (in 1884).

Description: This material comprises woody axes, up to 18 mm in diameter (Plate V, 1), which either lack a pith or show only a minute pith (up to 5–6 cells diameter; Plate V, 1, 4), and exhibit well-developed growth interruptions (Plate V, 2), which may be eccentric around the circumference. Another key feature of this material is a rather twisted/contorted appearance to the secondary xylem (Plate V, 3). Secondary xylem anatomy is similar to that described for Mesoxylon cf. sutcliffi above.

Identification: Such woody axes, with minimal pith, are characteristic of the cordaitalean genus, Amyelon, and probably represent root tissue. The twisted/contorted appearance of the secondary xylem is also characteristic of root wood. Our material is not well preserved, and limited sections exist in museum collections, but it is similar to that described recently from the Winterbourne Formation of Bristol (Falcon-Lang et al., 2011a).

Palaeoecology: Of palaeoecological importance is the development of growth interruptions, suggesting that these trees preferred better-drained facies.

Dadoxylon sp. Plate V, 3–9

Material: This is the most common taxon comprising a total of forty-three (or up to forty-five) specimens as follows: British Geological Survey, P.B. 311, M.P.K. 14135–14140, M.P.K. 14148–14150, M.P.K. 14158–14159, P.F. 7424–7427 (comprising six separate specimens of Dadoxylon sectioned 7–8 February 1912, 27–28 August 1913, 1–13 May 1925, 22 March 1926, by Evans); M.P.K. 14151–14153 (three sections prepared by Crookall from Evens’ material); M.P.K. 14145–14147; R.C. 1–6 and 17–18 (additional sections cut from Evens’ material by professional slide-maker, W. Hemingway and Crookall); P.F. 2949–2951, and one unregistered slide (from Mooretroon and Gelligroes). Other thin section material is in the Bristol City Museum and Art Gallery (Cc. 5201–5203), National Museum Wales (1911.9G.1–3; 28.3.G33–G40, 28.3.G48, 28.3.G32), and Natural History Museum (P. 405–406, 827; V. 537, V. 5237, V. 5875abc, V. 8909–8916, V. 8919–21, V. 8929–V. 8930, V. 9911–9912; 3 specimens). In addition, hand specimens from Conygar Quarry, comprising trunk-urks up to 210 mm diameter, are accessioned at the Bristol City Museum and Art Gallery (Acc 110/1558) and in the Sedgwick Museum, Cambridge.

Localities: Present at 19 of the 21 localities (with the exception of Hanham and Winterbourne localities).


Plate III. Mesoxylon cf. sutcliffi Maxlin 1911.

1. Woody axis with sediment-filled pith showing growth interruptions (g) and a small wound (w) overgrown by traumatic tissue, scale 2.5 mm, TS, BCMAG Cr. 5194.

2. Longitudinal section showing septate pith, scale 5 mm, RLS, BCMAG Cc. 5196.

3. Detail of pith septa and early formed xylem, scale 300 μm, RLS, BCMAG Cc. 5196.

4. Mesarch cauleine bundle with arrow pointing to protoxylem, and pith cells filled with dark contents (top), scale 125 μm, RLS, BGS M.P.K. 14123.

5. Departing leaf trace illustrating non-sympodial vasculature (left) and columns of rectangular parenchyma in the pith (right), scale 400 μm, RLS, BCMAG Cr. 5196.

6. Spiral thickening in tracheids of primary xylem, scale 50 μm, RLS, BCMAG Cr. 5196.

7. Biseriate, alternate, circular, bordered pitting on tracheids in secondary xylem, scale 100 μm, RLS, BCMAG Cr. 5196.

8. Rays, 1–7 cells high (mostly 1) close to the pith, scale 200 μm, TLS, BCMAG Cr. 5197.


10. Resin plugs in tracheids adjacent to rays (arrowed), scale 100 μm, RLS, BCMAG Cr. 5196.

Plate IV. Mesoxylon sp. 2. (see on page 38)

1. Woody axis, scale 1 mm, TS, BGS M.P.K. 14142.

2. Detail of solid (non-septate) parenchymatous pith, scale 250 μm, TS, BGS M.P.K. 14142.

3. Mesarch cauleine bundle with protoxylem (arrowed) and pith cells filled with dark content (below), scale 100 μm, TS, BGS M.P.K. 14142.

4. Multiseriate, oval, alternate bordered pits on tracheids, scale 50 μm, RLS, BGS M.P.K. 14143.

5. Elliptic or scalariform pits on early-formed (?)primary xylem) tracheids, scale 50 μm, RLS, BGS M.P.K. 14143.


7. Circular, alternate bordered pits on tracheids, scale 25 μm, RLS, BGS M.P.K. 14143.

8. Oval to elongate (almost scalariform), sub-opposite to alternate bordered pits on tracheids, scale 25 μm, TLS, BGS M.P.K. 14143.


10. Clusters of small, circular bordered pits on tracheid walls between adjacent rays, scale 25 μm, TLS, BGS M.P.K. 14143.


Plate V. Amyelon sp., 1–4, and Dadoxylon sp., 5–11. (see on page 39)

1. Axis showing minute pith (3–4 cells diameter), and a pronounced growth interruption, scale 2 mm, BMNH V. 673a.

2. Close-up of growth interruption shown in 1, illustrating reduction in tracheid diameter but emphasising the symmetry of the feature, scale 400 μm, TS, BMNH V. 5237E2.

3. Twisted structure of secondary xylem typical of root tissue, scale, TS, BMNH V. 5237E2.

4. Axis showing minute pith (4–6 cells diameter), scale 400 μm, TS, BMNH V. 5237E2.

5. Tracheids showing large, biseriate, alternate, circular pits with oblique, oval apertures, scale 40 μm, TS, BGS M.P.K. 14135.

6. Tracheids showing 1–4 seriate, circular, alternate, bordered pits, scale 70 μm, TLS, BMNH V. 5875a.

7. Close-up of circular, alternate bordered pits, scale 20 μm, TLS, BGS M.P.K. 14135.

8. Close-up of circular, alternate bordered pits showing hexagonal dividing walls beyond the area of the circular border, scale 20 μm, RLS, BGS M.P.K. 14135.

9. Uniseriate rays, 1–14 cells high, scale 100 μm, TLS, BGS M.P.K. 14139.

10. Uniseriate rays, 1–21 cells high, scale 100 μm, TLS, BGS M.P.K. 14137.

11. Atraecriptis cross-field pitting, poorly preserved, scale 500 μm, TLS, BGS M.P.K. 14135.
Plate IV (caption on page 36).
Plate V (caption on page 36).
date), W. Hemingway (unknown date), Jeffrey (in 1967), J. Pringle (in 1902), Storrie (in 1882), and W.D. Ware (unknown date).

Description: This material comprises pycnoxylic gymnosperm wood with the following characteristics: in RLS, tracheids, 56–78 μm diameter, show 2–5-seriate, circular bordered pits, contiguous and alternate, locally crowded and hexagonal (Plate V, 5–8). Rays comprise elongate parenchyma cells, up to 230 μm long, with oblique end-walls, and showing 2–9 poorly preserved araucarioid pits per cross-field (Plate V, 11). In TLS, tracheids are unipitted, and rays are 1–23 cells high, but typically <10 cells high, composed of cells 29 μm high by 28 μm wide (Plate V, 9, 10). Growth interruptions are rarely present and always very weakly developed.

Identification: This material could represent the wood of a variety of gymnosperms including cordaitaleans, conifers and even some pteridosperms; however, given the age of the material (mid/late Bolsovian–Asturian) and local biological connection with septate pith casts of Mesoxylon-type, a cordaitalean affinity seems most likely (Falcon-Lang and Bashforth, 2005). While specimens show a degree of anatomical variability, and may represent a number of species (cf. Doubinger and Marguerier, 1975), there is currently no satisfactory way of distinguishing ontogenetic and phylogenetic variants (Falcon-Lang, 2005), and we do not further subdivide our material into putative morphospecies.

7. Staplehill assemblage in the Winterbourne Formation

Recently, some of us described very similar permineralised fossils (to those dealt with here) from Staplehill, Bristol. These fossils occur in the mid/late Bolsovian Winterbourne Formation, which underlies the Pennant Sandstone Formation in this area of the Bristol Coalfield (Fig. 2; Falcon-Lang et al., 2011a). The Staplehill fossil assemblage, collected in 1905/6, had been considered ‘lost’ until its rediscovery in February 2011 in an unaccessioned collection at the British Geological Survey, Keyworth, UK. Since the publication of our paper, further museum specimens of the Staplehill assemblage have come to light. We therefore take this opportunity to briefly update knowledge of this material, before comparing it with the fossils from the Pennant Sandstone Formation.

7.1. Sedgwick Museum collection

The newly discovered Staplehill material was found in an unaccessioned collection in the Sedgwick Museum, Cambridge, in June 2011, by curator, Matt Riley, and augments knowledge of the assemblage while clarifying certain details of its history of investigation. As we reported in Falcon-Lang et al. (2011a), the Staplehill assemblage was originally collected by Hebert Bolton (1863–1936), curator of the Bristol Museum and Art Gallery, in 1905/6, initially studied in a somewhat superficial manner by biologist, Dennis G. Lillie (1884–1963) of St Johns College, Cambridge, in 1909/10 (Lillie, 1910a,b), and later re-examined by Robert Crookall at the British Geological Survey in 1926/27 (Crookall, 1927a,b, 1931).

In his original study, Lillie is believed to have examined 26 specimens from the Staplehill site, which he labelled using the letters A–Z. However, the material we recently described from a British Geological Survey collection (Falcon-Lang et al. (2011a) comprised only 18 of these specimens, of which most were cordaitalean (Amyelon, Dadoxylon, Mesoxylon) with single representatives of a pteridosperm (Succiella) and a lycopsid (indeterminate). The newly discovered thin section material in the Sedgwick Museum does not add to that diversity but does allow us to identify 21 of Lillie’s original 26 specimens (Table 3; only specimens J, V, W, X, and Y are currently unaccounted). Importantly, the Sedgwick Museum collection also contains hand specimens of some of Bolton’s original Staplehill collection, which may allow a more detailed investigation of the anatomy of these fossils in the future.

Archival material associated with Sedgwick Museum collection also allows us to revise the history of study of the Staplehill assemblage as follows: Herbert Bolton found the fossil site in 1905/6, but initially could not find anyone with the skills to describe the material. In late July 1908, Lillie visited Bolton in Bristol and borrowed the Staplehill material (Falcon-Lang et al., 2011a). He then discussed the fossils with palaeobotanist, William Thomas Gordon (1884–1950), who was a fellow student at Emmanuel College, Cambridge (and later long-time Professor of Palaeobotany at King’s College London; Taylor, 1951). In late 1908, Gordon facilitated the sectioning of the material at University College London (Lillie, 1910b; Crookall, 1927a,b). The first consignment of thin sections, all bearing the acronym U.C.M. (University College Museum), was delivered to Lillie on 2 February 1909 (as indicated by notes written on the slides by Gordon). A second consignment of U.C.M. slides was delivered in early 1910, and that same year, James Lomax (1857–1934), the professional slide maker based in Bolton (Howell, 2005), prepared many more slides.

However, Lillie was only able to complete a superficial study of the Staplehill material for two reasons: (1) he was suffering from mental illness (he was delusional and a manic depressive) and (2) in August 1910, he joined Scott’s fateful Terra Nova Expedition to Antarctica (Falcon-Lang et al., 2011a). Although Lillie donated Gordon’s U.C.M. slides to the Sedgwick Museum, the sections prepared by Lomax appear to have remained in his own private collection. Intriguingly, archival notes in Crookall’s ‘Slides’ register at the British Geological Survey indicate that the BGS purchased these Lomax slides from W.G. Crail, Professor of Botany, University of Aberdeen, on 13 April 1927, for the sum of £10 and 8 shillings. We can only speculate as to how Crail obtained this material; however, Lillie was admitted to Bethlem Hospital (a mental asylum), temporarily from 1918, and permanently from 1924, so it is probable that his family disposed of his personal belongings and the fossils eventually found their way into Crail’s hands.

In the course of his later study, Crookall (1927a,b) borrowed the U.C.M. slides from the Sedgwick Museum in addition to purchasing the Lomax slides. The U.C.M. slides were returned to the Sedgwick Museum on 2 March 1928 (as indicated by Crookall’s handwritten note that accompanies the specimens), but on arrival they were not accessioned in the museum’s register for some unknown reason, and remained ‘lost’ until their rediscovery. The larger, more important, collection of Lomax slides (described in Falcon-Lang et al., 2011a) remained in an unaccessioned collection of the British Geological Survey until their rediscovery in February 2011. Both collections are now fully accessioned with museum numbers (Table 3).

7.2. Comparison of assemblages

The permineralised assemblages from the Winterbourne and Pennant Sandstone formations together represent the finest example of permineralised flora in the British Pennsylvanian, and represent an important body of material that has been overlooked by previous workers. The composition of the two assemblages is remarkably similar, both in terms of shared taxa and their relative abundance (Table 4). In particular, both assemblages are dominated by the remains of cordaitaleans (about 87% of all specimens, Amyelon roots, Mesoxylon aerial axes, Dadoxylon trunk wood) and although there is relatively little correspondence between rare taxa, this disparity probably reflects the very low number of non-cordaitalean specimens. In fact, without the relatively large sample size utilised in this study it is unlikely that the rare taxa would have been detected at all (Henderson and Falcon-Lang, 2011). In the following section, we highlight that cordaitalean-dominated assemblages are unusual in Early and Middle Pennsylvanian strata and explore the palaeoecological implications of the two assemblages.
only 20 of the 21 sectioned specimens from the Winterbourne Formation are determinable. (Falcon-Lang et al., 2011a), and information about the general palaeoclimatic

Table 4

Comparison of the permineralised assemblages known for the Winterbourne Formation (Falcon-Lang et al., 2011a) and the Pennant Sandstone Formation (this paper). Note that only 20 of the 21 sectioned specimens from the Winterbourne Formation are determinable.

<table>
<thead>
<tr>
<th>Winterbourne Formation</th>
<th>Pennant Sandstone Formation Total</th>
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<tbody>
<tr>
<td></td>
<td>Number Percentage</td>
</tr>
<tr>
<td>Coniferopsida</td>
<td>18 90%</td>
</tr>
<tr>
<td>Amborella</td>
<td>5</td>
</tr>
<tr>
<td>Dadoxylon</td>
<td>15</td>
</tr>
<tr>
<td>Myeloxylon</td>
<td>12</td>
</tr>
<tr>
<td>Saccodendron</td>
<td>1</td>
</tr>
<tr>
<td>Filiocarpus</td>
<td>12</td>
</tr>
<tr>
<td>Psaronius</td>
<td>10</td>
</tr>
<tr>
<td>Lycopsids</td>
<td>4</td>
</tr>
<tr>
<td>Indeterminate</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>20 100%</td>
</tr>
</tbody>
</table>

8. Palaeoecology

In our earlier paper, we interpreted the cordaitalean-dominated assemblage from Staplehill, Bristol (mid/late Bolsovian Winterbourne Formation) as a subhumid dryland vegetation based on the widespread occurrence of growth interruptions in the woody axes, co-occurring calcite fragments, aspects of alluvial sedimentology (Falcon-Lang et al., 2011a), and information about the general palaeoclimatic context of this time interval (Besley et al., 1993; Glover et al., 1993; Jones et al., 2011; Waters and Davies, 2006). While the similar cordaitalean-dominated assemblage in the Pennant Sandstone Formation likely represents a comparable subhumid flora, it is more difficult to assess for two reasons.

First, the frequency and markedness of growth interruptions in cordaitalean woody axes (Amyelon and Mesoxylon) is rather less than in the Winterbourne Formation assemblage (Falcon-Lang et al., 2011a), or even when compared with trees that grow in the subhumid tropics today (Ash, 1983). This probably reflects an overall increase in rainfall during the deposition of the Pennant Sandstone Formation, consistent with the coarse-grained alluvial facies, which suggest that run-off and sediment supply markedly increased. In circumstances where rainfall is higher, it is harder to detect seasonality in woods because trees, especially in riparian settings, can be buffered against drought as a result of elevated water tables. Second, although both wetter (coals and platy grey shales) and drier (red beds with calcite nodules and silcrete) interfluve facies are inferred to have existed between the Pennant Sandstone channel facies, they are mostly very thin, laterally discontinuous, locally incised, and poorly exposed (Kellaway and Welch, 1993). As a result, it is impossible to reliably determine the degree of soil drainage on interfluves at the time that allochthonous permineralised material was being transported in the channels. Nonetheless there are two lines of evidence that support a dryland palaeoecology for the assemblage as follows.

