



**A QUANTITATIVE ANALYSIS OF THE DISPERSED SPORE  
AND POLLEN RECORD FROM THE MIDDLE JURASSIC OF  
YORKSHIRE, UK**

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## ABSTRACT:

Quantitative analysis of the distribution of dispersed sporomorphs (spores and pollen) has been used to assess vegetation change through the Middle Jurassic Ravenscar Group (Aalenian–Bathonian) from North Yorkshire, UK. Aalenian, Bajocian and Bathonian strata possess relatively distinct sporomorph assemblages regarding taxon occurrences, abundances and diversities (richness), suggesting a dynamic history regarding the nature of parent vegetation. Aalenian palynofloras are composed of a heterogeneous mixture of conifers, ferns, simple monosulcate pollen producers, sphenophytes and Caytoniales; Bajocian palynofloras are co-dominated by conifers and ferns; and Bathonian palynofloras are highly rich and contain assemblages of abundant ferns, conifers, lycophytes, pteridosperms/conifers and Caytoniales. Temporal variations in assemblages are a result of long-term depositional environmental changes that influence depositional taphonomic processes and parent vegetation. Comparison of the dispersed sporomorph and plant megafossil record through the Hasty Bank plant bed demonstrates that both fossil assemblages represent different aspects of the palaeoflora due to a multitude of ecological and taphonomic biases. Specifically, conifers and ferns are underrepresented in plant megafossil assemblages, bryophytes and lycopsids are represented only in sporomorph assemblages, and sphenophytes, pteridosperms, Caytoniales, Cycadales, Ginkgoales and Bennettitales are comparatively underrepresented in sporomorph assemblages. Biases between assemblages include, variation in sporomorph production levels, depositional environment and differential sporomorph and parent plant durability. Megaspore occurrences from the Middle Jurassic of Yorkshire are reviewed and a new megaspore genus, named *Reticuspinosporites whytei* is formally described. Transmission electron microscope analysis of the spore wall ultrastructure suggests lycopsid and possibly selaginellalean affinities.



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## CHAPTER 1: INTRODUCTION

Reconstructing palaeofloras is a crucial task in understanding ancient terrestrial environments as vegetation is a fundamental constituent of terrestrial ecosystems. The Middle Jurassic deposits of Yorkshire, UK represent a rare example of an extensive development of predominantly non-marine deposits of this age and therefore provide important insight into uncovering the workings of terrestrial ecosystems from this time. The sedimentary sequences are well studied in terms of their development and sedimentology (e.g. Alexander 1989) and are famous for their palaeontological significance, in particular for the exceptionally preserved plant megafossil remains (e.g. van Konijnenburg-van Cittert and Morgans 1999) and abundant dinosaur footprints (Whyte and Romano 1993, 2001a, 2001b; Romano *et al.*, 1999; Romano and Whyte 2003; Whyte *et al.*, 2006, 2007, 2010). Interestingly, the successions were among the first Middle Jurassic terrestrial deposits to be studied in detail (Young and Bird 1822) and hence provide important historical context in terms of reconstructing terrestrial environments in deep time. The rocks also yield exceptional dispersed sporomorph (spore and pollen) fossil assemblages, which offer an extensive source of data that can be used to reconstruct vegetation and thus provide insight into terrestrial ecosystems from the Middle Jurassic.

Numerous dispersed sporomorph studies have been carried out on these deposits, however much of this work remains unpublished as PhD and MSc theses at the University of Sheffield (e.g. Dodd 1975; Wilkinson 1975; Al-Jubori 1979; Cadman 1979; Fenton 1980; Stronach 1983; Hogg 1993; Trout 1996). The vast majority of published palaeobotanical work on the Middle Jurassic of Yorkshire focuses instead on the plant megafossil record (e.g. Harris 1941, 1944, 1952, 1953, 1961a, 1961b, 1964, 1969, 1978, 1979; van Konijnenburg-van Cittert 1972, 1975, 1978, 1981, 1989, 1996, 2008; Harris *et al.*, 1974; Spicer and Hill 1979; Hill 1990; Morgans 1999; van Konijnenburg-van Cittert and Morgans 1999), whilst dispersed sporomorph investigations are comparatively overlooked in the literature, with the exception of Couper (1958), Chaloner (1968), Chaloner and Muir (1968),

Riding and Wright (1989), Boulter and Windle (1993), Hubbard and Boulter (1997), and Srivastava (2011). Furthermore, much of the previous unpublished and published dispersed sporomorph work focuses on taxonomy and biostratigraphy (e.g. Couper 1958; Riding and Wright 1989; Srivastava 2011) and the use of sporomorphs in vegetation reconstructions from Yorkshire remains rare in the literature (e.g. Boulter and Windle 1993). To improve the understanding of vegetation change through the Middle Jurassic of Yorkshire, this study aims to use modern quantitative analysis of spore/pollen data to reconstruct vegetation change and compare sporomorph assemblages with the well-documented plant megafossil assemblages in order to explain any potential discrepancies between these fossil records.

This thesis has been written as a series of three distinct investigations undertaken throughout the PhD project, with an additional taxonomic chapter that lists all of the sporomorph taxa that have been encountered during the study and a brief conclusion chapter. Each of the three investigations is written up as a separate chapter with a self-contained introduction and methods section that outlines the aims, background information, previous work into similar studies, relevant geological information and details of how experiments were carried out. Although much of the methodology for the three experimental chapters (Chapters 4–6) is highly similar, there are key differences between these investigations, thus to avoid confusion regarding changes to methods, individual material and methods sections are provided for each of the three experimental chapters. The methodology for the taxonomic chapter (Chapter 3) follows that of Chapter 4, hence a material and methods section is not provided within Chapter 3. To avoid repetition, the general geological background information from the three experimental chapters has been amalgamated together into one geological setting chapter (Chapter 2).

## **1.1 Thesis Aims:**

1. Use modern quantitative analytical methods on dispersed sporomorph data to reconstruct vegetation and assess potential floral changes through the Middle Jurassic of Yorkshire.
2. Investigate the causes of any floral changes through the Middle Jurassic of Yorkshire.
3. Compare dispersed sporomorph and plant megafossil assemblages to, (i) assess the biases that shape these different fossil records, and (ii) provide more accurate vegetation reconstructions by using both fossil assemblages.
4. Investigate and describe any new taxa that arise during this study.

## **1.2 Thesis Framework:**

### ***Chapter 2: Geological Setting***

This chapter provides a geological background for the Middle Jurassic deposits of North Yorkshire.

### ***Chapter 3: Systematic Taxonomy of Dispersed Spores and Pollen***

This chapter lists and figures all sporomorphs encountered during this investigation.

Following detailed taxonomic studies by Couper (1958) and Srivastava (2011), and numerous unpublished PhD and MSc theses at the University of Sheffield (e.g. Dodd 1975; Wilkinson 1975; Al-Jubori 1979; Cadman 1979; Fenton 1980; Stronach 1983; Hogg 1993; Trout 1996), the identification and naming of sporomorphs from the Middle Jurassic of Yorkshire is very well constrained. The purpose of this chapter is to introduce the taxa encountered that are to be utilized in a novel study using modern quantitative analytical methods to assess vegetation dynamics of the Middle Jurassic of Yorkshire.

***Chapter 4: Middle Jurassic vegetation dynamics based on quantitative analysis of spore/pollen assemblages from the Ravenscar Group, North Yorkshire, UK***

This chapter attempts to use sporomorphs to reconstruct Middle Jurassic vegetation and describe and explain changes in sporomorph assemblages through time, relating such variations to potential causal mechanisms, including depositional and climatic changes. A manuscript version of this chapter has been accepted for publication in the journal *Palaeontology* (Slater and Wellman in press). Experiments were devised by SMS and CHW, conducted by SMS, and the chapter/manuscript was written by SMS under the guidance of CHW.

***Chapter 5: A quantitative comparison of dispersed spores/pollen and plant megafossil assemblages from a Middle Jurassic plant bed from Yorkshire, UK***

This chapter provides a detailed comparison of sporomorph and plant megafossil assemblages from a plant bed at Hasty Bank, North Yorkshire. Spicer and Hill (1979) carried out a comprehensive analysis of the plant megafossil contents of this bed; this study compares this data with new data on the dispersed sporomorph assemblages through the section. The differences between dispersed sporomorph and plant megafossil records are described and the reasons for discrepancies are investigated. A manuscript version of this chapter has been published in the journal *Paleobiology* (Slater and Wellman 2015). The experiment was devised by SMS and CHW, conducted by SMS, and the chapter/manuscript was written by SMS under the guidance of CHW.

***Chapter 6: Morphology and wall ultrastructure of a new and highly distinctive megaspore from the Middle Jurassic of Yorkshire, UK***

This chapter reviews the occurrence of megaspores in the Middle Jurassic of Yorkshire and describes a new megaspore genus. A manuscript version of this chapter has been published in the journal *Review of Palaeobotany and Palynology* (Slater *et al.*, 2015). The published article was written by SMS, with contributions from Wilson A. Taylor, David J. Batten and Christopher R. Hill, under the guidance of CHW.



## ***Chapter 7: Conclusions***

This chapter provides a brief summary of the key findings of the thesis.

## CHAPTER 2: GEOLOGICAL SETTING

### 2.1 Background to the Middle Jurassic

The Middle Jurassic ranges from 174 to 164 million years ago and is subdivided into the Aalenian (174–170 Ma), Bajocian (170–168 Ma), Bathonian (168–166 Ma) and Callovian (166–164 Ma) stages. The Jurassic period is marked by an overall gradual rise in sea level, interrupted by episodes of still-stand. Regional and global sea level changes are generally considered to be the result of the breakup of Pangea and formation of the Atlantic and Indian Oceans (Hallam 2001; Leinfelder *et al.*, 2002). The arrangement of the continents and the position of the UK are displayed in Figure 2.1 (Scotese 2000). The absence of permanent ice sheets at the poles from the Upper Permian to the Early Cretaceous and the presence of warm climatic floras in the Arctic and Antarctic indicate warm global climatic conditions through the Mesozoic (Vakhrameev 1991). High temperatures throughout the Jurassic are considered to be result of high atmospheric carbon dioxide levels. Estimates suggest atmospheric concentrations were between 2000 and 3000 ppmv (parts per million by volume) compared to modern levels of c. 400 ppm (parts per million) (Berner and Kothavala 2001; Gradstein *et al.*, 2004; Fletcher *et al.*, 2008; Monastersky 2013). Vakhrameev (1991) recognised three global latitudinal thermal zones within the Mesozoic world: (i) Temperate (Moderate)–Warm, (ii) Subtropical, and (iii) Tropical (Equatorial). Scotese (2000) named five climate zones: (i) Cool Temperate, (ii) Warm Temperate, (iii) Paratropical, (iv) Tropical, and (v) Arid (Figure 2.2).