8.1. Community composition

The permineralised assemblage in the Pennant Sandstone Formation is dominated by cordaitaleans (>62 specimens, 87%, including Amyelon roots, Dadoxylon trunks and Mesoxylon axial axes), with a few tree-ferns (>5 specimens, 7%, Psaronius, 2 species), rare pteridosperms (1 specimen, Myeloxylon, 1%), rare sphenopsids (2 specimens, 2.5%, Arthropitys) and rare lepidodendrids (2 specimens, 2.5%; Table 1). This assemblage differs substantially from the palynofloras obtained from coal seams interbedded with the coarse-grained fluvial channels. Those palynofloras are variable in their composition, with a few samples rich (>50%) in arborescent lycopsids, while most others comprise a fern or mixed fern- and lycopsid-dominated assemblage (Dimitrova et al., 2005; Pendleton and Wellman, in press). The permineralised assemblages also differ from megalofloral remains in roof shales, which are mostly dominated by pteridosperms, with some common ferns and sphenopsids (Crookall, 1929; Davies, 1929; Moore and Trueman, 1937, 1941; Dimitrova et al., 2005; Cleal, 2007; Pendleton et al., in press).

Thus, we conclude that the permineralised assemblage originated from a different community from either the mire forests (coals) or clastic swamp forests (roof shales).

Cordaitalean-dominance with relatively few pteridosperms is unusual for Pennsylvania wetland assemblages (e.g. although not
unknown, e.g., Raymond, 1988), but highly characteristic of Early and Middle Pennsylvanian red bed intervals interpreted as the deposits of subhumid drylands (DiMichele et al., 2010; Falcon-Lang, 2003b, 2004, 2006; Falcon-Lang et al., 2004, 2010, 2011a). Wetland cordaitaleans can be distinguished from those that occupied better-drained facies based on the presence of aerenchymatous tissue (Phillips, 1982; DiMichele and Phillips, 1994; Falcon-Lang et al., 2011a). As our cordaitalean trees (Amyelon) lack aerenchyma, both in the Pennant Sandstone Formation, and the underlying or laterally equivalent Winterbourne Formation, this suggests they favoured growth on a better-drained landsurface consistent with a dryland ecology.

8.2. Plant preservation

A second line of evidence for dryland ecology is the calcified preservation of our plant material, often preserving anatomy with a very high level of fidelity: this suggests mineralisation by alkali, carbonate-rich groundwaters within a few months, or maximally within a very few years, of deposition (Matsyová et al., 2010). Such groundwater conditions are most often found in dryland settings, where soils accumulate soil carbonate and silica, as calcrete and silcrete, respectively (Gibling and Rust, 1992; Tandon and Gibling, 1994); however, marine-influenced coastal wetlands may also receive carbonate-charged groundwaters (Scott and Rex, 1985). Nonetheless, there is relatively little evidence of coastal incursion in the Pennant Sandstone Formation, except for the Cambriense Marine Band near the base and a few possible brackish bands with nonmarine fauna (Moore and Trueman, 1937; Waters et al., 2009), and what evidence there is, is not directly associated with the fluvial channel facies. Thus, the weight of evidence implies that the calcified preservation mode originated under seasonally dry conditions (Matsyová et al., 2010).

8.3. Dryland or upland?

If we accept that the assemblages that we report here were of subhumid dryland-type and occupied better-drained soils than the Coal Forests, a key question is: where was this dryland vegetation located? One hypothesis is that permineralised remains represent plants that grew in extra-basinal terrains in the Variscan foothills (Falcon-Lang and Scott, 2000; Falcon-Lang and Bashforth, 2004, 2005; Bashforth et al., 2011; Dimitrova et al., 2011; Fig. 6). A second hypothesis is that permineralised plants grew in the lowland interfluvies, but during drier climatic intervals linked to glacial phases when the Coal Forests had temporarily retreated from the region (Falcon-Lang, 2004; Falcon-Lang and DiMichele, 2010; Dolby et al., 2011). Testing between these two hypotheses is challenging based on the limited data available. Although modern plant taphonomic studies show that most plant material incorporated in fluvial drainages originated in proximal levee settings rather than being transported huge distances downstream (Scheiheing and Pfefferkorn, 1984), this is little help in the case of the Pennant Sandstone Formation. This is because the Variscan Deformation Front lay only a few tens of kilometres south of our fossil plant sites (Fig. 6), meaning that an upland source cannot be entirely excluded, even though the frequency of material may suggest a relatively local source (within a few kilometres) was most likely.

8.4. Sequence stratigraphy holds the key

To further test between these two competing hypotheses, it is crucial that we develop a better understanding of the sequence stratigraphy of the Pennant Sandstone Formation. The occurrence of a single marine band and a few brackish bands (Moore and Trueman, 1937) between channel successions implies the occurrence of occasional highstand events reflecting eustatic rise, subsidence or combination of factors. In addition, the Pennant Sandstone channel facies also contain widespread evidence for incision, including evidence for cannibalisation of coals both from coeval interfluvies and older Early Pennsylvanian successes (Gayer and Pelek, 1992), which either reflects eustatic fall or drainage response to Variscan uplift, or a combination (Leveridge and Hartley, 2006). While it is tempting to speculate that the channel facies with permineralised plants were incised during glacial lowstands (cf. Gibling and Bird, 1994), and that cordaitalean-dominated floras reflect dryland ecosystems that replaced the Coal Forests when climatic conditions were drier (Falcon-Lang, 2004), currently this hypothesis is not fully testable and we cannot rule out the idea that permineralised assemblages comprise a record of extra-basinal vegetation. Thus, we leave open both possibilities until further data accumulate.

9. Conclusions

1. We describe Middle Pennsylvanian (mid/late Bolsovian–Asturian) permineralised plant assemblages from the Pennant Sandstone of southern Britain.

2. Fossils occur as allochthonous assemblages in the pebbly sandstone deposits of very large braided river channels draining the rising Variscan orogenic belt to the south.

3. Permineralised fossils (n = 72–77) are dominated by cordaitaleans (87%) with a few tree-ferns (7%), rare pteridosperms (1%), sphenopsids (2.5%) and rare lepidodendrids (2.5%), a very similar composition to that recently reported from the mid/late Bolsovian Winterbourne Formation (Falcon-Lang et al., 2011a).

4. Permineralised assemblages differ from palynoassemblages in interbedded coal seams and compressed plant assemblages in roof shales, which are pteridophyte- and pteridosperm-dominated, respectively.

5. The calcified preservational mode of the fossils and the occurrence of growth interruptions in woody axes imply that permineralised plant grew under seasonal (subhumid) conditions, either outside the wetland depocentre or during drier climatic phases when the Coal Forests had retreated.

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References


Appendix 11 – Published paper: Pendleton et al. (2012)
1. Introduction

The Bristol–Somerset Coalfield of southwest Britain (Fig. 1) has played an important role in the historical development of Pennsylvania palaeobotany, with many prominent palaeobotanists publishing on its plant fossil assemblages (e.g., Sternberg, 1820–1838; Bronniquart, 1826–1838; Kidston, 1888; Lillie, 1910a, 1910b; Arber, 1912, 1914, 1922; Crookall, 1925a, 1925b, 1925c, 1927, 1929, 1931; Moore and Trueman, 1937; Jongmans, 1940; Arber, 1838; Kidston, 1888; Lillie, 1910a, 1910b; Arber, 1912, 1914, 1922; Crookall, 1925a, 1925b, 1925c, 1927, 1929, 1931; Moore and Trueman, 1937; Jongmans, 1940; Moore, 1940). This intensive research effort largely coincided with the nineteenth to early twentieth century boom in the stone quarrying and coal mining industries, which allowed widespread access to plant-bearing strata (e.g., Cumberland, 1816; Woodward et al., 1876).

By the 1930s, however, those extraction industries had gone into sharp decline and by 1973 the last coal mine had closed (Bonsall, 1989; Green, 1992). Subsequently, access to fossil-bearing strata has been limited to degraded spoil tips of former coal mines (e.g., Allen, 1977), the most important being the Writhlington site, which has been designated a Geological Nature Reserve (Proctor, 1994; Thomas and Cleal, 1994). A few other sites, which have been designated as Sites of Special Scientific Interest (SSSIs) due to their scarcity, include brickpits (e.g., the Cattybrook SSSI; Cleal and Thomas, 1988, 1994, 1996), road and railway cuttings (e.g. the Winterbourne railway cutting SSSI; Cleal and Thomas, 1996), and abandoned stone quarries along the River Avon (e.g. the Bickley Wood SSSI; Cleal and Thomas, 1996). As a result of the paucity of new fossil material available, little research into the fossil plant assemblages of the Bristol–Somerset Coalfield has been undertaken over the past 75 years (Cleal and Thomas, 1996). These fossil plant assemblages are in urgent need of revision because of recent advances in our
since, although it has yet to be formally ratified, the IUGS scheme may eventually become globally applicable; however, about 80% of these deposits are concealed beneath widespread Mesozoic cover (Cleal and Thomas, 1996), resulting in a series of disjunct surface exposures. Throughout this paper we have identified the location of outcrops using the Ordnance Survey (OS) grid references usually used in the United Kingdom (Ordnance Survey, 2010).

2.2. Stratigraphy

Building on earlier work (e.g. Woodward et al., 1876; Moore and Trueman, 1937, 1939), Kellaway and Welch (1993) provided a detailed review of the stratigraphy of the Bristol–Somerset Coalfield, and showed that it contains an aggregate thickness of around 2600 m of coal-bearing strata. Recently, Waters et al. (2009) emended the stratigraphical terminology based on lithostratigraphical correlation of mapable geological units, as opposed to the broadly chronostratigraphical system of Kellaway and Welch (1993) (see also Waters et al., 2011). They defined the South Wales Coal Measures Group, containing coal-bearing sequences with marine bands...
The Warwickshire Group of the Bristol Coalfield, which has an aggregate thickness of up to 1200 m in the Coalpit Heath Syncline and an aggregate thickness of approximately 1900 m in the southern limb of the Kingswood Anticline, based on our own estimates from desktop based mapping and construction of a new stratigraphical interpretation (Fig. 3). Below, we summarise the key features of the three formations recognised in current stratigraphical nomenclature, from base to top, the Winterbourne, Pennant Sandstone and Grovesend formations (Waters et al., 2009).

2.3. Winterbourne Formation

The Winterbourne Formation is a 120–180 m thick unit whose distribution is restricted to the Coalpit Heath Syncline region of the northern part of the Bristol Coalfield (Green, 1992; Kellaway and Welch, 1993; Waters et al., 2009). The Winterbourne Marine Band (also known as the Cambriense Marine Band) defines the base of the Winterbourne Formation in the Coalpit Heath Syncline region, although this marine marker bed has not been found in the adjacent Kingswood Anticline region (Waters et al., 2009), likely reflecting a topographic high in this area. The top of the Winterbourne Formation is taken to be the base of the first major (>3 m thick), coarse-grained sandstone bed of the Pennant Sandstone Formation (Waters et al., 2009).

Only two limited surface exposures are known of the Winterbourne Formation; one is adjacent to a small stream in a wooded area between Fishponds and Speedwell (OS ST 632748), and the other comprises various points along the disused railway line between Staple Hill and Fishponds, especially near the Staple Hill tunnel (OS ST 651756). However, the Winterbourne Formation is much more thoroughly known from British Geological Survey (BGS) borehole cores including Harry Stoke B and C, Stoke Gifford 3, Yate Deep and Winterbourne (Kellaway and Welch, 1993), demonstrating its distribution over about 20 km². The Winterbourne Formation is also known from Stoke Gifford 2, and Westerleigh 1 and 2 boreholes, but due to the absence of the Winterbourne Marine Band in these areas only an estimated position of the lower boundary is possible.

The lower part of the Winterbourne Formation comprises a single basal marine band (in some areas), grey mudstone, locally containing the non-marine bivalves Anthracosuccisa philipi and a few coals, and channel sandstone bodies (Waters et al., 2009). The uppermost 40 m comprises mostly red mudstones and grey/green mottled mudstone beds and at least three beds of conglomerate bodies containing subangular polymictic clasts. The conglomerate beds are up to 2–3 m thick, fine-upwards into coarse-grained sandstone, and may show rooted upper surfaces, reworked caliche nodules and lithic clasts.
with oxidised rims. Associated permineralised tree-trunks show growth interruptions (Falcon-Lang et al., 2011b).

Falcon-Lang et al. (2011b) interpreted this succession as the de­posit of a poorly-drained coastal plain, over lain by the deposits of a well-drained alluvial plain subject to a seasonal (subhumid) tropical climate. Suppressed water table in these upper deposits was also likely linked to the first pulses of Variscan uplift, which centred on the Usk Anticline, and initiated the deposition of the closely associated conglomerates. The relative importance of climatic and tectonic influences on red bed formation at this time, which is widespread across Britain and northwest Europe (Besly and Turner, 1983; Besly and Fielding, 1989; Glover et al., 1993; Pagnier and van Tongeren, 1996; Fielding, 1989, 1993; Stubblefield and Trotter, 1957). Hence, the base of the formation is profoundly dia­chronous (younging from south to north), and time-equivalent to the Winterbourne Formation in its oldest part (Waters et al., 2009).

The top of the Pennant Sandstone Formation is defined at the Rudge Coal in the Somerset Coalfield, and in the Bristol Coalfield, at the High Coal in the Coalpit Heath Syncline (Kellaway, 1970). Due to the confusion regarding the stratigraphy of the southern limb of the Kingswood Anticline, we have constructed a new stratigraphical interpretation for this area, based on desktop mapping and field ob­servations (Fig. 3; based on J.L. Pendleton, unpublished data and field observations). Using this new stratigraphy the Rock Coal is des­ignated as the upper limit of the Pennant Sandstone in this southern region.

Previous authors have used a unified stratigraphy for the entire Bristol Coalfield, superimposing the Salridge Coal of the southern limb of the Kingswood Anticline onto the stratigraphy of the Coalpit Heath Syncline, 150–200 m below the High Coal. There appears to be no sound basis for this, despite this stratigraphical chart appearing in almost every paper relating to the Bristol Coalfield for the last few decades (Kellaway and Welch, 1993; Waters et al., 2009, 2011).

In the Bristol Coalfield, the Pennant Sandstone Formation is subdivided into the lower Downend Member (~150–600 m thick) and the upper Mangotsfield Member (~400 m thick). The boundary between the Downend and Mangotsfield members is taken as the lowest of the Mangotsfield coals in the Coalpit Heath Syncline and its equiva­lent, the Temple Cloud Coal, in the Somerset Coalfield. At this level, “Pennant-type” sandstone beds of the Mangotsfield Member rest sharply on top of the lowermost Mangotsfield coals. The Mangotsfield coals are not present in the southern limb of the Kingswood Anticline but based on the newly produced stratigraphy and field observations it is possible that the Salridge Coal may be its equivalent.

The Pennant Sandstone Formation is dominated by thickly bedded units of coarse-grained, feldspathic, lithic arenites organised into large-scale channel bodies. In extensive exposures in South Wales, these bodies typically rest on scours, several metres deep, and may be >100 m wide (Jones and Hartley, 1993); however, in the Bristol Coalfield, exposure is generally too poor to confirm channel geomet­ry, with channels and scours generally being larger than the outcrop scale. Nonetheless, there is no reason to assume that the channels of the Bristol Coalfield had a different geometry to those of South Wales.

Channel-fill comprises pebbly sandstone and coarse-grained sandstone, frequently trough cross-bedded, or locally showing tabular cross-stratification several metres high (Waters and Davies, 2006). Rare, fine-grained intervals between the sandstone beds comprise red mottled mudstone with caliche nodules or grey, platy shales with plant fossils and the non-marine bivalves Anthracostrea phillipsii, and a few lenticular coals (Kellaway and Welch, 1993; Falcon-Lang et al., 2012). The roof of the High Coal, which marks the top of the formation, contains the branchiopod crustacean Leaia (Crookall, 1929) in association with the non-marine bivalves, A. phillipsii and A. tenuis (Moore and Trueman, 1937).

The Pennant Sandstone Formation is interpreted as the deposits of large-scale braided fluvial systems (Jones and Hartley, 1993), which occupied a poorly-drained coastal plain setting as indicated by inter­vening coal-bearing strata, and at times, a well-drained alluvial plain as indicated by intercalating caliche-bearing red bed strata (Falcon­

Fig. 3. Stratigraphy of the Warwickshire Group of the Bristol Coalfield, north and south of the Kingswood Anticline, showing the position of the adpressed fossil sites consid­ered in producing the megafossil biostratigraphical chart (see Fig. 6). Location numbers as in Fig. 2b; * marks the ranges of the Harry Stoke B, C, and Winterbourne boreholes (Localities 1–3).