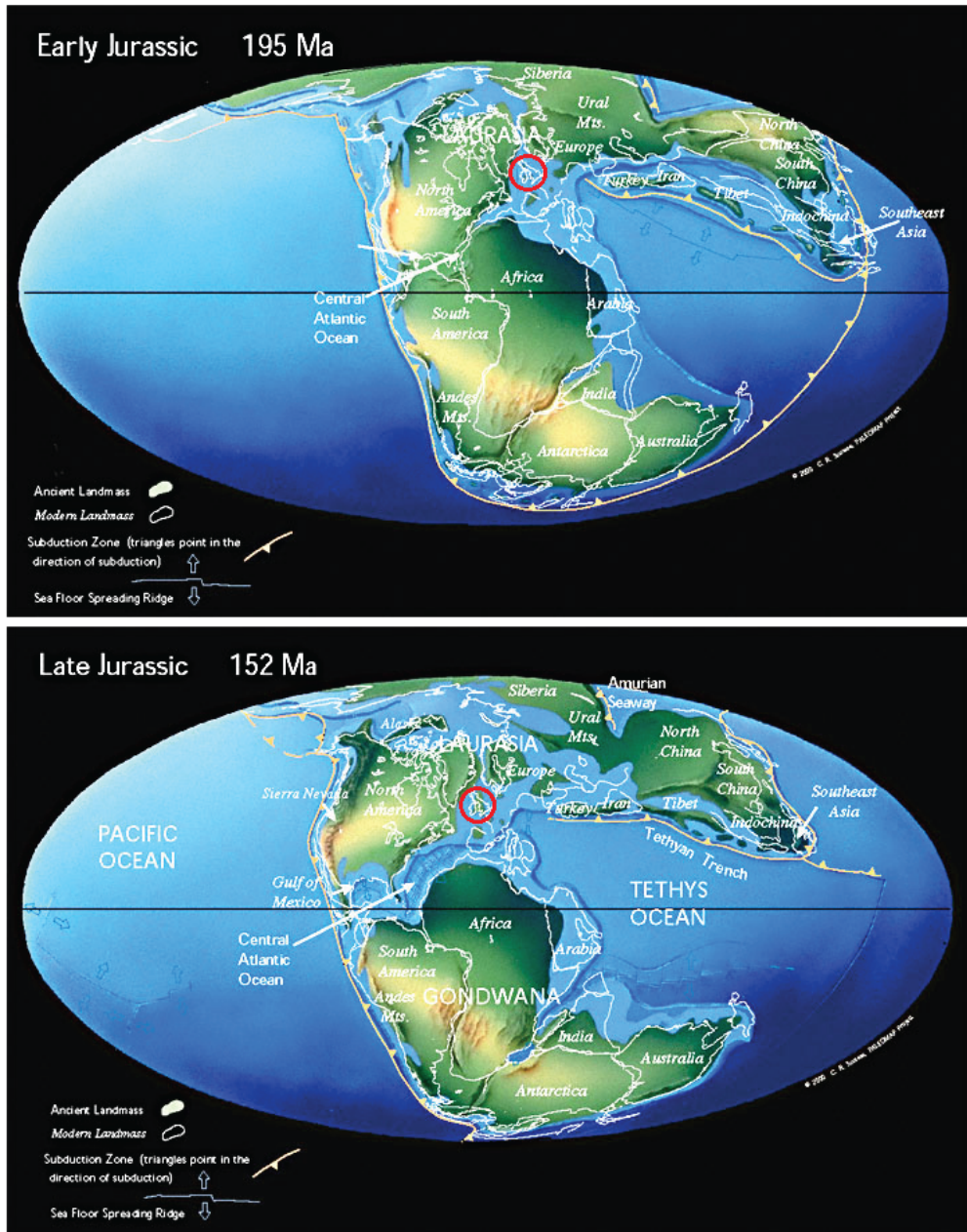
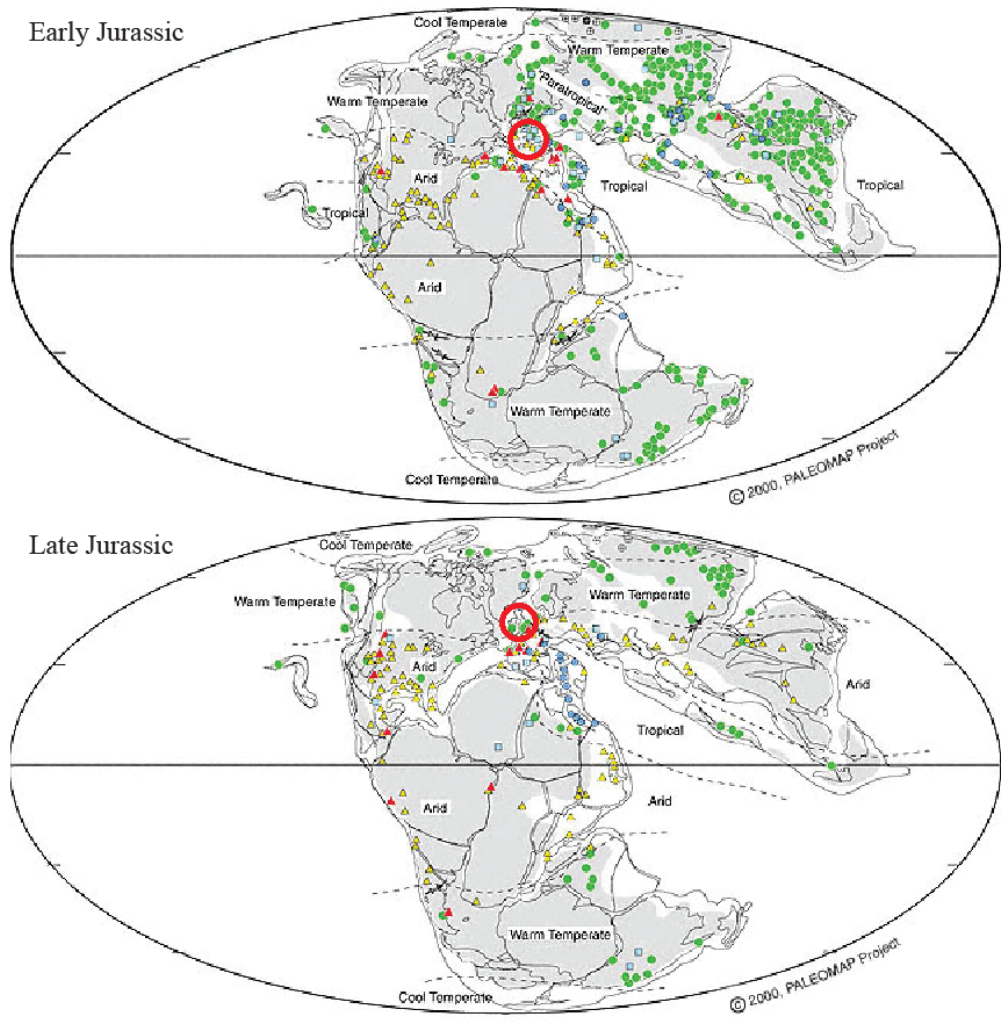


Figure 2.1: Worldwide palaeogeography from the Early to Late Jurassic. The position of the UK is circled. Taken from Scotese (2000).



### LEGEND

		WARM	COOL
WET	Tropical	● Coal ● Bauxite ● Laterite	● Coal & Tillites
	Warm Temperate	■ Kaolinite (& coal & evaporite) 🌴 Crocodiles 🌴 Palms & Mangroves	
	Arid	▲ Evaporite ▲ Calcrete	⊕ Cold Tillite ⊕ Dropstone ● Glendonite

"Paratropical" = High Latitude Bauxites

Figure 2.2: Worldwide palaeoclimate from the Early to Late Jurassic. The position of the UK is circled. Taken from Scotese (2000).

## **2.2 Middle Jurassic of the UK and Yorkshire**

The geology of the Mesozoic deposits of North Yorkshire has been intensively studied since the early nineteenth century (e.g. Young and Bird 1822) as these sequences offer well-exposed, extensive and often highly complex sedimentary successions from this time (e.g. Ielpi and Ghinassi 2014). Material studied here originates from the Cleveland Basin, North Yorkshire, UK (Figure 2.3). The palaeontological remains of the Jurassic of Yorkshire are of international importance and hence a number of Yorkshire Jurassic localities are recognized as Sites of Special Scientific Interest (SSSI) (see Cleal *et al.*, 2001). During the Middle Jurassic the UK was situated on the southern margin of the warm–temperate climatic latitude zone (Figure 2.2). Palaeoclimatic interpretations are suggestive of monsoonal conditions with distinct wet and dry seasons (Vakhrameev 1991; Hallam 1993; Scotese 2000). In the Middle Jurassic, high sea levels meant that parts of the southern UK was submerged underwater (Figure 2.4). The Cleveland Basin was, however dominantly non-marine and highlands to the north and west (Mid North Sea High and Pennine High respectively) supplied the inner basin with terrigenous material (Figure 2.5) (Bradshaw *et al.*, 1992). Transport of this sediment into the basin interior resulted in the accumulation of the coastal plain/deltaic sediments that now form the Ravenscar Group.

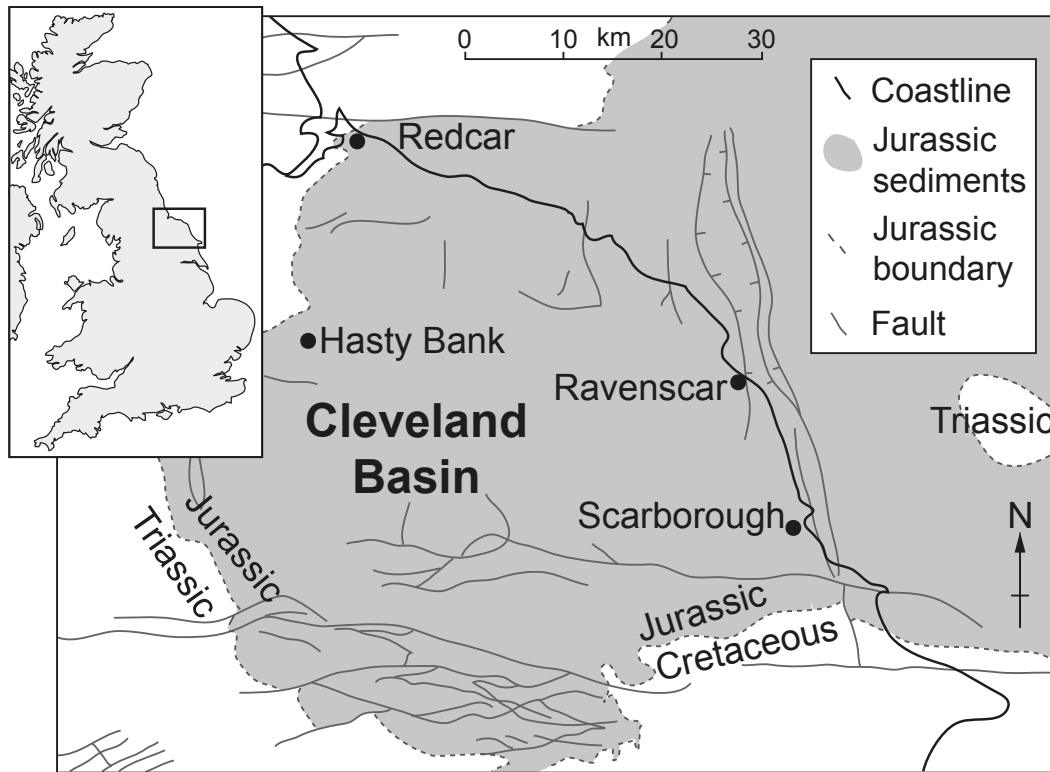


Figure 2.3: Generalized geological map of the North Yorkshire coast. Modified from Milsom and Rawson (1989); Mjøs and Prestholm (1993); Palliani and Riding (2000); Rawson and Wright (2000); Slater *et al.*, (2015); Slater and Wellman (2015).