2.4. Pennant Sandstone Formation

The Pennant Sandstone Formation is ~600–1000 m thick in the Bristol Coalfield and its base was originally formally defined as the Cambriense Marine Band (Kellaway and Welch, 1993). However, as already noted, in their lithostratigraphical revision, Waters et al. (2009) transferred the lowermost grey and red argillaceous beds encoun­tered in Coalpit Heath Syncline to the Winterbourne Formation. Consequently they moved the base of Pennant Sandstone Formation to a higher stratigraphical level defined by the lowermost mapable unit of thickly bedded (>3 m thick) “Pennant-type” sandstone. Usu­ally this occurs near the level of the Parrot (=Hen?) Coal in the Bris­tol Coalfield; however, in the Somerset Coalfield, the base of the Pennant Sandstone Formation is at the level of the Little Course Coal, 120 m below the Cambriense Marine Band (Stubblefield and Trotter, 1957). Hence, the base of the formation is profoundly dia­chronous (younging from south to north), and time-equivalent to the Winterbourne Formation in its oldest part (Waters et al., 2009).

The Pennant Sandstone Formation is interpreted as the deposits of the lowermost part of the Mangotsfield Formation in the Coalpit Heath Syncline, and is equivalent to the Rock Coal in the Somerset Coalfield. The Pennant Sandstone Formation, at this level, is defined by the Mangotsfield Member which is the uppermost unit of the Mangotsfield Formation, and is the horizon which marks the transition from non-marine and transitional marine deposits in the southern limb of the Kingswood Anticline, to marine deposits in the northern limb of the Kingswood Anticline (Kellaway and Welch, 1993; Falcon-Lang et al., 2011b). The Pennant Sandstone Formation is subdivided into two members, the Lower and Upper Mangotsfield Members, which are separated by a thick bed of caliche mudstone and pebbly sandstone (Kellaway and Welch, 1993; Falcon-Lang et al., 2011b). The Lower Mangotsfield Member is characterised by the presence of the branchiopod crustacean Leaia (Crookall, 1929) in association with the non-marine bivalves, A. phillipsii and A. tenuis (Moore and Trueman, 1937).

The Pennant Sandstone Formation is interpreted as the deposits of the lowermost part of the Mangotsfield Formation in the Coalpit Heath Syncline, and is equivalent to the Rock Coal in the Somerset Coalfield. The Pennant Sandstone Formation, at this level, is defined by the Mangotsfield Member which is the uppermost unit of the Mangotsfield Formation, and is the horizon which marks the transition from non-marine and transitional marine deposits in the southern limb of the Kingswood Anticline, to marine deposits in the northern limb of the Kingswood Anticline (Kellaway and Welch, 1993; Falcon-Lang et al., 2011b). The Pennant Sandstone Formation is subdivided into two members, the Lower and Upper Mangotsfield Members, which are separated by a thick bed of caliche mudstone and pebbly sandstone (Kellaway and Welch, 1993; Falcon-Lang et al., 2011b). The Lower Mangotsfield Member is characterised by the presence of the branchiopod crustacean Leaia (Crookall, 1929) in association with the non-marine bivalves, A. phillipsii and A. tenuis (Moore and Trueman, 1937).
Cross-beds indicate palaeoflow with a strong northerly to north westerly mode (also reported by Hartley and Warr, 1990; Cleal and Thomas, 1996), and as noted above, sediment was probably shed from the Variscan Deformation Front to the south (Heard, 1922); the diachronous lithostratigraphical base of the formation marking the northward proggradation of the fluvial system.

2.5. Grovesend Formation

The Grovesend Formation is the uppermost unit of the Bristol–Somerset Coalfield, resting on top of the Pennant Sandstone Formation, although the formation boundary is currently nowhere exposed, either in outcrop or borehole. In the Bristol Coalfield, it comprises the lower Farrington Member, <70 m thick, which is a succession of grey argillaceous strata with economic coals, overlain by the Barron Red Member, a red mottled mudstone succession, which is ~200 m thick in the Coalpit Heath Syncline area (Waters et al., 2009). These units interfinger at least in part.

Higher units of the Grovesend Formation do not occur in the Bristol Coalfield; however, in the Somerset Coalfield, the Radstock and Publow members overlie the Barron Red Member (Waters et al., 2009). Relatively little is known of the sedimentary facies and palaeontology of these units, beyond that they are dominated by grey mudstone with non-marine bivalves, “Pennant-type” sandstone bodies, and a few coals (Waters et al., 2009). They probably represent the deposits of poorly-drained coastal plains. The Hursley Hill borehole (OS ST 618 656), drifted just beyond the southern limit of the Bristol Coalfield outcrop (Fig. 2), provides access to the Radstock and Publow members in close proximity to the southern edge of the coalfield (Kellaway, 1970).

2.6. Correlation with marine-based global chronostratigraphy

A key stratigraphical marker bed for determining the age of the Warwickshire Group is the Aegiranum Marine Band. This is positioned ~200 m below the base of the group in the Harry Stoke B borehole, but lies close to the base of the group in the Somerset Coalfield due to the diachronous nature of the lower boundary. This widespread marine incursion defines the Duckmantian–Bolsovian boundary across northwest Europe (Davydov et al., 2010). The Aegiranum Marine Band contains Diplagnostus coloradoensis–Idiognathodus conodont faunas (Higgins, 1975; Boogard, 1983; Boogard and Bliss, 1983; Riley et al., 1985). Based on these conodonts, Riley and Turner (1995) have correlated it with the Winifred Shale (Atokan Stage) in the Appalachian Basin of North America, broadly coincident with the evidence of the associated megaflora (Blake et al., 2002).

The Cambriene Marine Band, which marks the base of the Winterbourne Formation (and the Warwickshire Group) in the Bristol Coalfield, is positioned near the lithostratigraphical middle of the Bolsovian succession (Waters et al., 2009). No conodonts have been reported from this unit (Phil Heckel, pers. comm., 2011), so its correlation with successions in the USA and the IUGS global chronostratigraphy is in doubt. The goniatites that are characteristic of this unit are described by Anochaeras cambriense (Bisat 1930), but were later simultaneously transferred to the genera Weideyoceras (Popov, 1979) and Donetzoceras (Saunders et al., 1979), the latter probably being the more correct name (Phil Heckel, pers. comm., 2011). Davydov et al. (2010), who used the genus, Weideyoceras, positioned their W. cambriense Zone as mid–Bolsovian, which would make it equivalent to the uppermost Bolsovian to lower Asturian in the western European regional chronostratigraphy. However, as all Donetzoceras cambriense specimens lack sutures crucial for ammonoid systematics (Saunders et al., 1979), comparison of the Russian and British material is uncertain, and in the absence of sutures also raises the question as to whether the whole taxon is a nomen dubium (Phil Heckel, pers. comm., 2011).

As no marine bands occur higher in the Warwickshire Group, there is considerable difficulty in correlating these beds with the global stratigraphy. However, as noted above, a number of non-marine bivalve bands containing Anochaeras philippisi occur in the Winterbourne and Pennant Sandstone Formation, with A. tenuis occurring at the base of the Grovesend Formation (Moore and Trueeman, 1957; Waters et al., 2009). Anochaeras philippisi is generally regarded as an upper Bolsovian index fossil with A. tenuis having a first occurrence just below the base of the Asturian Substage (although see Cleal, 1984 for a discussion on the practical problems of using these bivalves as biostratigraphical indices). In the Appalachian Basin, A. tenuis has a first occurrence in the upper Atokan Stage, at about the level of the Stockton or Upper Mercer Coal (Sager and Belt, 2003), which is also below the base of the Asturian Substage indicated by the megaflora (Blake et al., 2002). If we accept the correlations, the Warwickshire Group would be equivalent to a level somewhere in the earliest to mid-Moscovian Stage.

3. Material and methods

In this paper, we describe all known assemblages of adpression and sandstone-cast plant fossils in the Warwickshire Group of the Bristol Coalfield, and revise systematics in light of current taxonomy. We use these data to improve knowledge of the biostratigraphical framework of the Warwickshire Group and investigate patterns of plant diversity during the crucial evolutionary phase that preceded the peat mire floral community collapse in this region (Cleal et al., 2009a). We also compare our data with recently described permineralised assemblages (Falcon-Lang et al., 2011b, 2012) and palynofloras (Pendleton and Wellman, in press) in a facies context to analyse palaeoecology. Our inventory of marine and terrestrial plant assemblages is based on material at various museums, our own new field collections, and data mined from the literature as follows:

3.1. Museum repositories

In the course of our work we have examined material in six museum collections.

1. The Bristol City Museum and Art Gallery and Art Gallery collection contains material collected in the 1920s by palaeobotanist, Robert Crookall (Thomas, 1981), and amateur collector, Tom Fry (Large, 1994, 1997), whose photographs and short biographies appear in Falcon-Lang et al. (2012). Several specimens were also donated by other, presumably, amateur collectors and those affiliated with the then active coal mining and stone quarrying. We investigated 315 specimens from this collection; 21 adpressions from the Winterbourne Formation, 29 adpressions and 46 sandstone casts from the Pennant Sandstone Formation and 219 from the Farrington Member.

2. The University of Bristol collection contains specimens curated in its Geology Museum and its cabinets of teaching material. This includes material collected by Fry in the 1920s and sold to the university in 1934, and some of Leslie Moore’s Ph.D. material. We investigated 39 specimens from this collection, all adpressions from the Farrington Member.

3. The British Geological Survey, Keyworth (BGS) includes material collected by Robert Kidston (Thomson and Wilkinson, 2009), and plant fossils associated with boreholes mostly obtained in the 1950s. There are also several sandstone-cast fossils, some donated to Kidston by Crookall. We investigated 25 specimens from this collection; 3 adpressions and 10 sandstone casts from the Pennant Sandstone Formation and 12 adpressions from the Farrington Formation. In addition, 228 adpressions from the
Winterbourne Formation and lowermost Pennant Sandstone Formation from the Harry Stoke B and C boreholes, and ~1500 adpressions from the Grovesend Formation in the Hursley Hill borehole were investigated.

(4) The Natural History Museum (London) collection includes material obtained by Crookall and W.N. Edwards, the former curator of palaeobotany. We investigated 7 specimens from this collection; 1 sandstone cast from the Pennant Sandstone Formation and 6 adpressions from the Farrington Formation.

(5) The Sedgwick Museum (Cambridge) collection contains material from palaeobotanists Dennis Lille, E.A.N. Arber and Crookall (see Falcon-Lang et al., 2011b for historical details), mostly obtained between 1910 and the mid-1920s. We investigated 77 Farrington Member adpressions from this collection.

(6) The Hunterian Museum (Glasgow) collection contains a single specimen from the Farrington Member.

3.2. New field collections

We have also made collections of material from the following new sites and previously described sites as follows: (1) a newly discovered assemblage in the Mangotsfield Member at Dingle, Winterbourne Down (OS ST 656 793); (2) a newly discovered megafossil assemblage in the roof of the Salridge Coal located on the south bank of the River Avon, near Keynsham (OS ST 642 701); (3) a re-collection of a megafossil assemblage at Bickley Wood (OS ST 6417 7053), first identified and collected by Tom Fry, but unpublished except in manuscript form (Fry, 1922, 1926); and (4) numerous old and new localities where sandstone-cast fossils are preserved. All newly collected material is curated in the Department of Geology, National Museum Wales, Cardiff. Where percentages of species are mentioned, these are purely based on numbers of identifiable specimens recorded at the outcrop at the time the new collections were made.

3.3. Publications

We have also incorporated in our study megalfloral data from published work on the Warwickshire Group of the Bristol Coalfield (Kidston, 1888; Lillie, 1910b; Arber, 1912, 1914, 1922; Crookall, 1929; Moore and Trueman, 1937; Moore, 1940). In a few cases, we have not been able to track down the collections associated with these publications (due to incomplete or missing accession information). Most notably, we have been unable to locate the vast majority of Leslie Moore’s important fossil plant collection, obtained during his Ph.D. research at the University of Bristol under the supervision of Professor Arthur Trueman. As a result, our determinations are simply based on the updated nomenclature for published taxa, and may be in doubt in some cases. Such cases of doubtful identifications are marked on the entries in the data appendices.

Another major challenge of incorporating these historic published occurrences is that locality and stratigraphical data are often uncertain. This is because specimens were mostly collected from spoil tips and they were assumed to come from clastic rocks immediately adjacent to the coal being mined. This is problematic because (1) there was sometimes uncertainty as to exactly which coal was being mined, and (2) often a single pit mined more than one coal. Thus data were often presented in publications in such a way as to make it impossible to distinguish between the plant assemblages of different stratigraphical horizons (e.g., roof rocks). Even when specimens are available for re-examination they are often insufficiently curated with labels lacking necessary detail. Nonetheless, critical analysis of such assemblages is informative, even if not to their full potential due to inadequate documentation.

3.4. Biostratigraphy

The stratigraphical distribution of the plant megafossils in the Bristol Coalfield has been interpreted in terms of the biostratigraphy introduced by Wagner (1984) and modified by Cleal (1991) and Cleal and Thomas (1996). This scheme is based around what are now interval zones and subzones established from a synthesis by Wagner (1984) of the plant fossil distribution data from Euramerica, notably from the Variscan foreland and intramontane basins of Europe and the Canadian Maritimes, and India, with the Iberian Peninsula. Since the GSSPs of the subzones in the Heerlen Chronostratigraphical Scheme are located in these areas, it is relatively straightforward to relate the zones and subzones to those subzones, as summarised by Wagner (1984).

4. Location, stratigraphy and facies context of fossil assemblages

Based on these three sources of data (museum collections, field collections, and publications), we identified fifteen localities for which adpression plant fossils have been obtained in the Warwickshire Group of the Bristol Coalfield. We have used a combination of sources to ascertain, as accurately as possible, the locality, stratigraphical horizon and facies of each collection, including examination of historic maps and up to date geology maps (available via the digital map service, Digimap, www.edina.ac.uk/digimap), coal mine records and boreholes (available from the British Geological Survey), and field studies. For each collection we give an indication of the level of uncertainty of our stratigraphical determinations, and in some cases exclude collections from further analysis.

The fifteen adpression assemblages are described below, from oldest to youngest, and occur in two general facies contexts: (1) pale grey siltstone lenses, locally rooted, within major coarse-grained sandstone channel bodies in the Pennant Sandstone Formation, interpreted as channel abandonment and levee facies associated with large braided rivers, and (2) well-laminated shales in the roof of coals, locally with non-marine bivalves, in all three formations, interpreted as flooding horizons resulting from base-level rise. We do not give a similar list for localities with sandstone-cast material because such material is extremely widespread and most of our data come from poorly constrained sites in the Downend Formation of the Frome Valley, or the basal Mangotsfield Member of Winterbourne.

4.1. Winterbourne Formation and lower Downend Member boreholes (Localities 1–3)

The two known surface exposures of the Winterbourne Formation did not yield any identifiable adpression material. Although several BGS boreholes penetrate the Winterbourne Formation, only Harry Stoke B (OS ST 6321 7816, Locality 1) and Harry Stoke C (OS ST 6504 7677, Locality 2) have accessioned plant fossil material from this unit. A full summary log of the boreholes are in Kellaway and Welch (1993), and a more detailed log of the lower portion of the Harry Coke B and C borehole is in Falcon-Lang et al. (2011b), based on original borehole log records (BGS). From these rocks, megalfloral assemblages were obtained spanning the whole of the Winterbourne Formation, and the lowermost portions of the Downend Member. We have re-examined the specimens at the BGS, and made new determinations on the species composition for Harry Stoke B (Appendix 1) and Harry Stoke C (Appendix 2). We also considered the historical records of species obtained from the Winterbourne borehole (OS ST 2967 825, Locality 3), which also penetrated the same strata (Appendix 3). Plate 1 illustrates specimens from the Harry Stoke B and C boreholes.
4.2. Hanham Colliery (Locality 4)

The site of Hanham Colliery (OS ST 637 720) is situated on the northern bank of the River Avon, between Conham and Hanham; it operated between 1872 and 1926. Kellaway and Welch (1993) state Hanham Colliery worked the Red Ash (or Jubilee) and White Ash Veins of the South Wales Lower Coal Measures Group. However, these shafts would have also penetrated at least 275 m of Warwickshire Group, passing through several of the economic coals of the lowermost Pennant Sandstone and Winterbourne formations, which were specifically mined in other areas. It is likely, that at some point, Hanham Colliery did exploit these coals early in its history. However, as collections and observations by Crookall (1925a, 1925b, 1929) were made around the time that the colliery closed it is probable his material was indeed sourced from these older coals. Plant fossils recorded from Hanham Colliery were therefore excluded from this paper, as they were probably sourced from rocks below the Warwickshire Group.

Plate I. Adpressed plant fossils from the Laveineopteris rarinervis Subzone of the Winterbourne Formation. All specimens from Harry Stoke C (Locality 2). Scale bars 10 mm.

1. Lobanopteris miltoni (Artis) Wagner, Bo428; British Geological Survey, Keyworth.
2. Eupheneopteris trimus (Gothan) Novik, BF3021; British Geological Survey, Keyworth.
3. Linopteris oblata (Bunbury) Zeiller, Bo1397; British Geological Survey, Keyworth.
5. Reticulopteris muensteri (Eichwald) Gothan, Bo461; British Geological Survey, Keyworth.
6. Umatopteris tenella (Brongniart) Kidston, BF3114; British Geological Survey, Keyworth.
4.3. California Colliery, Oland Common (Locality 5)

This collection was obtained when, in 1876, an old shaft in Oland Common (OS ST 665 714) was deepened and renamed California Colliery. Prior to deepening, the pit is reported to have extended to a depth of around 70–75 m suggesting that it worked the uppermost coals of the lower Downend Member of the Pennant Sandstone Formation (the Millgrit, Rag and a small local seam named the Dibble Coal; Hawkins and Tomlinson, 1987). Following deepening the pit intersected the Parrot Coal and eventually reached the New Smith’s Coal at ~290 m. The Winterbourne Marine Band, which defines the base of the Warwickshire Group in the Bristol Coalfield, does not occur in the southern portion of the coalfield, but is likely equivalent to the interval between the New Smith’s Coal and Parrot Coal (Kellaway and Welch, 1993). Moore and Trueman (1937) reported a megafossil assemblage from the numerous tips associated with this colliery (Appendix 4). While it is likely that these plants come from the lowermost Pennant Sandstone Formation, and Winterbourne Formation, some may have come from just below the base of the Warwickshire Group.

4.4. St. Anne’s Park assemblage (Locality 6)

This collection was obtained from a small, disused quarry in St. Anne’s Park, south Bristol (OS ST 619 727) and reported in Moore and Trueman (1937). Material came from a fine-grained siltstone lens in the Pennant Sandstone Formation, and they noted that, "this horizon is probably not far above the base of the Pennant Series [= Pennant Sandstone Formation]". The quarry is recorded on historic maps and comparison with modern geological maps confirms a position in the Downend Member. We have been unable to locate Moore and Trueman’s (1937) material and the site has been landscaped for housing so new collections are impossible. Updated taxonomy for material listed in Moore and Trueman (1937) is given in Appendix 5.

4.5. Bickley Wood, Hanham Abbots (Locality 7)

This collection was obtained by Tom Fry from a disused quarry in Hanham Abbots, in the 1920s; further collections were later made by the present authors. Fry located his site as follows: “base of quarry, 280 yards [255 m] SSE of Castle Inn Farm, Hanham Abbots”. Using historic maps, we were able to re-locate this site precisely (OS ST 6417 7053). Cleal and Thomas (1996) referred to this site as the Bickley Wood SSSI. The material occurs in a grey siltstone lens apparently within a coarse-grained sandstone channel complex. Fry’s material is accessioned in the Bristol City Museum and Art Gallery and Art and Gallery and our own material is accessioned in the National Museum Wales, Cardiff. Cleal and Thomas (1996) noted that the taxon list provided by Moore and Trueman (1937) may include some misidentifications due to an unlikely combination of species. They suggested that the fossils indicated an age of early or even mid-Asturian, based on the presence of Neuropteris ovata Hoffmann. We have examined the material and provide a revised species list (Appendix 6). New material was extracted from a siltstone lens at the base of a quarry, which is situated very close to the inferred location of Fry’s site. The new material yielded abundant Bolsovan-Asturian ranging Laveineopteris dussartii (Laveine) Laveine (Plate II, 1), which superficially resembles the Asturian-restricted N. ovata Hoffmann (compare with Plate III, 4 for an example from the Grovesend Formation). Re-examination of Fry’s material in the Bristol City Museum and Art Gallery and Art and Gallery confirmed this was the case, Laveineopteris dussartii (Laveine) Laveine was overwhelmingly the dominant species in this lens, with subordinate Calamites sp. This collection comes from a north-facing quarry wall, on the western side of the A4174 road as it crosses the River Avon to the

Plate II. Adpressed plant fossils from the Laveineopteris rariusi subzone of the Pennant Sandstone Formation, including new specimens from Bickley Wood (Locality 7) and the Saltridge Coal, Keynsham (Locality 10). Scale bars 10 mm.

Plate III. Adpressed plant fossils from the Dicksoniites plumieri Subzone, of the Farrington Member. Scale bars 10 mm. (See on page 26)
Plate III (caption on page 24).
north west of Keynsham (OS ST 642 701). The quarry features Pennant-type channel sandstone bodies containing three siltstone lenses. This is overlain by 1.75 m of alternating, thinly bedded (0.2–0.3 m) mudstone and coal, developed on top of a 7.3 m thick seat earth. The sequence is capped by a 0.85 m thick coal with a pale beige/light brown roof; this likely represents the Salridge Coal proper. The beige colour of the roof rock does not appear to be the result of modern weathering, as this uniform colour was seen in fresh excavations of ~1 m into the outcrop made during two abseil runs. All plant material recovered from the substantial talus slope beneath the coal is also only present in this light mudstone. Adpression plant fossil assemblages were obtained directly from the roof. This locality likely represents a similar horizon to the “Chandos Lodge” site (Locality 9) of Moore and Trueman (1937). A species list is given in Appendix 9, with material illustrated in Plate II, 2–9.

4.9. Winterbourne Down (Dingle) leaf bed (Locality 11)

This newly discovered material was obtained from the upper part of the Pennant Sandstone Formation in a dissected quarry along the south bank of the River Frome in the Dingle, Winterbourne Down (OS ST 656 793). We estimate this horizon lies ~160–200 m above the Mangotsfield coals, in the middle Mangotsfield Member. It consists of a thin (~1 m) laterally inconsistent lenticular mudstone between thickly bedded sandstones characteristic of the Pennant Sandstone Formation. Small flutes casts on the sole of the overriding sandstone give a palaeocurrent towards the north–west. The leaves are well preserved, with isolated pinnules of Macroneuropteris scheuchzeri (Hoffmann) Cleal et al. being the vastly dominant taxon. These Macroneuropteris pinnules are generally smaller than is typical for the species, and are often torn parallel to the vein. A species list is provided in Appendix 10.

4.10. Crookall’s Grovesend Formation flora (Localities 12–13)

Crookall (1929) summarised all previous reports of adpression megafossils and other fossils from the former “Farrington Series” (= Farrington Member, Grovesend Formation) of his “northern area” (i.e., the Bristol Coalfield). This incorporated and built on previous work by a number of other authors. In his initial monograph of the adpression megafossils of the Bristol–Somerset Coalfield Kidston (1888) reported 15 taxa from the former “Farrington Series” (= Farrington Member) and a further 13 taxa were later added by other workers (Lilie, 1910b; Arber, 1914, 1922) including two species of the cone Lepidotrobus. Other occurrences were listed by Kidston and Jongmans (1917) and Kidston (1923–1925). These results were summarised and augmented by Crookall (1925a, 1925b, 1929) whose total list comprised 90 taxa. We have examined the Crookall collection at Bristol City Museum and Art Gallery and Art Gallery. Unfortunately the exact stratigraphical provenance of many of the specimens is unclear. This is unfortunate as the Bristol Farrington Member coalfields worked 3 or 4 coals, spanning up to 70 m of stratigraphy. Several other specimens, specifically the Lilie and Arber material, are accessioned in the Sedgwick Museum and were also investigated.

Appendix 11 features a full list of all species recorded as coming from the Farrington Member of Coapit Heath (Locality 12, OS ST 697 816) and Parkfield collieries (Locality 13, OS ST 690 777); this amalgamates all the historical records together with any miscellaneous species found during our museum investigations. Identifications were also checked, and necessary changes made. Plate III illustrates specimens from the Farrington Member of Coapit Heath and Parkfield collieries.

4.11. Shortwood Brickworks (Locality 14)

Moore and Trueman (1937) reported on an adpression megaflora recovered from the Farrington and Barren Red members of the Grovesend Formation from Shortwood brickworks (Locality 14, OS ST 682 768), some 2 km south–west of Parkfield Colliery. A coal, which is thought to represent the Hard Coal of Parkfield Colliery (i.e., the uppermost coal of the underlying Farrington Member) once outcropped at the very base of the brick-pit (Nick Chidlaw, pers. comm., 2011). This site is now a landfill site, although some strata are still exposed. We have visited the site on several occasions but did not find any new fossil material. Specimens from this location are accessioned in the Bristol City Museum and Art Gallery and Sedgwick Museum. Adjacent to Shortwood brickworks the four Parkfield coals were previously exposed in the old Dramway railway cutting (Kellaway and Welch, 1953). Specimens of Achithea polymorpha were recovered by the present authors from grey siltstones, which lie 1–2 m stratigraphically above the Hard Coal, and are accessioned in the National Museum Wales, Cardiff. Appendix 12 provides a species list from the uppermost Farrington and Barren Red members of Shortwood brickworks.

4.12. Hursley Hill borehole, Pensford (Locality 15)

The Hursley Hill borehole (OS ST 618 657?) was sunk for the National Coal Board in 1951, 3.3 km south–south–east of the southern limit of the Bristol Coalfield outcrop. This borehole penetrated 730 m of Grovesend Formation, including, from base to top, the Barren Red, Radstock, and Publow members. This borehole provides the only material from the Radstock and Publow members, which do not appear within the stratigraphy of the Bristol Coalfield outcrop. In this borehole the Radstock Member and Publow Member are 275 m and 305 m thick, respectively (580 m in total). The megafossils of the Hursley Hill Borehole were studied in the 1960s and 1970s by one of us (RHW) but details have not been published until now. Stratigraphically useful taxa are included on the range chart in Fig. 4. Plate IV illustrates some species from the Hursley Hill borehole.

5. Adpression megaflora

In this paper, we do not intend to give a full systematic revision of the adpression megafossils of the Bristol Coalfield, and surroundings. Here, we merely summarise and illustrate the main assemblages in a stratigraphical and facies context.

5.1. Overview of assemblages

All of the assemblages from the Winterbourne Formation are associated with grey shales and the roof and shale partings of the coals, i.e., clastic swamps (Plate I). It is also possible that at least some of these specimens represent the vegetation growing during the latest stage of mine development (Gastaldo et al., 1995). These assemblages contain 15 taxa including a high diversity of scrambling and arboreal cent pteridosperms (Eusphenopteris striata, Eusphenopteris neuropteroides, Laveineopteris spp., Macroneuropteris scheuchzeri, Mariopteris nervosa, Neopteris semireticulata and Reticulopteris muensteri), together with some marattialean ferns (Lobatopteris miltioni, Pecopteris plumosa), calamiteans (Annularia sphenophylloides, Annularia spinulosa), and sphenophylls (Sphenophyllum emarginatum, Sphenophyllum majus). Urnatopteris tenella, and Alethopteris cf. urophylla are restricted to the Winterbourne Formation, disappearing below the base of the Pennant Sandstone Formation. Pteridosperms are the dominant plant group in the Winterbourne Formation; Reticulopteris munsteri and Laveineopteris spp. are most common at the base of the assemblage, with Alethopteris cf. urophylla appearing in the upper portion of the formation.
In the Pennant Sandstone Formation ([Plate II]), assemblages are either associated with siltstone lenses within channel bodies (abandonment facies) or coal roofs (clastic swamps). Almost all the roof shale assemblages in the Pennant Sandstone Formation come from historic records (with the exception of Locality 10), therefore no comment can be made on species dominance patterns. Lobatopteris miltoni and Laveineopteris tenuifolia are restricted to the Downend Member in the roof shales or siltstone lenses, having their last occurrence in the roof of the Salridge (verified) and Mangotsfield coals (historical records). Most of the other species from the Winterbourne Formation continue into the Pennant Sandstone Formation roof shales, giving a similar overall species composition.

For the new siltstone lens collections, all available specimens were collected; so observations on dominance can be made with more certainty. Pteridosperms are the overwhelmingly dominant taxa in these beds, with a single species accounting for most of the assemblage; Laveineopteris dussartii (pinnate foliage and cyclopterids) represents 88% of identifiable megafossil specimens at Bickleys Wood, and Macroneuropteris scheuchzeri represents 80% of fossils in the Dingle leaf bed. Single specimens of other pteridosperms, Laveineopteris rarineris and Mariopetris cf. nervosa also occur in these assemblages. Nonpteridosperm assoxey taxa are limited to Annularia sp. and Calamites sp. Historic species list indicate the St Anne’s siltstone lens (Moore and Trueman, 1937) may be more diverse, although as these specimens are not available to check identification, it is possible that there are several misidentified taxa in this species list.

A significant increase in species diversity is seen in the Farrington Member ([Plate III]); the lowermost unit in the Grovesend Formation. These are mostly the first appearances of small ferns and tree-ferns (Actheca polymorpha, Alloiopteris radstockensis, Crossotheca crepini, Crossotheca pinnatifida, Cyathocarpus aff. arborescens, Lobatopteris cameronensis, Lobatopteris vestita, Oligocarpis brongniartianii) and pteridosperms (Alethopteris ambigua, Alethopteris larchitica, Alethopteris pseudograndinioides var. subzeilleri, Alethopteris serili, Dicksonites plukkeneti, Neuropteris ovata, Neuropteris flexuosa, Macroneuropteris macrophylla, Palmatopteris alatum). Pseudomariopteris cordatoovata and Callipteridium sp. (pteridosperms) first appear in the Radstock Member, Lobatopteris vianna (marattialean fern), Odontopteris bradui and Aethopteris var. subzeilleri (pteridosperms) appear in the Poldown Member, at the top of the succession. Plate IV illustrates fossils from the Radstock and Poldown formations.

Crookall (1925a) carried out a study of the species dominance in the Farrington Member roof shales, where he ranked the species on a scale from 1–2 (“very rare”) to 8–10 (“very common”). Lobatopteris vestita (recorded as Pecopteris miltoni, see below for discussion), a marattialean fern species, is the only species listed as “very common” at both collieries. Actheca polymorpha (marattialean fern), with Neuropteris flexuosa and Neuropteris ovata (pteridosperms) are listed as being “fairly common” at Parkfield; with the basal foliage Cyclopteris (Neuropteris) fimбриata also ranked as “fairly common” (2). Other taxa ranked as 5 at Parkfield are: Calamites citii (calamitalean), Cordaites (cordaitalean), Lepidodendron aculeatum (lycopsid) and Macroneuropteris scheuchzeri (pteridosperm). Lycopsis (Lepidodendron spp.) seem to be the “fairly common” taxa at rank 5 at Coalpit Heath, along with C. citii (calamitalean), Cyclopteris (Neuropteris) fimбриata (pteridosperm), M. scheuchzeri (pteridosperm) and Actheca polymorpha (marattialean fern).
It is difficult to make detailed comments on species dominance in the roof shale megafossil assemblages based on this limited data set. However, it may be tentatively suggested that the Parkfield assemblages show a dominance of ferns and pteridosperms, with subordinate calamiteans, whereas Coalpit Heath appears to be dominated by ferns with subordinate lycopsids and calamiteans.

It is important to note that most of the Pennant Sandstone floras were obtained from relatively small collieries or from isolated outcrops, whereas the collieries working the Fairlington Member coals were of much larger scale, and were much more intensively studied and collected. Due to the magnitude of the diversity increase, it is likely that this increase does reflect a true palaeoecological signal but the strong sampling bias must be acknowledged.
5.2. Taxonomic notes on biostratigraphically-important taxa

Most of the adpersion species dealt with in this paper are well documented from other areas such as from the Warwickshire Group of South Wales (e.g. Kidston, 1923–1925; Crookall, 1955–1976; Cleal, 1978, 1997; Cleal and Thomas, 1994) and the Sydney Mines Formation of Cape Breton (e.g. Bell, 1938; Zodrow and McCandlish, 1980; Zodrow, 1986) and require little further comment. The following notes are just intended to clarify the use of a few of the species, where this may not be immediately evident from this previous literature.

Annularia spinulosa Sternberg

This name is now used for the species traditionally referred to as Annularia stellata (Sternberg) Wood (see Kvaček and Straková, 1997; Barthel, 2004). This taxon first appears near the base of the Laveineopteris rarirevris Subzone, and Laveine (1977) used it as an indicator of the proximity of the base of the Asturian Substage. Annularia spinulosa occurs throughout the Grovesend Formation in the Bristol Coalfield, with historic records indicated this species may have a first occurrence in the uppermost Downend Member. However, no specimens in museums or from the new collections are available to validate these occurrences from the Pennant Sandstone Formation.