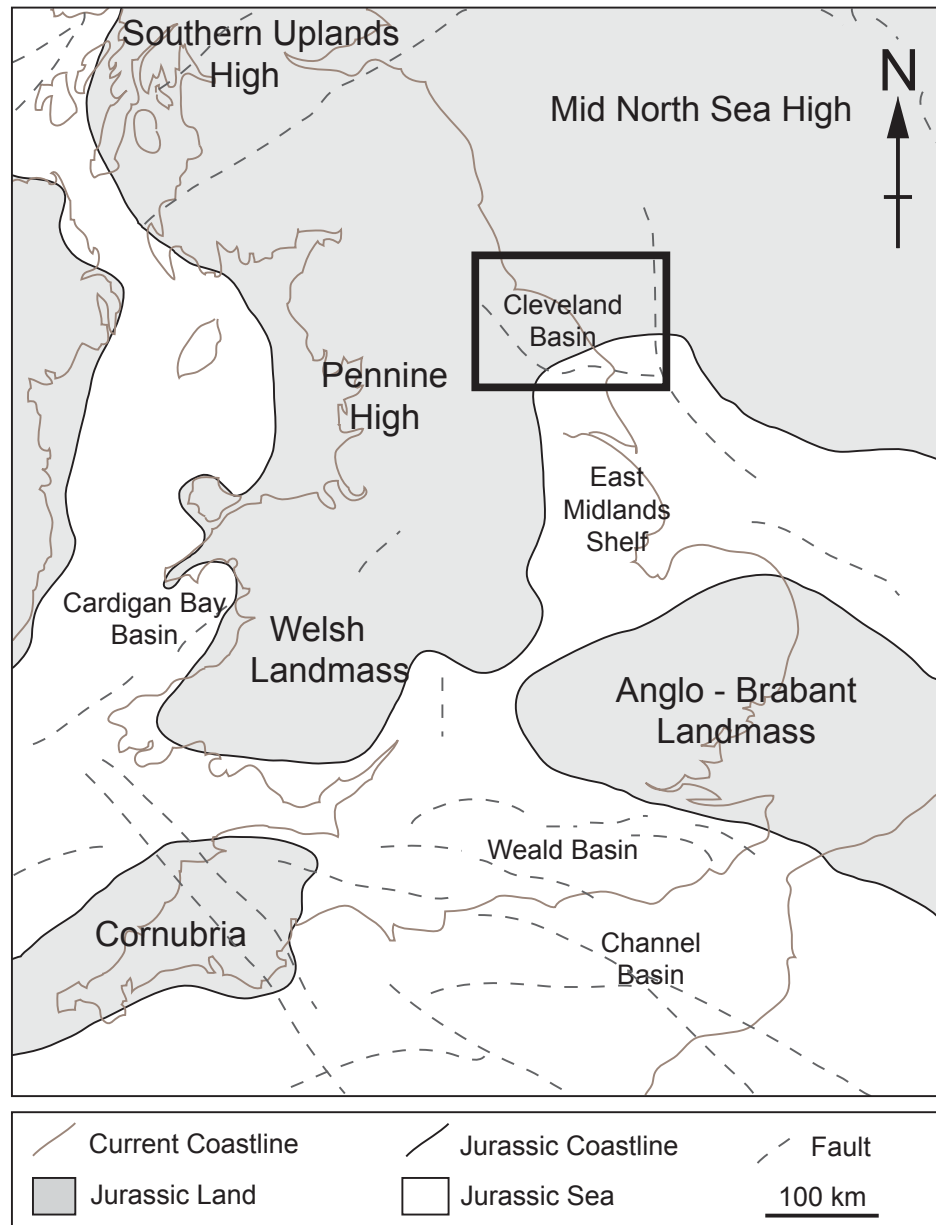
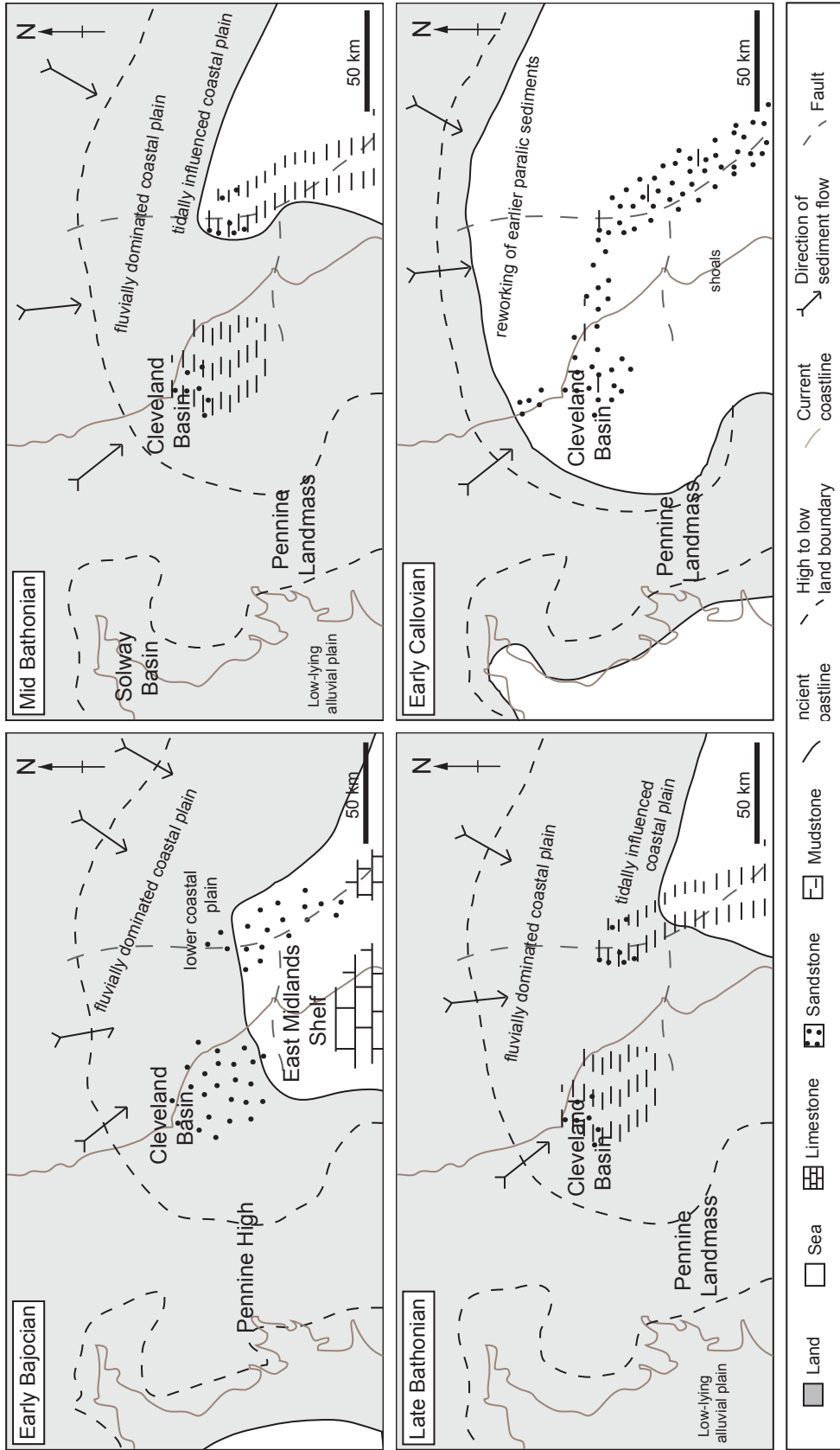


Figure 2.4: Middle Jurassic palaeogeographic map of the UK showing the major features controlling sedimentation. Modified from Bradshaw *et al.*, (1992).

Figure 2.5 (next page): Palaeogeographical development of the Cleveland Basin through the Middle Jurassic. Modified from Bradshaw *et al.*, (1992).





This study focuses on the dominantly non-marine sequences of the Middle Jurassic Ravenscar Group (Aalenian to Bathonian) (Figure 2.6). Unlike the dominantly marine sequences of the Lower Jurassic UK deposits, the Middle Jurassic sediments of North Yorkshire represent chiefly terrestrial sequences (Figure 2.6). Towards the end of the Permian subsidence of the Cleveland Basin began with differential subsidence progressing into the Triassic and Jurassic (Kent 1980). The present arrangement of sediments is a result of basin inversion during the late Cretaceous or Tertiary, followed by subsequent erosion. The buried Carboniferous landscape beneath played a major role in controlling deposition in the Cleveland Basin (Kent 1980). Few faults are known from the basin, with the exception of several N–S trending faults, which developed intermittently from the Triassic to the Tertiary. The most significant of these faults are the Red Cliff, Runswick, Whitby, Peak and Scarborough faults (Milsom and Rawson 1989; Rawson and Wright 2000). The various Middle Jurassic sedimentary units of the Cleveland Basin are discussed below. For a comprehensive review of the depositional history of the Jurassic of Yorkshire, see Powell (2010).

### ***2.2.1 Dogger Formation***

The Aalenian Dogger Formation represents the oldest Middle Jurassic formation in the Cleveland Basin. Thickness varies on the Yorkshire coast from 0.75–2 m. The Dogger Formation is a complex marine unit and rests unconformably on the Alum Shale (Riding 1984; Powell 2010). Oolitic and non-oolitic derived phosphate nodules occur at the base of the formation (Knox 1984). The majority of the formation comprises shallow marine ferruginous sandstones, conglomerates, ironstones, limestones and shales (Ivimey-Cook and Powell 1991; Palliani and Riding 2000).

Epoch	Stage	Lithostratigraphical Division		Age (Ma)	
<b>Middle Jurassic</b>	Lower Callovian	Cornbrash Formation		166	
	Bathonian	<b>Ravenscar Group</b>	Scalby Formation	Long Nab Member	168
	Upper Bajocian			Moor Grit Member	
	?		Scarborough Formation		170
	Lower Bajocian		Cloughton Formation	Gristhorpe Member	
		Lebberston Member			
			Sycarham Member		
	Aalenian		Eller Beck Formation		170
		Saltwick Formation		174	
		Dogger Formation			

Figure 2.6: Subdivision of Middle Jurassic of Yorkshire, marine units shaded. Modified from Rawson and Wright (2000); Slater *et al.*, (2015); Slater and Wellman (2015).

### 2.2.2 Ravenscar Group

The Ravenscar Group was laid down during the Middle Jurassic at a time of regional uplift and associated sea-level fall. The group is generally regarded to represent a predominantly terrestrial coastal plain environment with irregular marine incursions. Total thickness varies from 114–240 m. The deposits consist of mostly paralic, fluvial and lacustrine deposits, with three marine units that are present as a result of marine incursions from the south and east: the Eller Beck Formation, the Lebberston Member and the Scarborough Formation (Knox 1973; Hemingway and Knox 1973; Nami and Leeder 1978; Hancock and Fisher 1981; Livera and Leeder 1981; Kantorowicz 1985; Alexander 1989, 1992; Powell 2010).

### ***2.2.3 Saltwick Formation***

The non-marine Saltwick Formation (Aalenian), at the base of the Ravenscar Group overlies the marine Dogger Formation but often lies unconformably on the Lias Group in areas where the Dogger is absent due to erosion or non-deposition (Powell 2010). The Saltwick Formation is mostly composed of channel and crevasse-splay sandstones and floodplain mudstones (Morgans 1999), in which drifted and in situ plant megafossils are common (e.g. Spicer and Hill 1979). Thickness is typically around 50 m on the Yorkshire coast (Hemingway 1974; Milsom and Rawson 1989).

### ***2.2.4 Eller Beck Formation***

The Eller Beck Formation overlies the Saltwick Formation and represents a thin (c. 4 m thick), marine unit composed of marine sandstone, ooidal ironstone and lime mudstone (Knox 1973; Hemingway and Knox 1973; Powell 2010). Knox (1973) interpreted the Eller Beck Formation as a transgressive marine incursion onto the Saltwick Formation alluvial plain.

### ***2.2.5 Cloughton Formation***

The Cloughton Formation overlies the Eller Beck Formation and represents the thickest formation of the Ravenscar Group (c. 85 m). This is divided into three units: the Sycarham Member (non-marine), the Lebberston Member (marine), and the Gristhorpe Member (non-marine). The non-marine units of the Cloughton Formation are predominantly composed of cross-bedded sandstones, siltstones and mudstones throughout which plant beds and thin coal measures are common (van Konijnenburg-van Cittert and Morgans 1999). The Lebberston Member is laterally variable and is sub-divided into the Millepore Bed and Yons Nab Beds. In coastal exposures the Millepore Bed consists of a sandy ooidal limestone and calcareous sandstone, whereas inland exposures are more calcareous in composition and referred to as the 'Whitwell Oolite' (Hemingway 1949; Powell 2010). Samples from the Lebberston Member in this study are from coastal outcrops of the Millepore Bed.

### **2.2.6 Scarborough Formation**

Overlying the Cloughton Formation, the Scarborough Formation represents the most substantial marine incursion within the Ravenscar Group. Thickness varies in coastal exposures from c. 30 m at the Hundale Point type section (TA 026 949) (Gowland and Riding 1991) to c. 3 m at Yons Nab (Rawson and Wright 1992). Depositional interpretations for the Scarborough Formation include a brackish sandy embayment, a nearshore sandy and muddy shelf and an offshore mud-dominated shelf (Gowland and Riding 1991; van Konijnenburg-van Cittert and Morgans 1999).

### **2.2.7 Scalby Formation**

The Scalby Formation (maximum 60 m thick) is subdivided into the Moor Grit and Long Nab members, this overlies the Scarborough Formation and signifies a return to non-marine, fluviodeltaic conditions (Leeder and Nami 1979; Fisher and Hancock 1985; Riding and Wright 1989). The presence of sporadic marine palynomorphs and the distinctive marine Leberston Member indicate some marine influence within the dominantly non-marine Saltwick and Cloughton formations (Hancock and Fisher 1981; Fisher and Hancock 1985; Riding and Wright 1989). The Scalby Formation however displays the least amount of marine influence out of the dominantly non-marine formations (Rawson and Wright 2000). The Moor Grit Member is composed of medium to coarse-grained, cross-bedded channel sandstones, this represents a channel complex (Fisher and Hancock 1985; Riding and Wright 1989). The sequence fines-up gradationally into the siltstones, mudstones and fine-grained fluviodeltaic sandstones of the Long Nab Member (Ielpi and Ghinassi 2014). Depositional interpretations include alluvial, deltaic, swamp and river dominated deltaic conditions with some marine influence (Hancock and Fisher 1981; Livera and Leeder 1981; Fisher and Hancock 1985; Nami and Leeder 1978).

Although the boundary between the Scarborough and Scalby formations is erosive (Eschard *et al.*, 1991; Powell 2010), the age relationship of these deposits remains unresolved in the literature. One hypothesis suggests that there was no significant

stratigraphic gap between the two formations (Fisher and Hancock 1985; Riding and Wright 1989), whilst the other suggests a considerable time gap spanning the upper part of the Bajocian and lower and middle part of the Bathonian (Leeder and Nami 1979). This was supported by Hogg (1993) based on the appearance of certain palynological taxa in the Scalby Formation. However, isotopic analysis of fossil wood across the Scalby–Scarborough Formation boundary provides no evidence for a major stratigraphic gap (Hesselbo *et al.*, 2003) and Rawson and Wright (2000) speculated that the evidence for such a gap is slim.

### **2.2.8 Cornbrash Formation**

The Callovian Cornbrash Formation (maximum 10.5 m thick) lies unconformably on the Scalby Formation and is composed of the marine units of the Cornbrash Limestone, overlain by the shales of the Cornbrash. The unit represents marine transgression from the northeast; this reflects a worldwide marine transgression that started in the Lower Callovian (Wright 1977; Rawson and Wright 2000).

## **2.3 Jurassic vegetation**

Floral communities in the Jurassic were typically composed of conifers, ferns, cycads, ginkgos, Bennettitales, sphenopsids, lycopsids, and bryophytes. High latitude vegetation was generally made up of conifer and ginkgo forests with ferns and sphenopsids occupying the under story vegetation. Lower latitudes were characterised by low floral diversities with erratic conifer and cycad forests (Philippea *et al.*, 2004; Rees *et al.*, 2004). Mid latitudes possessed the highest floral diversities. Global phytogeographic belts for the Early Jurassic are displayed in Figure 2.7. Willis and McElwain (2002) described five distinct biomes: (i) Cool Temperate biome, (ii) Warm Temperate biome, (iii) Winterwet biome, (iv) Subtropical Desert biome, and (v) Summerwet (Tropical) biome.

**Cool temperate biome**—In high latitudinal (>60°) regions, floral diversities were low and vegetation composed of mostly deciduous plants. Ginkgos, large-leaved (macrophyllous) conifers, ferns and sphenopsids dominated this phytogeographic belt (Willis

and McElwain 2002). Growth rings in fossil wood recovered from this zone indicate seasonality (Vakhrameev 1991).

**Warm temperate biome**—Between latitudes of 60–40° floras were highly diverse and composed of ferns, sphenopsids, macrophyllous cycads and Bennettitales, conifers, and to a lesser degree, ginkgos (Willis and McElwain 2002). It should be noted that the warm temperate biome was, unlike modern phytogeographic realms, more diverse and productive than the tropical everwet biome (Rees *et al.*, 2000; Willis and McElwain 2002).

**Winterwet biome**—Occupying a band across central North America in the northern hemisphere, and southern South America, India, and western Australia, in the southern hemisphere, the winterwet biome was dominated by small-leaved (microphyllous) cycads, Bennettitales, conifers, and to a lesser extent ferns and sphenopsids (Rees *et al.*, 2000; Willis and McElwain 2002).

**Subtropical desert biome**—An absence of fossil plants in association with evaporites and aeolian sediments is suggestive of a subtropical desert biome. This region occupied the majority of modern day southern North America in the northern hemisphere, and central South America and southern Africa in the southern hemisphere (Willis and McElwain 2002).

**Summerwet (tropical) biome**—This biome occupied modern day Mexico, Cuba, Columbia, northern Brazil, northern Africa, and Isreal. The summerwet (tropical) biome was dominated by microphyllous Bennettitales, ferns and microphyllous conifers (including Cupressaceae and Podocarpaceae). Cycads were rare and ginkgos, and a number of conifer families (e.g. Pinaceae) were absent (Willis and McElwain 2002).

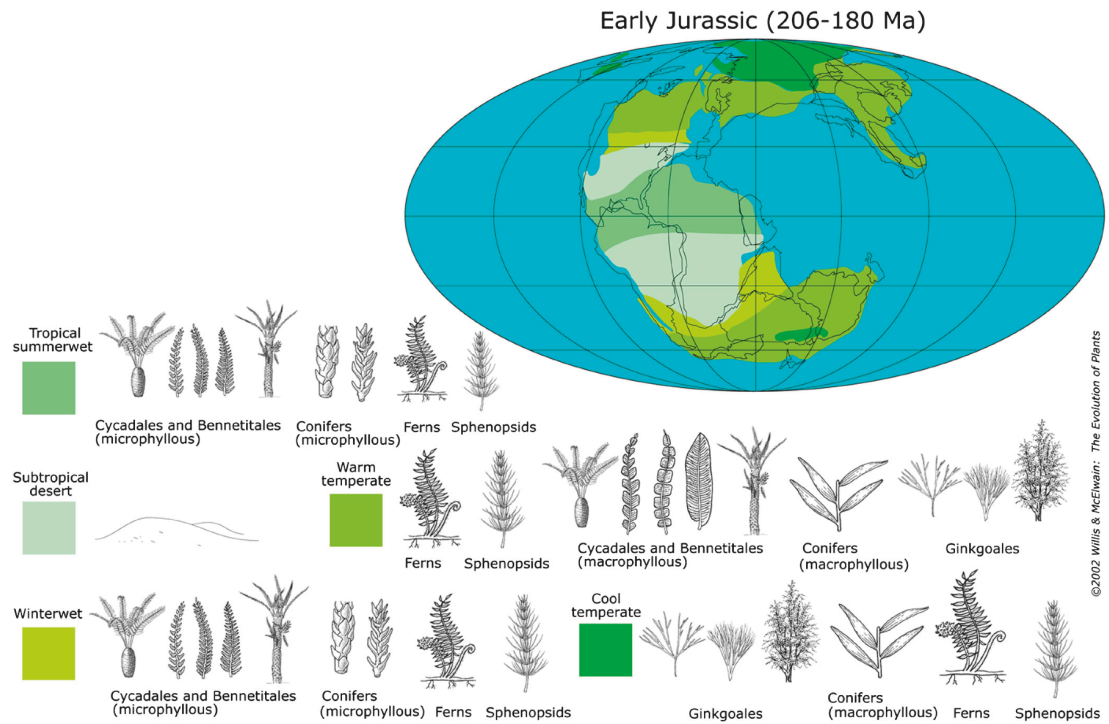


Figure 2.7: Biome map for the Early Jurassic (206–180 Ma). Taken from Willis and McElwain (2002).

The Jurassic deposits of Yorkshire are famous for their botanical remains, with the first floral investigations dating back Young and Bird (1822). Numerous subsequent palaeobotanical studies have followed, the most comprehensive of which comprises five volumes, entitled “The Yorkshire Jurassic flora” (Harris 1961, 1964, 1969, 1979; Harris *et al.*, 1974). The most abundant and best-preserved plant fossils are found within the numerous plant beds, scattered throughout the non-marine sequences of the Ravenscar Group (see van Konijnenburg-van Cittert and Morgans 1999; Cleal *et al.*, 2001). These beds often possess finely preserved vegetative fragments, inflorescences, fructifications, and spores and pollen (van Konijnenburg-van Cittert and Morgans 1999). This study will attempt to provide a more comprehensive reconstruction of the Jurassic palaeoflora of Yorkshire by using the overlooked, but exceptionally preserved dispersed sporomorph record of these deposits.