Lobatopteris miltoni (Artis) Wagner Plates I, 1 and II, 4; Lobatopteris vestita (Lesquereux) Wagner auct., Plate III, 3

The type specimen of Lobatopteris miltoni originated from the middle Westphalian Elicer Nine Feet Coal of Yorkshire (a lateral equivalent of the Barnsley Coal – Mitchell et al., 1947; Cleal et al., 2009b; Plenicka et al., 2009), and is characterised by relatively robust ultimate pinnules and bluntly terminated penultimate pinnules (Shute and Cleal, 1989). It ranges from the base of the Laveineopteris ishihi Subzone (middle Langsettian) through to the top of the Paripteris lingue-folia Zone (upper Bolsovian) and very rarely occurs in the lower Linopteris bunnurii Zone (lower Asturian) (Cleal and Thomas, 1994). The specimens from the Winterbourne and Pennant Formations (e.g., Plates I, 1 and II, 4) agree closely with this type. In contrast, those from the Grovesend Formation have more slender, delicate ultimate pinnules and gradually tapered penultimate pinnules that correspond to the species widely referred to as Lobatopteris vestita (see Plenicka et al., 2009 for a discussion on the nomenclatural problems surrounding this species). The confusion between L. vestita auct., which is a characteristic element of upper Asturian and Cantabrian fossil floras (Wagner and Alvarez-Vázquez, 1991), and L. miltoni which is typical of Langsettian to Bolsovian floras, has a long history dating back to Kidston (1923–1925). Lobatopteris miltoni is restricted to the Downend Member in the Bristol Coalfield.

Lobatopteris viannae (Teixeira) Wagner, Plate IV, 2

Wagner (1959) discussed the taxonomy of this species. Although it is most characteristic of Barruelian to Stephanian C megalofloras, Lobatopteris viannae has been reported from the Cantabrian Substage of both NW Spain (e.g., Wagner et al., 1983) and South Wales (Cleal, 1978). It was found in the Hursley Hill Borehole at depths of 114 m and 191 m, corresponding to the lower part of the Publow Member of the Grovesend Formation.

Alethopteris pseudograndinioides var. subzeilleri (Wagner) Zodrow & Cleal, Plate IV, 1

Wagner (1966) demonstrated that, in the lower Stephanian Stage, there was a transition from pinnules with more biconvex lateral margins and somewhat oblique veins of typical A. pseudograndinioides (= Alethopteris grandinioidea Wagner non Kessler; see Zodrow and Cleal, 1998) to the more parallel-sided pinnules with veins nearly perpendicular to the pinnule margin of A. pseudograndinioides var. subzeilleri. Most of the Hursley Hill specimens correspond to the type variety, but there is one specimen, from a depth of 460 m in the Publow Member of the Grovesend Formation, which shows pinnules of the var. subzeilleri form.

Laveineopteris dassartii (Laveine) Laveine, Plate II, 1

This species was established by Laveine (1977) for early Asturian fronds from northern France and subsequently recorded from the upper Bolsovian and Asturian of South Wales by Cleal (1978). It is similar to Neopteris ovata Hoffmann in the general shape of the pinnules, but the former are generally more oval, have a more consistently developed basiscopic auricle, and rather less dense veins. The presence of Laveineopteris dassartii at the Salridge Coal at Chandos Lodge accounts for the record of N. ovata from here by Moore and Trueman (1937).

Callipteridium spp., Plate IV, 4–5

Callipteridium is represented here by just a few rare fragments found at depths of 87.5 m, 151.5 m, 319.7 m and 557.5 m in the Hursley Hill Borehole, in both the Radstock and Publow members of the Grovesend Formation. This genus is extremely rare in Britain, having been previously reported as isolated fragments from the Somerset, South Wales and Severn coalfields (Kidston, 1923–1925; Cleal, 1978, 1986). Some of the Hursley Hill fragments have small pinnules similar to Callipteridium armassi (Zeiller) Wagner (Plate IV, 5) and others have larger pinnules of the Callipteridium jangmansi (Berr) Wagner type (Plate IV, 4). However, as there is a significant overlap in pinnule morphologies between these two species (see comments by Laveine et al., 1977), we cannot confidently assign our specimens to one or other of these species.

Fig. 5. Photographs of large sandstone-cast tree-trunks found in the Pennant Sandstone Formation in Fishponds, Bristol, between 1909 and 1926. (a) Sigillaria, and (b) Lepido- dendrid trunk >5 m long (courtesy of Bristol City Museum and Art Gallery and Art Gallery).
Odontopteris brardii (Brongniart) Brongniart, Plate IV, 3

Several fragments were found in the Hursley Hill Borehole at a depth of 279.5 m (lower Pliensbachian Member) that compare with Odontopteris brardii as recorded from the lower Cantabrian Substage of NW Spain (e.g., Wagner et al., 1983, pl. 7, fig. 1), in particular in having broadly attached pinnules with fine veins. The only other species with which it could be confused is Odontopteris reichiana Guttler, known from the upper Asturian Substage of Zwickau, Saarland and central and Western Bohemia (Dabner, 1955; Štětlik, 1977; Šimůnek and Čelákovský, 2004) but this has pinnules that are typically more constricted on the acroscopic side, and have a shorter midvein. Although O. brardii occurs most commonly in NW Spain in the Barroisian Substage, it can rarely occur as low as the lower Cantabrian Substage (Wagner et al., 1983).

6. Sandstone-cast axes

Sandstone cast fossils are common in the thick channel sandstone bodies of the Pennant Sandstone Formation, and historically, when quarrying proceeded at pace, very large specimens were recovered (Fig. 5).

6.1. Field studies

In order to determine the composition and relative abundance of taxa in these assemblages, we made field observations of sandstone-cast assemblages at four sites in north-east Bristol, three in the Downend Member (Eastville, Fishponds, Frenchay) and one in the Mangotsfield Member (Winterbourne Down). These sandstone-casts were mainly recovered as isolated blocks from spoil tips of stone quarries. Unfortunately, museum specimens often lack specific locality details beyond notation of a nearby conurbation. Presumably many were discovered during quarrying of the Pennant Sandstone Formation, which peaked in late nineteenth century, or on spoil tips from the mine shafts that penetrated this formation.

The names of several donors are noted on specimens in the Bristol City Museum and Art Gallery (e.g., J.W. Tutcher, W.J. Hawkins, A. Golding, T. Owen, J. Cornwell, A.E. Hudd, A. McNee, H.C. Harford) and several with “labelled in E.B.T.'s hand”. These people were likely local miners, quarrymen, and amateur collectors, and fossils were mainly obtained from the Downend Member in quarries close to the River Frome as it flows south westwards from Downend and Frenchay towards Stapleton (broadly, the same localities, where we undertook over field census). Other specimens came from Frampton Cotterell, Keynsham, Clevedon, Parkfield, and Golden Valley.

In order to document the composition of the sandstone-cast assemblages more completely, we also examined all available museum collections. Unfortunately museum specimens often lack specific locality details beyond notation of a nearby conurbation. Presumably many were discovered during quarrying of the Pennant Sandstone Formation, which peaked in late nineteenth century, or on spoil tips from the mine shafts that penetrated this formation.

Table 1: Censuses of sandstone-cast fossils in four regions of northeast Bristol in the Downend Member (Eastville, Fishponds and Frenchay) and the lower Mangotsfield Member (Winterbourne Down) showing the dominance of lycopsid trunks with subordinate calamitalean and cordaitalean axes.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Eastville</th>
<th>Fishponds</th>
<th>Frenchay</th>
<th>Winterbourne Down</th>
<th>Total %</th>
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<tr>
<td>Lycopsids</td>
<td>47.1</td>
<td>1.4</td>
<td>7.1</td>
<td>24.2</td>
<td></td>
</tr>
<tr>
<td>Stigmariaceae</td>
<td>47.1</td>
<td>1.4</td>
<td>7.1</td>
<td>24.2</td>
<td></td>
</tr>
<tr>
<td>Decorticated lycopsid</td>
<td>1.4</td>
<td></td>
<td>7.1</td>
<td>24.2</td>
<td></td>
</tr>
<tr>
<td>Sigillaria sp.</td>
<td>73.1</td>
<td>14.1</td>
<td></td>
<td>24.2</td>
<td></td>
</tr>
<tr>
<td>Calamites sp.</td>
<td>50.9</td>
<td>9.7</td>
<td>7.1</td>
<td>24.2</td>
<td></td>
</tr>
<tr>
<td>Filicites sp.</td>
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<td>1.4</td>
<td>7.1</td>
<td>24.2</td>
<td></td>
</tr>
<tr>
<td>Cycadites sp.</td>
<td>47.1</td>
<td>8.9</td>
<td>7.1</td>
<td>24.2</td>
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<tr>
<td>Pteridosperm axis</td>
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<td>3.5</td>
<td>7.1</td>
<td>24.2</td>
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<td>Coniferalean axis</td>
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<td>Indeterminate</td>
<td>152.9</td>
<td>29.5</td>
<td>24.2</td>
<td>516.1</td>
<td></td>
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</table>

Division Sphenophyta
Family Calamitaceae
Genus Calamites Brongniart

Identification: Calamites species are distinguished based primarily on the nature of the infranodal scars, which are not preserved on these specimens due to the coarse-grained nature of the sediment infill. However, we note that on better-preserved museum specimens from other coalfields, it is apparent that both the axis width and internodal length decrease gradually towards the junction between branches and stems, and are therefore not reliable criteria for separating species. It is also typical to find widely different internodal lengths within a single specimen (e.g., Croom, 1912), especially near the base (Falcons-Lang, 2006; DiMichele and Falcon-Lang, 2012). Therefore, many Calamites species may be of limited value. We note that almost all our observed specimens are unequivocally stem casts rather than what were formerly referred to as “pith casts” (DiMichele and Falcon-Lang, 2012).

Calamites cf. carinatus Sternberg, Plate V, 1
Description: Two specimens, with 72–77 mm wide axes (mean 74 mm). Internodes are straight sided, due to almost no constriction at the nodes. Nodes vary in prominence and sometimes almost seem to disappear when traced around the axes, making accurate measurements of internodes difficult. This is likely a result of the ribs crossing the internodes with almost no offset, and the lack of nodal constriction. Internodes are very variable, partly due to this varying prominence, but have been measured as ranging from 15 mm, up to 200 mm or more. Infranodal scars not visible. Internodal ribs are very slightly flexuose, which may be a feature of post-
mortem compression. Internodal ribs are prominent and have truncated apices with narrow (1 mm wide) interstitial furrows. The ribs constrict and converge in localised patches where they reach the nodes. This may mark the position of branch scars, but due to the coarse-grained nature of the sediment, these features were not preserved in detail.

Identification: The localised convergence of the ridges near the nodes, likely corresponding to branch scars, is a feature not seen in the other Calamites species. In addition, it has consistently broader ribs, lack of articulated internodes which are difficult to trace.

Calamites cf. suckowii Brongniart, Plate V, 2

Locality: 1von Weissenburg, frome way in winterbourne down, basal mangotsfield formation. 2Disused quarry on the dingle in winterbourne down, basal mangotsfield formation. 3Hanham, Downend member. 4Stapleton, lower downend member. 5Bristol coalfield. 6Clevedon (conygar quarry), undifferentiated pennant sandstone formation. 7Downend, upper downend member. 8Clevedon (Norton wood), undifferentiated pennant sandstone formation. 9Conham quarries, near top of Downend member. 10Keynsham (Fox's Wood), basal Mangotsfield member.

Description: Fifteen specimens, width axes ranging from 39 to 108 mm wide (mean 74 mm). Internodes 25–98 mm long (mean 56 mm). Internode length to axis width ratio 0.31 to 1.75 (mean 0.71). Internodes on any one specimen tend to be of more or less uniform length along the length of the visible axis. Constriction at the nodes, where rootlets would have been connected to this larger root system, is a feature not seen in the other Calamites species. In addition, it has consistently broader ribs, lack of articulated internodes which are difficult to trace.

Identification: Differentiated from other species by wider ribs, generally wider axes, consistently clear and large nodes, lack of constriction at the nodes, parallel-sided internodes and more or less constant internodal lengths. No evidence of constriction at site of branch scars.

Calamites sp. 1, Plate V, 3–4

Locality: 1Frome way in winterbourne down, basal mangotsfield member. 2Disused quarry on the dingle in winterbourne down, basal mangotsfield formation. 3Bristol coalfield, location uncertain. 4Clevedon (conygar quarry), undifferentiated pennant sandstone formation. 5Conham quarries, near top of Downend member.

Description: Ten specimens, with axes ranging from 26 to 60 mm wide; averaging 42 mm. Internodes 5–15 mm long (mean 11 mm). Internode length to axis width ratio 0.19–0.75 (mean 0.31). Internodes on any one specimen tend to be of variable length along the visible axis. Constriction at the nodes is variable, with specimens with longer internodes typically exhibiting only minor nodal constriction, while the shorter internoded specimens typically have pronounced nodal constriction, which causes the internodes to become barrel-shaped. Infranodal scars (tubercules) very rarely visible, extending for the full width of the internodal ribs and with a length roughly equal to twice this width. Longitudinal ribs narrow and straight, around 1–1.5 mm in width, with arcuate or slightly truncated apices. Interstitial longitudinal furrows around a half the width of the ribs. Specimens partially compressed, giving the axes an oval shaped profile.

Identification: Like Calamites cisti brongniart (Plate V, 1), grading into Calamites schutzteformis kidston and jongmans (Plate V, 2).

Division Lycophyta
Genus Sigillaria Brongniart
Sigillaria ficoides Brongniart, Plate V, 5

Locality: 1Disused quarry on the dingle in winterbourne down, basal mangotsfield formation. 2Golden valley (old pit), basal downend member.

Description: Three specimens. Surface with oval tubercles, 4–7 mm (mean 4) by 3–4 mm (mean 3 mm). Axis maximum diameter, 66–75 mm (measured from one specimen). Tubercles are spaced at approximately 4–13 mm intervals (mean 9 mm). At the centre of each tubercle sits a small 1 mm circular to oval pit, representing the site where rootlets would have been connected to this larger root axis.

Identification: The rootlet scars of Sigillaria stellata Göppert 1841 are bordered by short, strong radiating ribs.

Genus Halonia Lindley & Hutton
?Halonia, Plate V, 6
Material: Cg1558; Bristol City Museum and Art Gallery and Art Gallery.
Locality: Conham quarries, near top of Downend member.

Description: Axis 22–27 mm (mean 25 mm). 8 mm halonial scars spaced 8–12 mm apart. Axis ornamented with smaller, closely spaced 2 mm tubercles.

Identification: One specimen. Presence of halonial scars indicate Halonia; differentiation beyond generic level, not typically meaningful.

Knoria, Plate V, 7
Material: Cg2424; Cg06245; Bristol City Museum and Art Gallery and Art Gallery. Geol. soc. coll. 5245; British Geological Survey, Keyworth.

Locality: Stapleton, lower Downend Member.

Description: Three specimens of sandstone-cast axes; 73–131 mm diameter (mean 107 mm). Surface features give the appearance of small tubercles or short cylinders, 3–5 mm in diameter, lying near-parallel to the axis. Apices of projections typically rounded, or truncated.

Identification: While these fossils conform to the genus Knoria, traditionally interpreted as a decorticated lycopod, some superficially similar specimens show evidence for a possible martialean treefern affinity (discussed below as incertae sedis). The specimens retained here as Knoria however have a slightly different external ornament, more akin to traditional Knoria, and no internal preservation.

Family Sigillariaceae
Genus Sigillaria Brongniart
Sigillaria cf. trisellata Brongniart, Plate VI, 1
Locality: Disused quarry on the dingle in winterbourne down, basal mangotsfield formation.

Description: One specimen. Leaf cushions aligned in files, centred on longitudinal ribs which are 8–9 mm wide. 1 mm furrows
separate the ribs. Transverse furrow visible above each leaf scar, 4–5 mm wide and 10 mm long, which is convex upwards. Leaf cushions are broader than they are tall, 2–3 mm wide by 2 mm long, and appear to be broadly oval in shape. One or two depressions on the cushion are picked out by coal, which likely represent the parichnos and/or vascular bundle. Cushions are in an
alternating arrangement along each rib, suggesting a helical arrangement, and are spaced 6 mm apart.

Identification: Fine details of ornamentation are not preserved in sufficient detail to allow identification to species level. The generalised morphology, however, is similar to *Sigillaria teselato* Brongniart.

*Sigillaria* sp. 1, Plate VI, 2


Locality: Dragon Road in Winterbourne Down, basal Mangotsfield Formation.