### CHAPTER 3: SYSTEMATIC TAXONOMY OF DISPERSED SPORES AND POLLEN

This chapter lists and figures all terrestrial sporomorph taxa that were encountered within this study. The naming and identification of Middle Jurassic sporomorphs from Yorkshire is very well constrained following extensive published (Couper 1958; Srivastava 2011) and unpublished (Dodd 1975; Wilkinson 1975; Al-Jubori 1979; Cadman 1979; Fenton 1980; Stronach 1983; Hogg 1993; Trout 1996) taxonomic studies from these deposits. The purpose of this chapter is therefore to introduce spore/pollen taxa, which will be used in new quantitative analytical methods to improve vegetation reconstructions. In order to utilize sporomorphs in floral reconstructions, sporomorphs are arranged primarily based on their botanical affinities, and secondarily alphabetically within plant groups. Where possible, taxonomic groupings follow Taylor *et al.*, (2009). Synonymy lists of previous identifications of the same taxa are included for all species, parameters for inclusion within synonymy lists are; (i) original species names; (ii) all available UK Middle Jurassic onshore sporomorph studies; and (iii) changes to taxon names that the present author agrees with. Assigning parent plant groups to sporomorphs has only become possible following extensive work into spore and pollen in situ preservation (e.g. van Konijnenburg-van Cittert 1968, 1971, 1978, 1981, 1989, 1993, 2000; Pedersen *et al.*, 1989; Hill 1990; Osborn and Taylor 1993; Balme 1995; Friis and Pedersen 1996; Yang *et al.*, 2008) and TEM analysis of the spore wall ultrastructure (e.g. Batten and Dutta 1997), which now means that the majority of Middle Jurassic sporomorphs can be assigned to at least family-level plant classification. Botanical affinities for all sporomorph taxa are provided in Appendix 1. For sample collection and processing methods see chapter 4, section 4.2.



***Structure of Taxonomy:***

**3.1 Bryophytes**

**3.2 Spore-producing tracheophytes**

3.2.1 Lycophyta

3.2.1.1 Lycopodiales

3.2.1.2 ?Selaginellales

3.2.1.3 Isoetales

3.2.2 Sphenophytes

3.2.2.1 Equisetales

3.2.3 Ferns/Sphenophytes

3.2.4 Ferns

3.2.4.1 Marattiaceae

3.2.4.2 Osmundaceae

3.2.4.3 Gleicheniaceae

3.2.4.4 Dipteridaceae

3.2.4.5 Dipteridaceae/Matoniaceae

3.2.4.6 Matoniaceae

3.2.4.7 Schizaeaceae

3.2.4.8 Schizaeaceae/Cyatheaceae/Dicksoniaceae/Matoniaceae

3.2.4.9 Cyatheaceae/Dicksoniaceae/Gleicheniaceae

3.2.4.10 Dicksoniaceae

3.2.4.11 Cyatheaceae/Dicksoniaceae

3.2.4.12 Fern spores of unknown affinity

**3.3 Gymnosperms**

3.3.1 Pteridospermophyta/Conifers

3.3.1.1 Caytoniales

3.3.2 Conifers

3.3.2.1 Pinaceae

- 3.3.2.2 Podocarpaceae
- 3.3.2.3 Araucariaceae
- 3.3.2.4 Cheirolepidiaceae
- 3.3.2.5 Taxodiaceae
- 3.3.3 Cycadophytes/Ginkgophytes
  - 3.3.3.1 ?Bennettitales
- 3.3.4 Erdtmanithecales
- 3.3.5 Pollen of unknown affinity

### 3.1 Bryophytes

#### Genus *Foveosporites* Balme 1957

**Type species:** *Foveosporites canalis* Balme 1957.

**Diagnosis:** see Balme (1957), p. 17.

#### *Foveosporites moretonensis* De Jersey 1964

Pl. 1, fig. 1

1964 *Foveosporites moretonensis* De Jersey 1964, p. 7, pl. 1, fig. 7.

1993 *Foveosporites moretonensis* De Jersey 1964 in Hogg 1993, p. 75, pl. 4, fig. 9.

**Description:** see De Jersey (1964), p. 7.

**Remarks:** Conspicuous species from its foveo-reticulate sculpture.

#### Genus *Nevesisporites* (De Jersey and Paten 1964) Morbey 1975

**Type species:** *Nevesisporites vallatus* De Jersey and Paten 1964.

**Diagnosis:** see Morbey (1975), p. 19.

#### *Nevesisporites* (*Cingulatisporites*) *bigranulatus* (Levet-Carette 1965) Morbey 1975

Pl. 1, fig. 2

1965 *Cingulatisporites bigranulatus* Levet-Carette 1965, p. 290, pl. 25, fig. 4.

1975 *Nevesisporites bigranulatus* Levet-Carette 1965 comb. nov. in Morbey 1975, p. 19, pl. 4, figs. 9, 10.

1980 *Nevesisporites bigranulatus* (Levet-Carette 1964) Morbey 1975 in Fenton 1980, p. 132, pl. 6, fig. 12.

1993 *Nevesisporites bigranulatus* (Levet-Carette 1964) Morbey 1975 in Hogg 1993, p. 86, pl. 7, figs. 13, 14.

**Description:** see Levet-Carette (1965), p. 290.

#### Genus *Rogalskaisporites* Danzé-Corsin and Laveine 1963

**Type species:** *Rogalskaisporites* (*Sporites*) *cicatricosus* (Rogalska 1954) Danzé-Corsin and Laveine 1963.

**Diagnosis:** see Danzé-Corsin and Laveine (1963), p. 80.

*Rogalskaisporites (Sporites) cicatricosus* (Rogalska 1954) Danzé-Corsin and Laveine 1963

Pl. 1, fig. 3

1954 *Sporites cicatricosus* Rogalska 1954, p. 26, 44, pl. 12, fig. 11.

1963 *Rogalskaisporites cicatricosus* (Rogalska) comb. nov. in Danzé-Corsin and Laveine 1963, p. 80-81, pl. 6, figs. 19-21.

**Description:** see Rogalska (1954), p. 26.

**Remarks:** Highly conspicuous species. The exine is thicker in the central region of the distal side; this forms a ring with a dentate margin or a ring of verrucae.

**Genus *Stereisporites* Pflug in Thomson and Pflug 1953 emend. De Jersey 1964**

**Type species:** *Stereisporites (al. Sporites) stereoides* (Potonié and Venitz 1934) Pflug in Thomson and Pflug 1953.

**Diagnosis:** see De Jersey (1964), p. 4.

*Stereisporites* sp. Pflug in Thomson and Pflug 1953 emend. De Jersey 1964

Pl. 1, fig. 4

**Diagnosis:** see De Jersey (1964), p. 4.

**Remarks:** The present author follows De Jersey (1964) in including forms that show a distal polar crassitude.

### 3.2 Spore-producing tracheophytes

#### 3.2.1 Lycophyta

##### 3.2.1.1 Lycopodiales

#### Genus *Anapiculatisporites* Potonié and Kremp 1954

**Type species:** *Anapiculatisporites isselburgensis* Potonié and Kremp 1954.

**Diagnosis:** see Potonié and Kremp (1954), p. 133.

*Anapiculatisporites* sp. Potonié and Kremp 1954

Pl. 1, fig. 5

1993 *Anapiculatisporites* spp. Potonié and Kremp 1954 in Boulter and Windle 1993, p. 132, pl. 9, fig. 1-17.

**Diagnosis:** see Potonié and Kremp (1954), p. 133.

**Remarks:** Conspicuous genera, recognisable from the apiculate elements.

#### Genus *Densoisporites* (Weyland and Krieger 1953) Dettmann 1963

**Type species:** *Densoisporites velatus* Weyland and Krieger 1953.

**Diagnosis:** see Dettmann (1963), p. 83.

*Densoisporites (Psilatriteles) circumundulatus* (Brenner 1963) Playford 1971

Pl. 1, fig. 6

1963 *Psilatriteles circumundulatus* Brenner 1963, p. 67, pl. 20, figs. 4-5.

1971 *Densoisporites circumundulatus* (Brenner 1963) comb. nov. in Playford 1971, p. 541, pl. 105, figs. 6, 7.

1993 *Densoisporites circumundulatus* (Brenner 1963) Playford 1971 in Hogg 1993, p. 74, pl. 5, fig. 5.

1996 *Densoisporites circumundulatus* (Brenner 1963) Playford 1971 in Trout 1996, p. 71, pl. 1, fig. 5.

**Description:** see Brenner (1963), p. 67.

**Remarks:** Higher degree of folding compared to *Densoisporites velatus*.

*Densoisporites velatus* Weyland and Krieger 1953

Pl. 1, fig. 7

1953 *Densoisporites velatus* Weyland and Krieger 1953, p. 12, pl. 4, figs. 12-14.

- 1958 *Densoisporites perinatus* n. sp. in Couper 1958, p. 145, pl. 23, figs. 6-9.
- 1975 *Densoisporites velatus* Weyland and Krieger 1953 in Dodd 1975, p. 35, pl. 8, fig. 11.
- 1979 *Densoisporites velatus* Weyland and Krieger 1953 in Cadman 1979, p. 50, pl. 2, fig. 9.
- 1980 *Densoisporites velatus* Weyland and Krieger 1953 emend. Krasnova 1961 in Fenton 1980, p. 136, pl. 7, fig. 11.
- 1988 *Densoisporites microrugulatus* Brenner 1963 in Walton 1988, p. 70, pl. 5, fig. 1.
- 1993 *Densoisporites velatus* Weyland and Krieger 1953 in Hogg 1993, p. 75, pl. 5, figs. 6 and 7.
- 1996 *Densoisporites velatus* Weyland and Krieger 1953 in Trout 1996, p. 71, pl. 1, fig. 4.
- 2011 *Densoisporites perinatus* Couper 1958 in Srivastava 2011, p. 151, pl. 3, fig. 7.
- 2011 *Densoisporites velatus* Weyland and Krieger 1953 in Srivastava 2011, p. 151, pl. 3, fig. 8.

**Description:** see Weyland and Krieger (1953), p. 12.

**Remarks:** Conspicuous species. Lower degree of folding compared to *Densoisporites circumundulatus*.

*Densoisporites cf. velatus* Weyland and Krieger 1953

Pl. 1, fig. 8

**Description:** Trilete, biconvex, amb roundly triangular. Laesurae are straight, long ( $\frac{3}{4}$  of spore radius) and enclosed within membranous lips. Sclerine two-layered, cavate, proximally attached. Sculptine 10-20  $\mu\text{m}$  thick, thicker in equatorial regions, surface pattern scabrate, inner layer scabrate, *c.* 5  $\mu\text{m}$  thick.

**Dimensions:** Equatorial diameter (1 specimen), overall 87  $\mu\text{m}$ , inner layer 57  $\mu\text{m}$ .

**Remarks:** *Densoisporites cf. velatus* is larger than *Densoisporites velatus* and the inner wall layer is scabrate, this is smooth in *D. velatus*.

**Genus *Kraeuselisporites* (Leschik 1956) Scheuring 1974**

**Type species:** *Kraeuselisporites dentatus* Leschik 1956.

**Diagnosis:** see Scheuring (1974), p. 199.

*Kraeuselisporites whitfordensis* Backhouse 1988

Pl. 1, fig. 9

1988 *Kraeuselisporites whitfordensis* sp. nov. in Backhouse 1988, p. 60, pl. 6, figs. 4-6, pl. 13, fig. 7.

1993 *Kraeuselisporites whitfordensis* Backhouse 1988 in Hogg 1993, p. 63, pl. 1, figs. 1-6, pl. 2, fig. 1.

**Description:** see Backhouse (1988), p. 60.

**Remarks:** Distinguished from *Kraeuselisporites* sp. 1 by the presence of strongly developed spines at the equator.

*Kraeuselisporites* sp. 1

Pl. 1, fig. 10

1975 *Kraeuselisporites* sp. A in Dodd 1975, p. 39, pl. 7, figs. 1-12.

1980 *Kraeuselisporites hyalinus* sp. nov. in Fenton 1980, p. 141, pl. 8, figs. 1-5.

1993 *Kraeuselisporites scalbiensis* n. sp. in Hogg 1993, p. 62, pl. 2, figs. 6, 7, 9.

**Description:** see Hogg (1993), p. 62.

**Remarks:** The present author follows Hogg (1993) in the description of this species, however, *K. scalbiensis* has not been formally named in published literature, and hence this taxon is referred to as *Kraeuselisporites* sp. 1 here. The name *Kraeuselisporites* sp. 1 has been used in manuscripts derived from this PhD project, thus to keep consistency the same name is applied here.

**Genus *Lycopodiacidites* (Couper 1953) Potonié 1956**

**Type species:** *Lycopodiacidites bullerensis* Couper 1953.

**Diagnosis:** see Potonié (1956), p. 39.

*Lycopodiacidites (Lycopodiumsporites) cerniidites* (Ross 1949) Brenner 1963

Pl. 2, fig. 1

1949 *Lycopodium cerniidites* Ross 1949, p. 30, pl. 1, figs. 1, 2.

1958 *Lycopodiumsporites cerniidites* (Ross 1949) Delcourt and Sprumont 1955 in Couper 1958, p. 132, pl. 15, figs. 6-9.

1963 *Lycopodiacidites cerniidites* (Ross) in Brenner 1963, p. 43, pl. 5, fig. 2.

- 1975 *Lycopodiumacidites cerniidites* (Ross 1949) Brenner 1963 in Dodd 1975, p. 57, pl. 5, figs. 14-15.
- 1975 *Lycopodiumacidites cerniidites* (Ross 1949) Brenner 1963 in Wilkinson 1975, p. 76, pl. 3, figs. 12-14.
- 1979 *Lycopodiumacidites cerniidites* (Ross 1949) Brenner 1963 in Al-Jubori 1979, p. 56, pl. 3, fig. 1.
- 1980 *Lycopodiumsporites cerniidites* (Ross 1949) Brenner 1963 in Fenton 1980, p. 113, pl. 4, fig. 11.
- 1983 *Lycopodiumsporites cerniidites* (Ross 1949) Brenner 1963 in Stronach 1983, p. 27, pl. 3, figs. 4, 5.
- 1996 *Lycopodiumsporites cerniidites* (Ross 1949) Brenner 1963 in Trout 1996, p. 73, pl. 2, fig. 1.
- 1993 *Lycopodiacidites cerniidites* (Ross) Brenner 1963 in Boulter and Windle 1993, p. 130, pl. 2, figs. 6-28.

**Description:** see Ross (1949), p. 30.

**Remarks:** Distinguishable from *Lycopodiacidites rugulatus* from the more triangular equatorial contour and reduced ornament at the proximal pole.

*Lycopodiacidites (Perotrilites) rugulatus* (Couper 1958) Schulz 1967

Pl. 1, fig. 2

- 1958 *Perotrilites rugulatus* sp. nov. Couper 1958, p. 147, pl. 25, figs. 7, 8.
- 1967 *Lycopodiacidites rugulatus* (Couper 1958) comb. nov. in Schulz 1967, p. 573, pl. 7, figs. 15-16.
- 1975 *Lycopodiacidites rugulatus* (Couper 1958) Schulz 1967 in Wilkinson 1975, p. 79, pl. 3, fig. 15.
- 1979 *Lycopodiacidites rugulatus* (Couper 1958) Schulz 1967 in Al-Jubori 1979, p. 57, pl. 3, fig. 2.
- 1980 *Lycopodiacidites rugulatus* (Couper 1958) Schulz 1967 in Fenton 1980, p. 114, pl. 4, fig. 12.
- 1993 *Lycopodiacidites rugulatus* (Couper 1958) Schulz 1967 in Hogg 1993, p. 80, pl. 7, figs. 7 and 8.

**Description:** see Couper (1958), p. 147.

**Remarks:** Possesses a more distinct rugulate sculpture and the equatorial contour is more rounded than *L. cerniidites*.

**Genus *Neoraistrickia* Potonié 1956**

**Type species:** *Neoraistrickia (Triletes) truncatus* (Cookson 1953) Potonié 1956.

**Diagnosis:** see Potonié (1956), p. 34.

*Neoraistrickia (Triletes) truncatus* (Cookson 1953) Potonié 1956

Pl. 2, fig. 3

- 1953 *Triletes truncatus* Cookson 1953, p. 471, pl. 2, fig. 36.



- 1956 *Neoraistrickia* (*al. Trilites*) *truncatus* (Cookson 1953) nov. comb. in Potonié 1956, p. 34, pl. 3, fig. 32.
- 1958 *Lycopodiumsporites gristhorpensis* Couper 1958, p. 133, pl. 15, figs. 14-16.
- 1975 *Lycopodiumsporites gristhorpensis* Couper 1958 in Dodd 1975, p. 57, pl. 5, fig. 9.
- 1975 *Baculatisporites truncates* (Cookson 1953) Balme 1957 in Dodd 1975, p. 50, pl. 5, fig. 4.
- 1979 *Neoraistrickia truncata* (Cookson 1953) Potonié 1956 in Al-Jubori 1979, p. 52, pl. 2, figs. 9, 12.
- 1979 *Neoraistrickia gristhorpensis* (Couper 1958) Tralau 1967 in Cadman 1979, p. 40, pl. 1, fig. 17.
- 1980 *Neoraistrickia gristhorpensis* (Couper 1958) Tralau 1967 in Fenton 1980, p. 104, pl. 3, fig. 10.
- 1983 *Neoraistrickia gristhorpensis* (Couper 1958) Tralau 1968 in Stronach 1983, p. 24, pl. 2, fig. 4.
- 1993 *Neoraistrickia truncata* (Cookson 1953) Potonié 1956 in Hogg 1993, p. 92, figs. 1 and 2.
- 1996 *Neoraistrickia truncata* (Cookson 1953) Potonié 1956 in Trout 1996, p. 78, pl. 2, fig. 7.

**Description:** see Cookson (1953), p. 471.

**Remarks:** Conspicuous species from the presence of stout, flat topped bacula.

#### **Genus *Retitriletes* Van der Hammen 1956 ex Pierce 1961 emend. Döring *et al.*, 1963**

**Type species:** *Retitriletes globosus* Pierce 1961.

**Diagnosis:** see Döring *et al.*, (1963), p 16.

#### *Retitriletes* (*Lycopodiumsporites*) *austroclavatidites* (Cookson 1953) Döring *et al.*, 1963

Pl. 2, fig. 4

- 1953 *Lycopodium austroclavatidites* Cookson 1953, p. 469, pl. 2, fig. 35.
- 1963 *Retitriletes austroclavatidites* (Cookson) Döring *et al.*, 1963 in Krutzsch 1963, p. 16.
- 1975 *Lycopodiumsporites austroclavatides* (Cookson 1953) Potonié 1956 in Dodd 1975, p. 56, pl. 5, figs. 7-8.
- 1975 *Lycopodiumsporites austroclavatidites* (Cookson 1953) Potonié 1956 in Wilkinson 1975, p. 82, pl. 4, fig. 3.
- 1979 *Lycopodiumsporites austroclavatidites* (Cookson 1953) Potonié 1956 in Al-Jubori 1979, p. 59, pl. 7, figs. 2, 10, 11.
- 1979 *Lycopodiumsporites austroclavatidites* (Cookson 1953) Potonié 1956 in Cadman 1979, p. 46, pl. 2, fig. 4, 5.
- 1980 *Retitriletes australoclavatidites* (Cookson 1953) Döring *et al.*, 1963 in Fenton 1980, p. 108, pl. 4, fig. 6.
- 1993 *Retitriletes austroclavatidites* (Cookson 1953) Döring *et al.*, 1963 in Hogg 1993, p. 81, pl. 6, fig. 4.

- 1993 *Retitriletes austroclavitudites* (Cookson 1953) Döring *et al.*, 1963 in Boulter and Windle 1993, p. 130, not figured.
- 1996 *Retitriletes australoclavitudites* (Cookson 1953) Döring *et al.*, 1963 in Trout 1996, p. 76, pl. 2, fig. 5.
- 2011 *Retitriletes austroclavitudites* (Cookson 1953) Döring, Krutzsch, Mai and Schulz in Krutzsch 1963 in Srivastava 2011, p. 157, pl. 6, figs. 4-6.

**Description:** see Cookson (1953), p. 469.

**Remarks:** Distinguished from *Retitriletes clavatooides* by the more abundant and thinner muri and smaller lumina.

*Retitriletes (Lycopodiumsporites) clavatooides* (Couper 1958) Döring *et al.*, 1963

Pl. 2, fig. 5

- 1958 *Lycopodiumsporites clavatooides* Couper 1958, p. 132, pl. 15, figs. 10-11.
- 1963 *Retitriletes clavatooides* (Couper 1958) Döring *et al.*, 1963, p. 16.
- 1993 *Retitriletes clavatooides* (Couper 1958) Döring *et al.*, 1963 in Hogg 1993, p. 81, pl.6, fig. 5.
- 2011 *Retitriletes clavatooides* (Couper 1958) Döring, Krutzsch, Mai and Schulz in Krutzsch 1963 in Srivastava 2011, p. 158, pl. 6, figs. 7, 8.

**Description:** see Couper (1958), p. 132.

**Remarks:** Differs from *Retitriletes austroclavitudites* in possessing fewer and thicker muri and larger lumina.

*Retitriletes (Lycopodiumsporites) semimuris* (Danzé-Corsin and Laveine 1963) McKellar

1974

Pl. 2, fig. 6

- 1963 *Lycopodiumsporites semimuris* Danzé-Corsin and Laveine 1963 p. 79, pl. 6, figs. 15a-b.
- 1974 *Retitriletes semimuris* (Danzé-Corsin and Laveine 1963) McKellar 1974, p. 14, pl. 5, fig. 6.
- 1975 *Lycopodiacidites semimuris* (Danzé-Corsin and Laveine 1963) nov. comb. in Wilkinson 1975, p. 78, pl. 4, fig. 1.
- 1980 *Lycopodiacidites semimuris* Danzé-Corsin and Laveine 1963 comb. nov. in Fenton 1980, p. 116, pl. 5, fig. 3.
- 1983 *Lycopodiacidites semimuris* (Danzé-Corsin and Laveine 1963) comb. nov. Reiser and Williams 1969 in Stronach 1983, p. 27, pl. 3, fig. 7.

1993 *Retitriletes (Lycopodiacidites) semimuris* (Danzé-Corsin and Laveine 1963) McKellar 1974 in Hogg 1993, p. 82, pl. 6, figs. 9-11.

**Description:** see Danzé-Corsin and Laveine (1963), p. 79.

**Remarks:** Recognised by the incomplete reticulate ornamentation and rounded triangular equatorial contour.

#### *Retitriletes singhii* Srivastava 1972

Pl. 2, fig. 7

1964 *Lycopodiumsporites marginatus* n. sp. in Singh 1964, p. 41, pl.1, figs. 7-10.

1972 *Retitriletes singhii* n. name in Srivastava 1972, not figured.