Description: One specimen. Leaf cushions arranged into files on 9–10 mm wide ribs. Leaf cushions are offset between each rib, likely being arranged helically around the trunk. Leaf cushions only represented by 2–3 mm oval tubercles which are broader than they are tall, which are spaced at 7–8 mm intervals. Under oblique lighting faint lateral lines can be seen to extend downwards from each leaf cushion, which appear to terminate at around the midpoint between the leaf cushion and the one below.

Identification: Although no leaf cushion detail is preserved, the broad scar and long lateral lines suggests *Sigillaria laevigata* Brongniart or *Sigillaria rugosa* Brongniart, or similar form.

*Sigillaria elegans* (Stnemb) Brongniart Plate VI, 3

Material: cg1575; Bristol City Museum and Art Gallery and Art Gallery.

Locality: "Bristol Coalfield", location uncertain.

Description: One specimen. Axis, 67–80 mm wide. Hexagonal cushions ~8 mm tall by 7 mm wide, raised with a domed profile. No inter-areas visible. Leaf cushions may be arranged in files (hence *Sigillaria* genus assignment).

Identification: It is unclear, due to oblique compression of the axis, whether the hexagonal cushions are arranged in files.

Genus *Syringodendron* Sternberg

*Syringodendron* sp. 1 Plate VI, 4


Locality: 1 Dragon Road in Winterbourne Down, basal Mangotsfield Formation. 2 Frenchay, upper Downend Member. 3 Stapleton, lower Downend Member. 4 Keynsham, basal Mangotsfield Member.

Description: One specimen. Axis, 67–80 mm wide. Hexagonal cushions ~8 mm tall by 7 mm wide, raised with a domed profile. No inter-areas visible. Leaf cushions may be arranged in files (hence *Sigillaria* genus assignment).

Identification: Although no leaf cushion detail is preserved, the broad scar and long lateral lines suggests *Sigillaria laevigata* Brongniart or *Sigillaria rugosa* Brongniart, or similar form.

*Syringodendron* elegans (Stnemb) Brongniart Plate VI, 3

Material: cg1575; Bristol City Museum and Art Gallery and Art Gallery.

Locality: "Bristol Coalfield", location uncertain.

Description: One specimen. Axis, 67–80 mm wide. Hexagonal cushions ~8 mm tall by 7 mm wide, raised with a domed profile. No inter-areas visible. Leaf cushions may be arranged in files (hence *Sigillaria* genus assignment).

Identification: It is unclear, due to oblique compression of the axis, whether the hexagonal cushions are arranged in files.

Identifications: Two specimens, four in negative impression and two in positive impression, with longitudinal ribs 9–19 mm wide (mean 14 mm), separated by 2–4 mm (mean 3 mm) wide "U"-shaped furrows. Longitudinal ribs ornamented with long striations along their length. On the ribs are pairs of elongated crescentic sub-cortical scars of reniform or tear shape. Each scar is around 9–14 mm long and 1–4 mm wide, averaging 4 mm length and 2 mm width. Due to the small size of the scars and the very coarse sandstone they are preserved in, some paired sub-cortical scars appear fused at one end or along most of their length to produce a horseshoe-shape or oval scar. Each scar is spaced 21–29 mm, averaging 26 mm, from the next one along the longitudinal rib. These scars represent the aeration channels (parichnos).

Identification: The consistently smaller, more widely spaced scars and thinner ribs differentiate this species from *Syringodendron* sp. 1. This difference could represent different *Sigillaria* species or a more apical or branch location of the specimen. *Syringodendron* sp. 1 is also only seen in positive compression, whereas *Syringodendron* sp. 2 is more typically seen in negative compression. It is also possible that these two *Syringodendron* species represent different stages of decortication of similar *Sigillaria*; with one being casts of the decorticated stem and the other being a cast of the outer "bark" layer after it had come away from the trunk.

Family Lepidodendraceae

Genus *Lepidodendron* Sternberg

*Lepidodendron* cf. aculeatum Sternberg Plate VI, 6


Locality: 1 Disused quarry on The Dingle in Winterbourne Down, basal Mangotsfield Formation. 2 Frenchay, upper Downend Member. 3 Stapleton, lower Downend Member.

Description: One well preserved specimen, on which the description is mostly based upon, together with two moderately preserved and one poorly preserved specimen. Rhomboidal leaf cushions that are taller than wide (width to height ratios of 0.45–0.42, 22–24 mm (average 22 mm) tall and 9–9 mm (average 8 mm) in width, with inflexed apical and basal angles, and rounded lateral angles. Leaf cushions taller than wide, with. Inter-areas between cushions on the best preserved specimen are narrow, around 3 mm thick. In the other specimens, leaf cushions abut each other with no inter-areas. The preserved axis is 103 mm wide, and is likely an incomplete representation due to the irregular edges of the cast.

The best preserved specimen features a discernible elliptical-rhombic leaf abscission (folar) scar, approximately 3 mm in diameter, positioned approximately half way between the cushion midpoint and the apical and basal angles. A longitudinal furrow (keel) runs from the base of the foliar scar, to the basal angle of the leaf cushion. Another keel likely runs through the upper leaf bolster to the apical angle, but this is not seen as the upper bolster is obscured due to the oblique nature of the cast. On some foliar scars, a small 1 mm tubercle may be present; likely representing the ligule. Due to the coarse nature of the sediment, no infra-foliar parichnos are preserved. Slightly below the foliar scar, two small tubercles may be discernible; likely representing a pair of inter-foliar parichnos channels.

Identification: The following features suggest these specimens may be *Lepidodendron aculeatum* Sternberg; flexuose-rhombic leaf cushions which are taller than wide, featuring a distinctive keel and small, rhombic leaf scale which is offset towards the apical angle of
Lepidodendron aculeatum Sternberg also is known to show secondary stem growth, which produced inter-areas between the normally abutting leaf cushions.

Lepidodendron worthenii Lesquereux, Plate VI, 7
Material: Geol. Soc. Coll. 5298; British Geological Survey, Keyworth
Locality: Downend, upper Downend Member.
Description: One specimen. 12–14 mm wide axis, featuring roughly rhombohedral leaf cushions; 4 mm long and 1.5 mm wide. At the top of the leaf cushion is a small tubercle 2 mm long by 1 mm wide, with a longitudinally orientated slit, representing the leaf scar. Leaves depart from the stem axis at 45–50°; which are 8–9 mm long and < 1 mm wide at the base. Leaves straight to moderately curved.
Identification: Species conforms to descriptions of Lepidodendron wortheni Lesquereux. Lepidodendron lycopodioides Sternberg has broader based leaves, which typically depart at a shallower angle from the axis (<45°). The leaves of Lepidodendron similre Kidston also depart the axis at a shallower angle, and have a distinct “S”-shape.

Lepidodendron sp. 1, Plate VI, 8
Material: cg15671, cg15592; Bristol City Museum and Art Gallery. Geol. Soc. Coll. 52853; British Geological Survey, Keyworth
Locality: 1Clevedon (Norton Wood), undifferentiated Pennant Sandstone Formation. 2Conham quarries, near top of Downend Member. 3Bristol Coalfield, location uncertain.
Description: Three specimens. 30–31 mm lycophytes axis, featuring rhombohedral leaf cushions 5–6 mm long and 2–4 mm wide. No leaf cushion detail preserved, and no leaf scars or parichnos channels visible.
Identification: Likely represents shoots of species like Lepidodendron c.f. aculeatum Sternberg, or Lepidodendron wortheni Lesquereux without leaf cushion preservation.

Genus Lyginodendron Gourlie
Lyginodendron sp. 1, Plate VII, 1
Locality: 1Disused quarry on The Dingle in Winterbourne Down, basal Mangotsfield Formation. 2Bristol Coalfield, location uncertain. 3Stapleton, lower Downend Member. 4Golden Valley (Old Pit), basal Downend Member. 5Conham quarries, near top of Downend Member.
Description: Six specimens of decorticated lycopsid. Shorter and neatly rhombic to lenticular scars appear on some specimens. As axis width increases the length of the scars dramatically increases and the scars become very elongate but retain their overall lenticular shape. The width of the scars varies from 3 to 14 mm, whereas their length varies from 7 mm on the smallest specimen (42 mm axes) to up to 60 mm on the largest (140 mm axes) specimen. On the larger specimens the apical terminations of the scars also become less distinct, and in places the terminations of the scars may appear joined.
Identification: Gourlie (1844) established the genus Lyginodendron (type species Lyginodendron landsburgii Gourlie) based on a cast of a lycophyte stem. Williamson (1873) later misinterpreted the genus and used it for anatomically preserved stems of a lyginopteridalean (pteridosperm), a mistake pointed out by Potonié (1897), who established the alternative name Lyginopteris. The name Lygino- dendron in the original sense of Gourlie (1844) has not been subsequently used in the literature. However, the specimen that we figure in Pl. VI, 7 is so remarkably similar to Gourlie’s type, and so dissimilar to the other decorticated lycopsid stems from the Bristol Pennant Sandstone Formation, that we feel justified in allocating these specimens to the genus (rather than relegating them to Incerta sedis).

Division Pteridophyta
Family Marattiaceae
Genus Caulopteris Lindley & Hutton
Caulopteris cf. petilgra Brongniart, Plate VII, 2
Material: Cg1564; Bristol City Museum and Art Gallery.
Locality: There is some discrepancy between the location details on the labels (Conham, near top of Downend Member) and the tray details (Yate Concrete Works, uncertain position in Pennant Sandstone Formation).
Description: One specimen. Axes 48–53 mm. Oval shaped leaf scars, 50 mm long by 24 mm wide, with long axis parallel to stem axis. Leaf scars are arranged into four files, helically offset. Longitudinally aligned striations in the centre of the leaf scar for a 35 mm by 14 mm raised oval area, concentric with the leaf scar outline. The striations are 1–2 mm wide, extend for up to 4 mm in length and have rounded terminations with straight or slightly curved sides.
Identification: Similar to Caulopteris petilgra Brongniart from the roof shales of the Grovesend Formation of Coalpit Heath; originally identified as Caulopteris macrodiscus Brongniart by Kidston, but renamed in Crookall (1929). Caulopteris petilgra lacks the coarsely striated, raised portion at the centre of the leaf scar.

Caulopteris sp. 1, Plate VII, 3
Material: Cg1562; Bristol City Museum and Art Gallery.
Locality: There is some discrepancy between the location details on the labels (Conham, near top of Downend Member) and the tray details (Yate Concrete Works, uncertain position in Pennant Sandstone Formation).
Description: One specimen. Axes 69 mm. Tear-shaped/flash shaped leaf scars with rounded upper limit and open side facing towards the base of the stem, 77–80 mm long (mean 79 mm) and 20 mm broad at the widest point; 29–41 mm spaced, average 36 mm. Leaf scars are arranged into eight files, helically offset. Longitudinal striations occur in the lower half of the scar, at the open side of the scar. No vascular detail is preserved at the top of the scar.

Division Coniferophyta
Order Cordaitales
Genus Artisia Sternberg, 1838
Artisia approximata Lindley & Hutton, Plate VII, 4
Material: Cg15741, cg15601, cg15552; Bristol City Museum and Art Gallery and Art Gallery.
Locality: 1Conham quarries, near top of Downend Member. 2Troopers Hill, Downend Member.
Description: Three pith cast specimens, 31–41 mm diameter (mean 35 mm). Around the axes are 1 mm transverse ridges, which are typically concentric with few truncations. Ridges occur at a density of 7–9 per cm (mean 8). Longitudinal striations occur randomly but appear to form discrete clusters, and extend for several centimetres before terminating; likely representing leaf scars.
Identification: Artisia transversa Sternberg does not feature leaf scars.

Artisia transversa (Artis) Sternberg, Plate VII, 5
Locality: 1Dragon Road in Winterbourne Down, basal Mangotsfield Formation. 2Disused quarry on The Dingle in Winterbourne Down, basal Mangotsfield Formation. 3Downend, upper Downend Member.
Description: Four pith cast specimens, 17–24 mm diameter (mean 21 mm). Around the axes are 0.8–1 mm (mean 0.9 mm) wide transverse ridges. Ridges at a density of 1–2 per mm (mean 1.1). Ridges mostly concentric around the axes, with very few truncations.
One specimen retains the original trunk outline, which is 107–111 mm in diameter. In this specimen the pith cast occupies 12–16% of the total diameter, and appears to be slightly skewed to one side by 10–12%.
Identification: Artisia transversa Sternberg can be differentiated from the other species, Artisia approximata Lindley and Hutton, by its lack of longitudinal leaf scars.
Remarks: The skewed pith implies that the tree grew on inclined slope, or that the axes represent a branch (Creber, 1975; Fritts, 1976).
Division incertae sedis
Incertae sedis, Plate VII, 6–7
Material: cd62771, cg14952; Bristol City Museum and Art Gallery and Art Gallery.
Localities: 1Stapleton, lower Downdenn Member. 2Clevedon (Norton Wood), undifferentiated Pennant Sandstone Formation.

Description: Two specimens. Sandstone-cast axes ornamented with short cylinders lying near-parallel to the long axis, with rounded or truncated. This ornament is similar to that of Knorria.

One specimen (cg14955) has been partially mineralised by ironstone, shortly after being sandstone-cast, and preserves some three-dimensional structure. Most prominent in transverse view is a large "C"-shaped cavity, 17 x 25 mm diameter, showing fine, longitudinal striations. This is surrounded by other cavities, triangular in transverse view, which may be helically arranged. Surface features give the appearance of small cylinders, 2–3 mm in diameter, lying near-parallel to the axis, and overlapping in the direction that the axes widen, such that they are visible for only 8–13 mm (mean 10 mm) of their length. Apices of projections typically rounded, or truncated.

Identification: Most Knorria specimens, which feature similar external ornament to these specimens, comprise decorticated trunks of lycopsids; this is how the generic name has been traditionally used. However, the appearance of our specimen is suggestive of marattiaceous tree-ferns, with the systems of external, overlapping cylinders, aligned parallel to the axis, representing a cast of the outer root mantle, and the system of internal cavities in one specimen, preserving details of stellar anatomy and departing petioles. Due to the uncertainty surrounding the affinity of this very unusual specimen, it is retained within incertae sedis.

7. Biostratigraphy and stratigraphical implications

The Warwickshire Group of the Bristol Coalfield has always been contentious in terms of its age and various aspects of its stratigraphy, especially the correlation of the successions in the Coalpit Heath Syncline and Kingswood Anticline. Traditionally these strata have been biostratigraphically dated based on the fauna of the marine bands, megafossil floral assemblages and associated terrestrial faunal remains (e.g., Moore and Trueman, 1937; Kellaway and Welch, 1993; Waters et al., 2009). Here we present a range chart of the biostratigraphically most important megafossil taxa for the Warwickshire Group of the Bristol Coalfield, based on re-evaluation and re-identification of existing museum collections, and our newly collected material (Fig. 4).

7.1. Biozonation

The base of the Warwickshire Group in the Bristol Coalfield is marked by the mid-Bolsovian Winterbourne Marine Band (= Cambridgian Marine Band). We show that megafossil assemblages from the Winterbourne and Pennant Sandstone Formation belong to the Laveineopteris rariniensis Subzone of the Paripteris linguefolia Zone indicating a mid- to late Bolsovian age. Specifically, these formations contain L. rariniensis, Annnularia sphenophylloides, and Reticulopteris muensteri which have their lowest stratigraphical occurrences in the mid-Bolsovian, at the base of this subzone. These reflect floral changes in the mid-Bolsovian; correlating to the base of Kidston’s “Staffordian Series” (Kidston, 1905), Dix’s Floral Zone G (Dix, 1934) and the “Morganian Substage” (Dix and Tuenman, 1937). In the Wagner (1984) biostatigraphical scheme, the lowest stratigraphical occurrence of Sphenophyllum emarginatum is in the underlying Neuropteris semireticulata Subzone, usually in the upper part of that subzone. Alethopteris urophylla has a highest stratigraphical occurrence within the lower portion of this biozone (see Wagner and Alvarez-Vázquez, 2008 for a detailed review of this species) and A. cf. urophylla is present in the Winterbourne Formation. Laveineopteris linguefolia and Lobatopteris miltoni similarly do not normally range up into the overlying Linopterus obliqua Zone (e.g. Cleal, 2007).

The Farrington to Radstock members of the Grovesend Formation, in contrast, have megafossil assemblages belonging to the Dicksonites pluknetii Subzone of the Lobatopteris vestita Zone, indicating a late Asturian age. Actidicea polymorpha, L. vestita and D. pluknetii have first occurrences in the late Asturian and define the base of this subzone. Sphenophyllum majus has a last occurrence in the late Asturian, just above the base of the D. pluknetii Subzone. The presence of Odontopteris bradii Brongniart, Lobatopteris viannae (Teixeira) Wagner and Alethopteris pseudograndidioides var. subzellieri (Wagner) Zodrow and Cleal in the Publow Member suggests the presence of Cantabrian aged rocks (Odontopteris cantabrica Zone).