2011 *Retitriletes singhii* Srivastava 1972 in Srivastava 2011, p. 158, pl. 6, figs. 9, 10.

**Description:** see Singh (1964), p. 41.

**Remarks:** Conspicuous species from its relatively large size and prominent margin.

Srivastava (1972) transferred *Lycopodiumsporites marginatus* to *Retitriletes*, however *Retitriletes marginatus* (Singh) n. comb. would have been a homonym of *Retitriletes marginatus* (Kara-Murza 1954) Krutzsch 1963, thus Srivastava (1972) renamed the species.

#### **Genus *Leptolepidites* Couper 1953**

**Type species:** *Leptolepidites verrucatus* Couper 1953.

**Diagnosis:** see Couper (1953), p. 28.

#### *Leptolepidites (Trilites) bossus* (Couper 1958) Schulz 1967

Pl. 2, fig. 8

1958 *Trilites bossus* n. sp. Couper 1958, p. 148, pl. 25, figs. 11, 12.

1967 *Leptolepidites bossus* (Couper) in Schulz 1967, p. 559, pl. 2, figs. 4-6.

1975 *Triletes bossus* Couper 1958 in Dodd 1975, p. 34, pl. 3, fig. 13.

1979 *Leptolepidites bossus* (Couper 1958) Schulz 1967 in Cadman 1979, p. 39, pl. 1, fig. 16.

1980 *Leptolepidites bossus* (Couper 1958) Schulz 1967 in Fenton 1980, p. 101, pl. 3, fig. 6.

1993 *Leptolepidites bossus* (Couper 1958) Schulz 1967 in Hogg 1993, p. 89, pl. 9, figs. 3 and 4.

1993 *Rotverrusporites bossus* Fensome 1987 in Boulter and Windle 1993, p. 131, not figured.

1996 *Leptolepidites bossus* (Couper 1958) Schulz 1967 in Trout 1996, p. 84, pl. 3, fig. 4.

**Description:** see Couper (1958), p. 148.

**Remarks:** Differs from *Leptolepidites major* in its smaller size and the verrucae are rarely in contact.

*Leptolepidites crassibalteus* Filatoff 1975

Pl. 2, fig. 9

1975 *Leptolepidites crassibalteus* n. sp. Filatoff 1975, p. 49, pl. 5, figs. 4-6.

**Description:** see Filatoff (1975), p. 49.

**Remarks:** Distinguished from *Leptolepidites bossus*, *L. equatibossus* and *L. major* by the thickened equatorial exine, which is often indented at the apices.

*Leptolepidites (Trilites) equatibossus* (Couper 1958) Tralau 1968

Pl. 2, fig. 10

1958 *Trilites equatibossus* n. sp. Couper 1958, p. 148, pl. 25, fig. 13-14.

1968 *Leptolepidites equatibossus* (Couper 1958) in Tralau 1968, p. 48, pl. 8, fig. 3.

1975 *Trilites equatibossus* Couper 1958 in Dodd 1975, p. 34, pl. 3, figs. 14-16.

1993 *Leptolepidites equatibossus* (Couper 1958) Tralau 1968 in Hogg 1993, p. 89, pl. 9, fig. 5.

1993 *Rotverrusporites equatibossus* Fensome 1987 in Boulter and Windle 1993, p. 130, pl. 3, figs. 18-41.

**Description:** see Couper (1958), p. 148.

**Remarks:** Differs from *Leptolepidites bossus* in having ornament confined to the equatorial regions.

*Leptolepidites major* Couper 1958

Pl. 2, fig. 11

1958 *Leptolepidites major* n. sp. Couper 1958, p. 141, pl. 21, figs. 7-8.

1975 *Leptolepidites major* Couper 1958 in Dodd 1975, p. 48, pl. 4, fig. 6-10.

1979 *Leptolepidites major* Couper 1958 in Al-Jubori 1979, p. 48, pl. 2, fig. 4.

1979 *Leptolepidites major* Couper 1958 in Cadman 1979, p. 39, pl. 1, fig. 15.

1980 *Leptolepidites major* Couper 1958 in Fenton 1980, p. 102, pl. 3, fig. 5.

- 1983 *Leptolepidites major* Couper 1958 in Stronach 1983, p. 23, pl. 2, figs. 4, 5.
- 1993 *Leptolepidites major* Couper 1958 in Hogg 1993, p. 89, pl. 9, fig. 8.
- 1993 *Rotverrusporites major* Fensome 1987 in Boulter and Windle 1993, p. 130, pl. 3, figs. 1-17.
- 1996 *Leptolepidites major* Couper 1958 in Trout 1996, p. 83, pl. 3, fig. 3.
- 2011 *Leptolepidites major* Couper 1958 in Srivastava 2011, p. 155, pl. 5, figs. 4, 5, pl. 10, fig. 3.

**Description:** see Couper (1958), p. 141.

**Remarks:** Differs from *Leptolepidites bossus* in its larger size and verrucae that are commonly in contact.

### **Genus *Sestrosporites* (Couper 1958) Dettmann 1963**

**Type species:** *Sestrosporites (Foveotriletes) irregularis* (Couper 1958) Dettmann 1963.

**Diagnosis:** see Dettmann (1963), p. 66.

#### *Sestrosporites (Cingulatisporites) pseudoalveolatus* (Couper 1958) Dettmann 1963

Pl. 2, fig. 12

- 1958 *Cingulatisporites pseudoalveolatus* Couper 1958, p. 147, pl. 25, fig. 5, 6.
- 1963 *Sestrosporites pseudoalveolatus* (Couper 1958) comb. nov. in Dettmann 1963, p. 66, pl. 13, figs. 11-16.
- 1975 *Sestrosporites pseudoalveolatus* (Couper 1958) Dettmann 1963 in Dodd 1975, p. 42, pl. 8, figs. 13-14.
- 1979 *Sestrosporites pseudoalveolatus* (Couper 1958) Dettmann 1963 in Al-Jubori 1979, p. 67, pl. 3, figs. 7-9, 11.
- 1979 *Sestrosporites pseudoalveolatus* (Couper 1958) Dettmann 1963 in Cadman 1979, p. 48, pl. 2, fig. 7.
- 1980 *Sestrosporites pseudoalveolatus* (Couper 1958) Dettmann 1963 in Fenton 1980, p. 124, pl. 6, fig. 4.
- 1993 *Sestrosporites pseudoalveolatus* (Couper 1958) Dettmann 1963 in Hogg 1993, p. 76, pl. 5, figs. 2, 3, and 4.
- 1996 *Sestrosporites pseudoalveolatus* (Couper 1958) Dettmann 1963 in Trout 1996, p. 79, pl. 2, fig. 8.
- 1993 *Vallizonosporites pseudoalveolatus* Fensome 1987 in Boulter and Windle 1993, p. 131, pl. 4, figs. 1-19.
- 2011 *Sestrosporites pseudoalveolatus* (Couper 1958) Dettmann 1963 in Srivastava 2011, p. 159, pl. 6, figs. 11, 12.

**Description:** see Dettmann (1963), p. 66.

**Remarks:** Conspicuous species from the presence of distinctive foveolate ornamentation.

### Genus *Staplinisporites* Pocock 1962

**Type species:** *Staplinisporites (Cingulatisporites) caminus* (Balme 1957) Pocock 1962.

**Diagnosis:** see Pocock (1962), p. 49.

*Staplinisporites* sp. Pocock 1962

Pl. 2, fig. 13

1993 *Staplinisporites* spp. Pocock 1962 in Boulter and Windle 1993, p. 130, pl. 1, figs. 1-28.

**Diagnosis:** see Pocock (1962), p. 49.

**Remarks:** Refers to all specimens that belong to this genus with the exception of *Staplinisporites mathurii*. Rugulate elements coalesce to form a distal thickening, surrounded by an irregular concentric element, distinguishing this genus from *Lycopodiacidites*.

*Staplinisporites mathurii* (Srivastava 1966) Filatoff 1975

Pl. 2, fig. 14

1966 *Triangulatisporites mathurii* Srivastava new species in Srivastava 1966, p. 91, pl. 2, fig. 5.

1975 *Staplinisporites mathurii* (Srivastava) comb. nov. in Filatoff 1975, p. 44, pl. 3, figs. 5-7.

**Description:** see Srivastava (1966), p. 91.

**Remarks:** *Staplinisporites mathurii* differs from other *Staplinisporites* taxa in this study by its slightly larger size, thicker exine and rugulate sculpture on the distal equatorial area. Three specimens were found.

### Genus *Uvaesporites* Döring 1965

**Type species:** *Uvaesporites glomeratus* Döring 1965.

**Diagnosis:** see Döring (1965), p. 39.

*Uvaesporites (Stenozonotriletes) argentiformis* (Bolkhovitina 1953) Schulz 1967

Pl. 2, fig. 15

1953 *Stenozonotriletes argentiformis* sp. nov. in Bolkhovitina 1953, p. 51, pl. 7, fig. 9.

- 1967 *Uvaesporites argentiformis* (Bolkhovitina 1953) comb. nov. in Schulz 1967, p. 560, pl. 2, figs. 10-11, pl. 23, fig. 2.
- 1980 *Uvaesporites argentiformis* (Bolkhovitina 1953) Schulz 1967 in Fenton 1980, p. 105, pl. 4, fig. 3.
- 1993 *Uvaesporites argentiformis* (Bolkhovitina) Schulz 1967 in Boulter and Windle 1993, p. 133, pl. 9, figs. 18-31.
- 2011 *Uvaesporites argentiformis* (Bolkhovitina 1953) Schulz 1967 in Srivastava 2011, p. 160, pl. 7, figs. 5, 6, pl. 10, figs. 5-6, pl. 11, figs. 1-4.

**Description:** see Bolkhovitina (1953), p. 51.

**Remarks:** *Uvaesporites* differs from *Leptolepidites* in having typically larger verrucae near the equator and *Leptolepidites* spores are generally darker and have a thicker exine. Verrucae on the distal face are typically irregular and fused together to form an irregular reticulum, distinguishing this species from *Leptolepidites major*.

### 3.2.1.2 ?Selaginellales

#### Genus *Reticuspinosporites* Slater *et al.*, 2015

**Type species:** *Reticuspinosporites whytei* Slater *et al.*, 2015.

**Diagnosis:** see Slater *et al.*, (2015), p. 35-41.

*Reticuspinosporites whytei* Slater *et al.*, 2015

See Chapter 6

**Description:** see Chapter 6.

**Remarks:** see Chapter 6.

### 3.2.1.3 Isoetales

#### Genus *Paxillitriletes* Hall and Nicholson 1973

**Type species:** *Paxillitriletes reticulatus* (Mädler 1954) Hall and Nicholson 1973.

**Diagnosis:** see Hall and Nicholson (1973), p. 319.

*Paxillitriletes (Triletes) phyllicus* (Murray 1939) Hall and Nicholson 1973

Pl. 3, figs. 1-6; Pl. 4, figs. 1-6

- 1939 *Triletes phyllicus* Murray 1939, p. 482, pl. text-figs. 7-8.  
1961 *Triletes phyllicus* Murray 1939 in Harris 1961b, p. 48, text-figs. 13 I, J, 14.  
1973 *Paxillitriletes phyllicus* (Murray 1939) Hall and Nicholson 1973, p. 319.  
1993 *Paxillitriletes phyllicus* (Murray 1939) Hall and Nicholson 1973 in Hogg 1993, p. 110, pl. 2, fig. 8.  
1996 *Paxillitriletes phyllicus* (Murray 1939) Hall and Nicholson 1973 in Trout 1996, p. 72, pl. 1, fig. 6.