One important implication of our new biostatigraphical data concerns the correlation of the strata in the Coalpit Heath Basin with that on the southern limb of the Kingswood Anticline. Desktop mapping suggested to us that the Salridge Coal was far more likely to correlate with the Mangotsfield coals than ~120–150 m below the high vein (the position typically marked where the stratigraphy is displayed in both older and recent publications). Our biostratigraphical studies seem to be in support of this interpretation. Although good megafossil assemblages were recovered from the roof of the Salridge Coal and underlying strata at Bickley Wood, these were of limited biostratigraphical value. What is clear is that the assemblage has much more in common with the Pennant Sandstone Formation (Laveineopteris rariniensis Subzone) than the Grovesend Formation (Dicksonites pluknetii Subzone). This confirms that the Salridge Coal almost certainly belongs to the Pennant Sandstone Formation, as do field observations of identical thick Pennant-type sandstones above and below this coal (J.L. Pendleton, unpublished data; Nick Chidlaw, pers comm., 2011).

The presence of Laveineopteris linguefolia in the roof of the Salridge Coal, a species which has not been recorded above the Mangotsfield coals of the northern component of the basin, also lends support to our correlative stratigraphy.

Another important implication of our biostratigraphical studies is that the absence of the Linopterus obliqua Zone and Lobatopteris micromitron Subzone from the Bristol Coalfield (Fig. 4) indicates a major hiatus between the Pennant Sandstone Formation and the Grovesend Formation. This was suggested previously by Cleal (1997) but the lack of detailed biostratigraphical evidence from the Pennant Sandstone Formation then available made the idea difficult to confirm. Having examined in detail all of palaeobotanical evidence from the Pennant Sandstone Formation, we can now confirm the absence of any of the biozonal units indicative of the lower or middle Asturian Substage. This hiatus appears to be part of the regional tectonic activity referred to as the Leonian Phase of the Variscan Orogeny (sensu Wagner, 1965), which in southern Britain is also manifested by a disconformity in eastern South Wales (Cleal, 1978), and the onset of coal-bearing deposition in the Forest of Dean, Severn, Newent and Oxfordshire coalfields (Cleal, 1986, 1987, 1997). However, on-going palynological work (Pendleton and Wellman, in press), which includes well preserved and biostatigraphically useful assemblages from near the top of the Mangotsfield Member, indicates that the very top of the Pennant Sandstone Formation may extend into the early Asturian Substage, which would slightly diminish the duration of this hiatus. This would also confirm that the Salridge Coal is more likely correlated with the Bolsovian Mangotsfield coals, rather than Asturian-aged measures at the top of the Pennant Sandstone Formation.

7.2. Correlation with South Wales and adjoining areas

Establishing the distribution of the megafossil biozones in the Bristol Coalfield now allows the sequence here to be more accurately
correlated with the other coalfields in southwest Britain. The most complete succession of Westphalian and lower Stephanian megafossil biozones have been identified by Cleal (1978, 1997). Fig. 6 illustrates a correlation of megafossil biostratigraphy of the Bristol Coalfield with the South Wales Coalfield (Cleal, 2007). The new data suggest that the onset of sedimentation of Pennant-type deposits was more or less coincident in both the Bristol and South Wales coalfields, and earlier further south in the Somerset Coalfield, confirming that it was a genetically linked event in both areas to the rising Variscan hinterland to the south (Kelling, 1974; Gayer and Jones, 1989; Jones, 1991; Hartley, 1993). However, the Pennant Sandstone Formation of the Bristol Coalfield correlates with only the lower part of that formation in South Wales — the Llwyn and Rhondda members. The beds overlying the Pennant Sandstone Formation in the Bristol Coalfield, yielding *D. plukenetii* Subzone megafossils, correlate with the Grovesend Formation or possibly part of the Swansea Member in South Wales; there is no evidence in the Bristol Coalfield of beds equivalent to the Brithdir and Hughes members of South Wales. In the easternmost part of the South Wales Coalfield, there is a disconformity in the upper Asturian part of the succession, with the Swansea and upper part of the Hughes members missing, which Cleal (1997) related to the Leonian Phase of Variscan tectonic activity. This disconformity would seem to be related to the disconformity below the Grovesend Formation in the Bristol Coalfield.

Between the Bristol and South Wales coalfields there are a number of small outcrops of Carboniferous coal-bearing strata, notably the Forest of Dean, Newent and Severn coalfields (Wagner and Spinner, 1972; Cleal, 1986, 1987, 1997); these all have broadly similar successions, consisting of Pennant Sandstone Formation overlain by Grovesend Formation (Waters et al., 2011); a broadly similar situation also exists further east, in the Oxfordshire Coalfield (Cleal, 1997; Waters et al., 2011). The Pennant Sandstone Formation in these areas has yielded no megafossils of biostratigraphical significance, but the Grovesend Formation has yielded floras of the *Dicksonites plukenetii* Subzone in its lower part and the *Odontopteris canadrica* Formation in the upper part. This would suggest a correlation with the Radstock and Piblow members of the Grovesend Formation in the Bristol Coalfield. This has two consequences. Firstly, the onset of sedimentation in the Forest of Dean and adjacent coalfields would seem correlated with the onset of sedimentation of the Grovesend Formation in the Bristol and South Wales coalfields, and is thus related to the Leonian Phase of tectonic activity. Secondly, the influx of Pennant-like clastic sediment seems to have been significantly later in the Forest of Dean and adjacent coalfields than in the Bristol and South Wales
coalfields. As with the Pennant Sandstone Formation of South Wales, these deposits in the Forest of Dean and adjacent areas are of south-easterly provenance (Gayer and Stead, 1971; Hartley, 1993), and so the diachronous onset of Pennant-like sedimentation across the area suggests shifting drainage patterns during very late Westphalian and early Stephanian times — perhaps another response to the northwards migration of the Variscan Deformation Front.

8. Palaeoecology

The Warwickshire Group of the Bristol Coalfield contains common plant assemblages in various preservational states and facies contexts, including permineralised axes (Falcon-Lang et al., 2011b, 2012), palynofloras (Pendleton and Wellman, in press), and adpressed megafossils and sandstone-cast fossils (this paper); thus, reconstructing plant palaeoecology is complex, requiring understanding of the composition of each assemblage in a taphonomic context. Here, we review the different taphofloras below and make inferences about communities and palaeoecosystems.

8.1. Plant communities in peat mires and swamps

Palynofloras obtained from the coals in the Winterbourne and Pennant Sandstone formations are variable in their composition, with a few samples rich (＞50%) in lepidodendrid lycopsids, while most others comprise a fern or mixed fern- and lycopsid-dominated assemblage (Pendleton and Wellman, in press). While different plant groups would have produced pollen and spores in varying abundance, and while it is challenging to correct for these production biases (Willard, 1993), palynoassemblages probably indicate that the peat mires were dominated by a lycopsid-fern vegetation, consistent with studies of similar-aged coals in this part of Euramerica (Dimitrov et al., 2005). The peat mires of the late Asturian Grove-send Formation, by contrast, feature a palynoflora dominated by fern and tree-ferns (Pendleton and Wellman, in press) as these groups began to fill some of the ecological niches of the arborescent lycopsids during this time.

Adpression assemblages from roof shales in part of the Winterbourne Formation, Pennant Sandstone Formation (n=2 assemblages; Mangotsfield coals, the Salridge Coal), and Grovesend formations, directly associated with these coal, contain a diverse megafossil assemblages. These include lycopsids (“Lepidodendron”, Lepidophloios, Sigillaria), calamitaleans, sphenophylls, tree-ferns (Lobatopteris, Pecopteris, Psychocarpus), herbaceous ferns (Renauldia, Sphenopteris, Zeilleria), diverse pteridosperms (Eusphenopteris, Lavoeropteris, Linopteris, Macroleucope, Marioperis, Neuropteris, Odontopteris, Parapertis, Ricetopteris), and cordaitaleans.

The origin of roof shales has been debated (Gasaldo et al., 1995), but they probably represent parautochthonous assemblages preserved during the final stages of peat mire drowning (DiMichele et al., 2007; DiMichele and Falcon-Lang, 2011) or plants that grew in clastic swamps that replaced the mires (e.g., Falcon-Lang, 2009). Our findings are consistent with other studies of Middle Pennsylvanian wetlands, which indicate that peat mires were generally lycopsid-fern dominated, while areas of standing water that attracted clastic sediment contained a much greater abundance and diversity of pteridosperms and other plants, perhaps reflecting input from a variety of somewhat heterogeneous sub-environments (e.g., levees, swamps, coasts) and soil chemistries (e.g., DiMichele and Phillips, 1994; DiMichele et al., 2001, 2007; Bashforth et al., 2010, 2011).

8.2. Plant communities associated with large fluvial systems

Remains of somewhat different plant communities are associated with the coarse-grained channel deposits in the Winterbourne and Pennant Sandstone formations. Allotrichous sandstone-cast assemblages, which are restricted to the Pennant Sandstone Formation, are dominated by lycopsid tree-trunks (mostly Sigillaria, with a few lepidodendrids), common calamitaleans and cordaitaleans, and rare tree-ferns and pteridosperms. Sandstone-cast axes are commonly poorly preserved and occur in the bases of braided fluvial channel deposits where they are frequently seen with attached to coaly fragments.

However, given that this material is dominated by Sigillaria (and not lepidodendrids), it does not seem likely that these fossils were reworked from peat mire communities or clastic swamps. More likely these Sigillaria-dominated assemblages comprised riparian stands that grew along the margins of fluvial systems and were introduced to the drainages during floods and avulsive episodes (Bashforth et al., 2010); most plant material in channel deposits is riparian in origin (Scheiing and Pfefferkorn, 1984). This is supported by the occurrence of rare Stigmaria, which are probably autochthonous and confirm that lycopsids were rooted in sandy riparian soils. Sigillaria is thought to have been common colonisers of channel margins and fringing non-peat forming wetlands (DiMichele and Phillips, 1994), which would seem to fit into this interpretation. This would suggest that channel margins dominated by Sigillaria, calamitaleans and some cordaitaleans were a common feature at this time.

A few megafossil assemblages that occur in channel abandonment facies (n=3 assemblages; St. Anne’s Park, Bickle Wood, The Dingle) within the Pennant Sandstone Formation, provide further information about composition and heterogeneity of communities associated with these high energy fluvial systems. These megafossil assemblages are of low diversity (typical ＜5 whole plant taxa) and dominated by pteridosperms (especially Lavoeropteris, Macroleucope, Marioperis, Ricetopteris) with usually one taxon dominant. Calamitaleans are present in subordinate numbers. These parautochthonous assemblages record pteridosperm-calamitalean stands living within the active channel belt directly comparable to communities reported from similar contexts and ages elsewhere in tropical Euramerica (Bashforth et al., 2010, 2011).

Also found in the coarse-grained deposits of the large fluvial systems is fourth type of plant assemblage, which comprises calcified axes. These axes are often found closely associated with reworked coal clasts, but rarely, if at all, with sandstone-cast axes. The calcified assemblages are dominated by cordaitaleans, with a few tree-ferns, and rare medulosalean pteridosperms, calamitaleans and lycopsids (Falcon-Lang et al., 2011b, 2012). In many cases, calcified axes are fragmented and abraded, suggesting that this material was transported and may contain components derived from a more distal area. Association with reworked caliche nodules, and the occurrence of growth interruptions in the woody axes of cordaitaleans, also implies that these allochthonous remains may represent a dryland (sub-humid) community that either existed in elevated terrains outside the basin, or grew in depositional lowlands during drier climatic phases (Falcon-Lang et al., 2009, 2012).

8.3. Geographic or temporal relation of communities

Summarising these inferences, we identify a variety of plant communities within the Warwickshire Group. Peat mires were dominated by lepidodendrids and ferns during the Bolsovian, and were replaced by tree fern and fern mires in the late Asturian. These mires were fringed by areas of clastic swamp, containing a relatively high diversity of pteridosperms, calamitaleans and ferns. Low diversity pteridosperm-calamitalean communities lived in disturbed riparian niches of the braided fluvial systems (cf. Bashforth et al., 2010, 2011). Sigillaria, calamitalean and cordaitalean communities were also common along the margins of the large fluvial system; often being incorporated into channel lags due to undercutting of the river banks. Large cordaitaleans were common in drier interfluvies and/or transported in from hinterland areas outside the basin (cf. Falcon-Lang and Bashforth, 2004).
As an alternative to this “Walther’s Law” interpretation of the plant assemblages, the data may also be interpreted to represent two temporally distinct vegetative landscapes (Falcon-Lang, 2004; Falcon-Lang et al., 2009, 2012). In this view, the landscape sometimes consisted of lycopsid-fern mires, with the fringing clastic swamp covered by a diverse flora of pteridosperms, calamitaleans and ferns. However, at other times the basin may have been dominated by braided fluvial systems with low diversity pteridosperm–calamitalean communities living in disturbed riparian niches and with large cordaitalean trees dominating dryland, inter-flows or hinterland areas. The temporal alternation of these two vegetation landscapes may have been linked to high frequency climate fluctuations (Falcon-Lang, 2004) or autocyclic switching of major drainage networks (Bashforth et al., 2011).

9. Conclusions

(1) We present, for the first time, a megafossil biostratigraphical scheme for the Warwickshire Group of the Bristol Coalfield, based on re-evaluation of historic records, museum collections, recollection of old field sites and collections from new field locations.

(2) Megafossil assemblages from the Winterbourne and Pennant Sandstone formations indicate a mid- to late Bolsovian age (Lavoineopteris rarifernis Subzone). The Farrington to Radstock members of the Grovesend Formation, in contrast, have floral assemblages indicating a late Asturian age (Dicksonites plukettii Subzone). There is evidence that the uppermost Pubnowl Formation may be Cantabrian in age (Odontopteris canadensis Zone).

(3) Absence of early- to mid-Asturian megafossil biozones (Linopteris oblique Zone and Lobopteris micromitom Subzone) from the coalfield between the Pennant Sandstone Formation and the Grovesend Formation. This hiatus is likely part of the regional tectonic activity referred to as the Leonian Phase of the Variscan Orogeny, thought to have produced a similar hiatus in South Wales, and to be associated with the appearance of coal-bearing deposits in the Forest of Dean, Severn, Newent and Oxfordshire coalfields.

(4) Bolsovian peat mires of the Winterbourne and Pennant Sandstone formations were dominated by lepidodendrids and ferns, and were replaced by tree fern and fern mires in the late Asturian Grovesend Formation. High diversity pteridosperm, calamitalean and fern clastic swamps fringed and interfaced these mires.

(5) Bolsovian braided fluvial systems created disturbed riparian niches that were colonised by low diversity pteridosperm–calamitalean communities and Sigillaria–calamitalean–cordaitalean communities. Large cordaitaleans were common in drier interfluves and hinterland areas.

(6) Switching between stable mire/swamp communities and disturbed fluvial communities either reflects autocyclic channel switching or alloyclic alternations driven by climate change.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.revpalbo.2012.04.003.

References


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Appendix 12 - Supplementary data for Pendleton et al., (2012)

Lists of fossil plant taxa preserved as adpressions and sandstone-casts in the Warwickshire Group of the Bristol Coalfield. These lists were compiled from new field collections, examination of museum collections, and revised determinations gleaned from published literature. Material is listed by locality, and arranged approximately from oldest to youngest. Where historic records have been taxonomically revised, the original identification is recorded first with our new determinations following in brackets. Species entries marked with a star (*) indicate likely misidentification in a historic record (where we do not have access to specimens to check); these inferences are based on misidentifications confirmed by the present authors in material from other assemblages from the Bristol Coalfield.

Appendix 1. Harry Stoke B borehole at depths, 145.01 m to 3.0 m (OS ST 6321 7816, locality 1 on Figure 3b); Winterbourne Formation. Identifications from borehole material by Cleal and Pendleton.

- Annularia radiata (Brongniart) Sternberg
- Annularia sphenophylloides (Zenker) Gutbier
- Calamites carinatus Sternberg
- Calamites suckowii Brongniart
- Cordaicarpus sp.
- Cordaites sp.
- Cyperites bicarinatum Lindley & Hutton
- Eusphenopteris striata (Gothan) Novik
- Laveineopteris rarinervis (Bunbury) Cleal et al.
- Laveineopteris tenuifolia (Schlotheim ex Sternberg) Cleal et al.
- Lepidophloios laricinus Sternberg
- Linopteris cf. neuropteroides (Gutbier) Zeiller
- Lobatopteris miltoni (Artis) Wagner
- ?Macroneuropteris scheuchzeri (Hoffmann) Cleal et al.
- Mariopites nervosa (Brongniart) Zeiller
- ?Paleostachya sp.
Appendix 2. Harry Stoke C borehole at depths 143.73 m to 3.53 m (OS ST 6504 7677, locality 2 on Figure 3b); Winterbourne Formation. Identities from borehole material by Cleal and Pendleton.

*Pecopteris plumosa* (Artis) Stur

*Pinnularia capillacea* Lindley & Hutton

*Renaultia* sp.

*Reticulopteris munsteri* (Eichwald) Gothan

*Sigillaria scutellata* Brongniart

*Sphenophyllum emarginatum* Brongniart

*Sphenophyllum majus* (Brongniart) Brongniart

*Stigmaria ficoides* (Sternberg) Brongniart

*Urnatopteris tenella* (Brongniart) Kidston

*Appendix 2.* Harry Stoke C borehole at depths 143.73 m to 3.53 m (OS ST 6504 7677, locality 2 on Figure 3b); Winterbourne Formation. Identifications from borehole material by Cleal and Pendleton.

*Alethopteris* cf. *urophylla* (Brongniart) Presl

*Annularia radiata* (Brongniart) Sternberg

*Annularia sphenophylloides* (Zenker) Gutbier

*Asterophyllites equisetiformis* (Schlotheim) (with unattached *Paleostachya*)

*Calamites* sp.

*Cordaicarpus* sp.

*Cordaites* sp.

*Eusphenopteris striata* (Gothan) Novik

*Eusphenopteris* cf. *neuropteroides* (Boulay) Novik

*Laveineopteris rarinervis* (Bunbury) Cleal *et al.*

*Lepidostrobophyllum* sp.

*?Linopteris* cf. *neuropteroides* (Gutbier) Zeiller

*Linopteris obliqua* (Bunbury) Zeiller

*Lobatopteris miltoni* (Artis) Wagner

Lyco phyte shoots

*Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.*

*Mariopteris nervosa* (Brongniart) Zeiller

*Neuropteris semireticulata* Josten

*Neuropteris* sp.

*Pecopteris plumosa* (Artis) Stur

*Renaultia* sp.
Appendix 3. Winterbourne borehole at depths, 274.47 m to 103.28 m (OS ST 646 801, locality 3 on Figure 3b); Winterbourne Formation, and lowermost Downend Member, Pennant Sandstone Formation. Based on British Geological Survey logs by Cantrill and Smith and summary in Cantrill and Smith (1919). Identifications from borehole material by Cleal and Pendleton.

Asterophyllites equisetiformis (Schlotheim)
Asterophyllites sp.
Calamites sp.
Eusphenopteris sp.
Cordaites sp.
Lepidophyllum minus Goode
Lepidophyllum sp.
Lobatopteris miltoni (Artis) Wagner

* Linopteris obliqua (Bunbury) Zeiller
Pecopteris sp.

Appendix 4. California collieries, New Smith’s Vein to Parrot Vein (OS ST 665 714, locality 5 on Figure 3b); Winterbourne Formation. Historic record by Moore and Trueman (1937)

Annularia sphenophylloides (Zenker) Gutbier
Annularia cf. radiata (Brongniart) Sternberg
Asterotheca miltoni (Artis) Zeiller (= Lobatopteris miltoni (Artis) Wagner)
Calamites sp.
Lepiodendron lycopodioides Sternberg
Lepidodendron rimosum Sternberg
Linopteris sub-brongniartii (Grand’Eury) Carpentier

* Linopteris obliqua (Bunbury) Zeiller
Linopteris munsteri (Eichwald) Potonié (= Reticulopteris muensteri (Eichwald) Gothan
Mariopteris latifolia (Brongniart) Zeiller (= Fortopteris latifolia (Brongniart) Boersma)

Mariopteris sp.

Neuropteris rarinervis Bunbury (= Laveineopteris rarinervis (Bunbury) Cleal et al.)

Neuropteris tenuifolia Schlotheim ex Sternberg (= Laveineopteris tenuifolia (Schlotheim ex Sternberg) Cleal et al.)

Neuropteris cf. flexuosa Sternberg

Renaultia chaerophylloides (Brongniart) Zeiller

Sphenopteris cf. spiniformis Kidston

Sphenopteris cf. laurenti Andrae

Sphenopteris sp.

* Sphenophyllum cuneifolium (Sternberg) Zeiller

Sphenophyllum cf. majus (Bronn) Bronn

Sphenophyllum ermarginatum Brongniart

Appendix 5. St. Anne’s Park megafloral bed (OS ST 619 727, locality 6 on Figure 3b); Downend Member, Pennant Sandstone Formation. Historic record by Moore and Trueman (1937)

Asterotheca cf. cyathea (Schlotheim) (= Cyathocarpus cf. cyatheus (Schlotheim ex Brongniart) Mosbrugger

Asterotheca sp. (= Cyathocarpus sp.)

Annularia stellata (Sternberg) Wood (≡ Annularia spinulosa Sternberg)

Annularia radiata (Brongniart) Sternberg

Annularia sphenophyloides (Zenker) Guttber

Linopteris cf. munsteri (Eichwald) Potonié (= Reticulopteris cf. muensteri (Eichwald) Gothan

Neuropteris tenuifolia Schlotheim ex Sternberg (= Laveineopteris tenuifolia (Schlotheim ex Sternberg) Cleal et al.)

* Neuropteris obliqua (Brongniart) Zeiller

Appendix 6. Bickley Wood, near Elm Tree Inn, Hanham Abbots (OS ST 6417 7053, locality 7 on Figure 3b); upper Downend Member, Pennant Sandstone
Formation. New specimens collected by Pendleton and Cleal, with re-evaluation of Fry’s material in the Bristol City Museum and Art Gallery.

- *Annularia* sp.
- *Calamites* sp.
- *Cyclopteris orbicularis* Brongniart
- *Laveineopteris dussarti* (Laveine) Laveine (incorrectly identified as *Neuropteris ovata* by Fry)
- *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.*
- *Laveineopteris rarinervis* (Bunbury) Cleal *et al.*

Appendix 7. Mangotsfield seams at Church Lane (Farm) and Wallsend collieries (OS ST 668 763 and OS ST 664 766, respectively, locality 8 on Figure 3b); coal seams dividing the Downend and Mangotsfield members, Pennant Sandstone Formation. Historic record by Moore and Trueman (1941).

- *Annularia stellata* (Schlotheim ex Sternberg) Wood (≡ *Annularia spinulosa* Sternberg)
- *Calamites* sp.
- *Cordaites* sp.
- *Lepidodendron* sp.
- *Neuropteris scheuchzeri* Hoffmann (= *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.*)
- *Neuropteris rarinervis* Bunbury (= *Laveineopteris rarinervis* (Bunbury) Cleal *et al.*)
- *Odontopteris lindleyana* Sternberg (= *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.*)

Appendix 8. Keynsham Hams, near Chandos Lodge (OS ST 644 695, locality 9 in Figure 3b); coals likely part of the Salridge Vein dividing the Downend and Mangotsfield members, Pennant Sandstone Formation. Historic record by Moore and Trueman (1937)

- *Annularia sphenophylloides* (Zenker) Gutbier
- *Cyclopteris orbicularis* Brongniart
Lepidodendron lycopodioides Sternberg
Mariopteris cf. nervosa (Brongniart) Zeiller
Neuropteris rarinervis Bunbury (= Laveineopteris rarinervis (Bunbury) Cleal et al.)
* Neuropteris flexuosa Sternberg
Neuropteris scheuchzeri Hoffmann (= Macroneuropteris scheuchzeri (Hoffmann) Cleal et al.)
Neuropteris tenuifolia Schlotheim ex Sternberg (= Laveineopteris tenuifolia (Schlotheim ex Sternberg) Cleal et al.)
* Neuropteris cf. obliqua (Brongniart) Zeiller
Neuropteris cf. linguaeolia Bertrand (= Paripteris cf. linguaeolia (Bertrand) Laveine)
Ptychocarpus unitus (Brongniart) Zeiller
Odontopteris sp.
Sphenophyllum emarginatum Brongniart
Sphenophyllum. cf. majus (Bronn) Bronn
Sphenopteris sp. (cf. S. artemisaefolioides Crépin)
Sphenopteris cf. neuropteroides (Boulay) Zeiller (= Eusphenopteris cf. neuropteroides (Boulay) Novik
* Mixoneura (Neuropteris) ovata (Hoffman) Zalessky (= Neuropteris ovata Hoffmann)

Appendix 9. Taxa from the newly discovered Salridge Vein roof site on south bank of the River Avon, north east of Keynsham (OS ST 642 701, locality 10 on Figure 3b); coal seam dividing the Downend and Mangotsfield members, Pennant Sandstone Formation. Collected and identified by Pendleton and Cleal).

Annularia sphenophylloides (Zenker) Gutbier
?Cordaites sp.
Asterophyllites equisetiformis Brongniart
Eusphenopteris ?neuropteroides (Boulay) Novik
Laveineopteris rarinervis (Bunbury) Cleal et al.
Laveineopteris tenuifolia (Sternberg) Cleal et al
Lepidodendron shoot
Lobatopteris miltoni (Corsin) Wagner
Macroneuropteris scheuchzeri (Hoffmann) Cleal et al.,
?Mariopteris sp.
Neuropteris sp.
“Odontopteris lindleyana” Sternberg (= incised pinnules of
Macroneuropteris scheuchzeri (Hoffmann) Cleal et al.)
Sigillaria sp.
Sphenophyllum emarginatum Brongniart

Appendix 10. Taxa from the newly discovered Dingle leaf bed, Winterbourne Down
(OS ST 656 793, locality 11 on Figure 3b); lower Mangotsfield Member, Pennant
Sandstone Formation. Collections by Wellman, Pendleton and Cleal. Identifications
by Cleal and Pendleton.
Calamites cisti Brongniart
Laveineopteris rarinervis (Bunbury) Cleal et al.
Macroneuropteris scheuchzeri (Hoffmann) Cleal et al.,
Mariopteris cf. nervosa (Brongniart) Zeiller

Appendix 11. Parkfield and Coalpit Heath collieries (OS ST 690 777 and OS
ST 697 816, respectively, localities 12 and 13 on Figure 3b); Farrington
Member, Grovesend Formation; Historic records from Kidston (1888), Lillie
(1910b), Arber (1914), Arber (1922), Kidston and Jongmans (1917), Kidston
(1923 – 1925) and Crookall (1925a, 1925b, 1929). Includes re-evaluation of
museum collections to check species identification, where available.
Acitheca polymorpha Brongniart
Alethopteris ambigua (Lesquereux) Zodrow & Cleal
Alethopteris cf. costei Zeiller
Alethopteris integra Gothan
Alethopteris lonchitica Sternberg
Alethopteris pontica Zeiller
Alethopteris pseudograndinioides Zodrow & Cleal
Alethopteris serlii (Brongniart) Göppert
Alloiopteris radstockensis Kidston
Alloiopteris sp.
Annularia cf. radiata (Brongniart) Sternberg
Annularia radiata (Brongniart) Sternberg
Annularia sphenophalloides (Zenker) Gutbier
Annularia spinulosa Sternberg
Aphlebia crispa (Gutbier) Presl
Aphlebia sp.
Asolanus camptotaenia Wood
Asterophyllites equisetiformis Brongniart 1828
Asterophyllites longifolius Sternberg
Bothrodendron sp.
Calamites carinatus Sternberg
Calamites cisti Brongniart
Calamites suckowii Brongniart
?Cordaicarpus sp.
Caulopteris peltigera (Brongniart)
Caulopteris sp.
Cordaites sp.
Crossotheca crepini Zeiller
**Crossotheca pinnatifida** Gutbier
Cyathocarpus aff. arborescens (Schlotheim)
Cyathocarpus cf. cyatheus (Schlotheim ex Brongniart) Mosbrugger
Cyclopteris fimbriata Lesquereux
Cyclopteris orbicularis Brongniart
Cyclopteris sp.
Dicksonites pluckenettii (Sternberg) Sterzel
Diplotmema geniculatum Germar and Kaulfuss
Eupecopteris fletti Kidston
Eupecopteris sp.
Eusphenopteris neuropteroides (Boulay) Novik
Eusphenopteris striata (Gothan) Novik
Excipulites callipteridis Schimp
Laveineopteris cf. nicolausiana Gothan
Laveineopteris rarinervis (Bunbury) Cleal et al.
?Lepidodendron obovatum Sternberg
Lepidodendron aculeatum Sternberg  
Lepidodendron cf. glincanum Eichwald  
Lepidodendron cf. jaraczewskii Zeiller  
Lepidodendron dichotomum Zeiller  
Lepidodendron lanceolatum Lesquereux  
Lepidodendron loricatum Arber  
Lepidodendron lycopodioides Sternberg  
Lepidodendron obovatum Sternberg  
Lepidodendron ophiurus Brongniart  
Lepidodendron rimosum Sternberg  
Lepidodendron simile Kidston  
Lepidodendron worthenii Lesquereux  
Lepidophloios laricinus Sternberg  
Lepidostrobophyllum majus (Brongniart) Hirmer  
Lepidostrobophyllum sp.  
Lepidostrobus brevifolius Lesquereux  
Lepidostrobus hastatus Lesquereux  
Lepidostrobus lanceolatus Lindley & Hutton  
Lepidostrobus majus Brongniart  
Lepidostrobus minor Goode  
Lobatopteris camertonensis (Kidston) Wagner  
Lobatopteris vestita (Lesquereux) Wagner (often identified as Pecopteris miltoni Artis)  
Macroneuropteris macrophylla Brongniart  
Macroneuropteris scheuchzeri (Hoffmann) Cleal et al.  
Macrostachya cf. infundibuliformis Brongniart  
Mariopteris nervosa (Brongniart) Zeiller  
Mariopteris sp.  
cf. Megaphyton sp.  
Neuropteris flexuosa Sternberg  
Neuropteris macrophylla Brongniart  
Neuropteris ovata Hoffmann  
Neuropteris sp.  
Oligocarpa brongniarti Stur
Palmatopteris alatum (Brongniart) Potonié
Pecopteris bucklandii Brongniart
Pecopteris oreopteridia Schlothheim
Pecopteris plumosa (Artis) Stur
Pinnularia capillacea Lindley & Hutton
Ptychocarpus unitus (Brongniart) Zeiller
Radstockia sp.
Radstockia sphenopteroides Kidston
Renaultia chaerophylloides (Brongniart) Zeiller
Rhabdocarpus lillianus Arber
Rhacophyllum crispum Gutbier
Rhacophyllum filiciforme Gutbier
Rhacophyllum goldenbergii Weiss
Rhacophyllum spinosum Lesquereux
Schizopteris lactuca Presl
Sigillaria candollei Brongniart
Sigillaria deutschiana Brongniart
Sigillaria discophora Konig
Sigillaria elongata Brongniart
Sigillaria major Lindley & Hutton
Sigillaria mamillaris Brongniart
Sigillaria reniformis Brongniart
Sigillaria rugosa Brongniart
Sigillaria tessellata Stein
Sigillaria voltzi Brongniart
Sigillaria sp.
?Sphenophyllum oblongifolium Germar & Kaulfuss
Sigillariophyllum bicarinatum Lindley & Hutton
Sphenophyllum ermarginatum Brongniart
Sphenophyllum longifolium Germar
Sphenophyllum sp.
Sphenopteris ovatifolia Lillie
Sphenopteris pecopteroides Kidston
Sphenopteris sp.
Stigmaria ficoides (Sternberg) Brongniart
Trigonocarpus sp.
Trigonocarpus noeggerathi (Sternberg)

Appendix 12. Shortwood brick-works (OS ST 682 768, location 14 on Figure 3b); Farrington and Barren Red members, Grovesend Formation. Historic record by Moore and Trueman (1937). Includes newly collected specimens of Acithea polymorpha Brongniart from the adjacent Dramway exposure.

Acithea polymorpha Brongniart
Asterotheca cf. cyathea (Schlotheim) (= Cyathocarpus cf. cyatheus)
(Schlotheim ex Brongniart) Mosbrugger
Asterotheca sp. (= Cyathocarpus sp.)
Annularia sphenophylloides (Zenker) Gutbier
Annularia stellata (Schlotheim ex Sternberg) Wood (≡ Annularia spinulosa Sternberg)
Carpolithus membranaceus Goeppert
cf. Eupecopteris fletti Kidston
Sphenophyllum emarginatum Brongniart
Sphenopteris ovatifolia Lillie
Ptychocarpus unitus (Brongniart) Zeiller