**Description:** see Murray (1939), p. 482.

**Remarks:** Highly conspicuous species due to its large size. Specimens agree with descriptions provided by Murray (1939) and Harris (1961b). Due to their sub-opaque appearance, specimens are best studied using reflected light or a scanning electron microscope.

### 3.2.2 Sphenophytes

#### 3.2.2.1 Equisetales

##### Genus *Calamospora* Schopf *et al.*, 1944

**Type species:** *Calamospora hartungiana* Schopf *et al.*, 1944.

**Diagnosis:** see Schopf *et al.*, (1944), p. 51.

##### *Calamospora mesozoica* Couper 1958

Pl. 5, fig. 1

- 1958 *Calamospora mesozoica* n. sp. Couper 1958, p. 132, pl. 15, figs. 3-4.  
1975 *Calamospora mesozoica* Couper 1958 in Dodd 1975, p. 132, pl. 15, fig. 3.  
1979 *Calamospora mesozoica* Couper 1958 in Al-Jubori 1979, p. 34, pl. 1, fig. 1.  
1980 *Calamospora mesozoica* Couper 1958 in Fenton 1980, p. 82, pl. 1, fig. 12.  
1983 *Calamospora mesozoica* Couper 1958 in Stronach 1983, p. 17, pl. 4, fig. 4.  
1993 *Calamospora mesozoica* Couper 1958 in Hogg 1993, p. 66, pl. 3, fig. 1.  
1993 *Calamospora mesozoica* Couper 1958 in Boulter and Windle 1993, p. 131, pl. 4, figs. 34-39.  
1996 *Calamospora mesozoica* Couper 1958 in Trout 1996, p. 69, pl. 1, fig. 3.

**Description:** see Couper (1958), p. 131.



**Remarks:** Often difficult to identify as the spore folds easily, concealing the short laesurae. Filatoff (1975) recorded the presence of granules at the contact areas, this feature was also observed in this study.

### 3.2.3 Ferns/Sphenophytes

#### **Genus *Laevigatosporites* Ibrahim 1933 emend. Schopf *et al.*, 1944**

**Type species:** *Laevigatosporites (Sporites) vulgaris* (Ibrahim 1932) Ibrahim 1933.

**Diagnosis:** see Schopf *et al.*, (1944), p. 36.

*Laevigatosporites* sp. Ibrahim 1933 emend. Schopf *et al.*, 1944

Pl. 5, fig. 2

**Diagnosis:** see Schopf *et al.*, (1944), p. 36.

**Remarks:** Conspicuous species recognised from its oval shape and monolete laesura.

### 3.2.4 Ferns

#### 3.2.4.1 Marattiaceae

#### **Genus *Marattisporites* Couper 1958**

**Type species:** *Marattisporites scabratus* Couper 1958.

**Diagnosis:** see Couper (1958), p. 133.

*Marattisporites scabratus* Couper 1958

Pl. 5, fig. 3

1958 *Marattisporites scabratus* Couper 1958, p. 133, pl. 15, fig. 20.

1975 *Marattisporites scabratus* Couper 1958 in Dodd 1975, p. 63, pl. 9, fig. 3.

1980 *Marattisporites scabratus* Couper 1958 in Fenton 1980, p. 144, not figured.

1993 *Marattisporites scabratus* Couper 1958 in Hogg 1993, p. 98, pl. 11, fig. 2.

1993 *Marattisporites scabratus* Couper 1958 in Boulter and Windle 1993, p. 131, pl. 4, figs. 40-48.

1996 *Marattisporites scabratus* Couper 1958 in Trout 1996, p. 86, pl. 3, fig. 6.

**Description:** see Couper (1958), p. 133.

**Remarks:** As noted by Couper (1958), a few specimens possess a faint trilete mark, but this species is typically monolete.

### 3.2.4.2 Osmundaceae

#### Genus *Baculatisporites* Thomson and Pflug 1953

**Type species:** *Baculatisporites (Sporites) primarius* (Wolff 1934) Thomson and Pflug 1953.

**Diagnosis:** see Thomson and Pflug (1953), p. 56.

*Baculatisporites (Trilites) comaumensis* (Cookson 1953) Potonié 1956

Pl. 5, fig. 4

- 1953 *Trilites comaumensis* Cookson 1953, p. 470, pl. 2, figs. 27-28.
- 1956 *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956, p. 33, pl. 3, fig. 31.
- 1975 *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956 in Wilkinson 1975, p. 70, pl. 3, fig. 5.
- 1979 *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956 in Al-Jubori 1979, p. 44, pl. 1, figs. 10, 11.
- 1979 *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956 in Cadman 1979, p. 36, pl. 1, fig. 12.
- 1980 *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956 in Fenton 1980, p. 95, pl. 2, fig. 8.
- 1983 *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956 in Stronach 1983, p. 21, pl. 3, figs. 11, 12.
- 1993 *Baculatisporites comaumensis* Cookson 1953 ex Potonié 1956 in Hogg 1993 p. 96, pl. 10, fig. 10.
- 2011 *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956 in Srivastava 2011, p. 147, pl. 1, figs. 1, 2.

**Description:** see Cookson (1953), p. 470.

**Remarks:** Differs from *Conbaculatisporites mesozoicus* in possessing a circular to sub-circular equatorial contour.

#### Genus *Osmundacidites* Couper 1953

**Type species:** *Osmundacidites wellmanii* Couper 1953.

**Diagnosis:** see Couper (1953), p. 20.

*Osmundacidites wellmanii* Couper 1953

Pl. 5, fig. 5

- 1953 *Osmundacidites wellmanii* Couper 1953, p. 20, pl. 1, fig. 5.  
1958 *Osmundacidites wellmanii* Couper 1953 in Couper 1958, p. 134, pl. 16, figs. 4, 5.  
1975 *Osmundacidites wellmanii* Couper 1953 in Dodd 1975, p. 52, pl. 4, fig. 14.  
1975 *Osmundacidites wellmanii* Couper 1953 in Wilkinson 1975, p. 68, pl. 3, figs. 7, 8.  
1979 *Osmundacidites wellmanii* Couper 1953 in Al-Jubori 1979, p. 54, pl. 2, figs. 10, 11.  
1979 *Osmundacidites wellmanii* Couper 1953 in Cadman 1979, p. 41, pl. 1, fig. 18.  
1980 *Osmundacidites wellmanii* Couper 1953 in Fenton 1980, p. 94, pl. 2, fig. 7.  
1983 *Osmundacidites wellmanii* Couper 1953 in Stronach 1983, p. 24, pl. 3, figs. 8, 9.  
1993 *Osmundacidites wellmanii* Couper 1953 in Hogg 1993, p. 96, pl. 10, fig. 11.  
1993 *Osmundacidites* spp. Couper 1953 in Boulter and Windle 1993, p. 131, pl. 5, figs. 1-32.

**Description:** see Couper (1953), p. 20.

**Remarks:** Conspicuous species, recognisable from the rounded equatorial contour, granular-papillate sculpture, and typical dark brown colour in these deposits.

**Genus *Todisporites* Couper 1958**

**Type species:** *Todisporites major* Couper 1958.

**Diagnosis:** see Couper (1958), p. 134.

*Todisporites major* Couper 1958

Pl. 5, figs. 6, 7

- 1958 *Todisporites major* n. gen. n. sp. in Couper 1958, p. 134, pl. 16, figs. 6-8.  
1975 *Todisporites major* Couper 1958 in Dodd 1975, p. 32, pl. 2, fig. 1.  
1975 *Todisporites major* Couper 1958 in Wilkinson 1975, p. 65, pl. 1, fig. 15.  
1979 *Todisporites major* Couper 1958 in Cadman 1979, p. 35, pl. 1, fig. 9.  
1980 *Todisporites major* Couper 1958 in Fenton 1980, p. 85, pl. 1, fig. 7.  
1983 *Todisporites major* Couper 1958 in Stronach 1983, p. 19, pl. 1, fig. 7.  
1993 *Punctatisporites major* (Couper 1958) Kedves and Simoncsics 1964 in Hogg 1993, p. 69, pl. 3, fig. 14.

**Description:** see Couper (1958), p. 134.

**Remarks:** Identified from *Todisporites minor* by its larger size.

*Todisporites minor* Couper 1958

Pl. 5, figs. 8, 9

- 1958 *Todisporites minor* Couper 1958, p. 135, pl. 16, figs. 9, 10.  
1975 *Todisporites rotundiformis* (Mal.) Pocock 1970 in Dodd 1975, p. 32, not figured.  
1958 *Todisporites minor* Couper 1958 in Wilkinson 1975, p. 64, pl. 1, figs. 13, 14.  
1979 *Todisporites minor* Couper 1958 in Cadman 1979, p. 35, pl. 1, figs. 10, 11.  
1980 *Todisporites minor* Couper 1958 in Fenton 1980, p. 85, pl. 1, fig. 6.  
1983 *Todisporites minor* Couper 1958 in Stronach 1983, p. 20, pl. 1, fig. 8.  
1993 *Punctatisporites minor* (Couper 1958) Brenner 1986 in Hogg 1993, p. 70, pl. 3 fig. 15.

**Description:** see Couper (1958), p. 135.

**Remarks:** Identified from *Todisporites major* by its smaller size.

**3.2.4.3 Gleicheniaceae**

**Genus *Gleicheniidites* Ross 1949**

**Type species:** *Gleicheniidites senonicus* Ross 1949.

**Diagnosis:** see Ross (1949), p. 31.

*Gleicheniidites senonicus* Ross 1949

Pl. 5, fig. 10

- 1949 *Gleicheniidites senonicus* Ross 1949, p. 31, pl. 1, fig. 3.  
1958 *Gleicheniidites senonicus* Ross 1949 in Couper 1958, p. 138, pl. 19, figs. 13-15.  
1975 *Gleicheniidites senonicus* Ross 1949 in Dodd 1975, p. 44, pl. 3, fig. 5.  
1979 *Gleicheniidites senonicus* Ross 1949 in Al-Jubori 1979, p. 65, pl. 3, fig. 6.  
1980 *Gleicheniidites senonicus* Ross 1949 in Fenton 1980, p. 128, pl. 6, fig. 6.  
1983 *Gleicheniidites senonicus* Ross 1949 emend Skarby 1964 in Stronach 1983, p. 32, pl. 1, figs. 5, 6.  
1993 *Gleicheniidites senonicus* Ross 1949 in Hogg 1993, p. 68, pl. 3, fig. 10.  
1993 *Gleicheniidites senonicus* Ross 1949 in Boulter and Windle 1993, p. 132, pl. 8, figs. 1-14.  
1996 *Gleicheniidites senonicus* Ross 1949 in Trout 1996, p. 86, pl. 3, fig. 7.  
2011 *Gleicheniidites senonicus* Ross 1949 in Srivastava 2011, p. 153, pl. 4, figs. 4, 5.

**Description:** see Ross (1949), p. 31.

**Remarks:** Distinguished from *Dictyophyllidites harrisii* and *Deltoidospora minor* by the presence of sharp apices between which the exine thickens.

#### 3.2.4.4 Dipteridaceae

##### Genus *Conbaculatisporites* Klaus 1960

**Type species:** *Conbaculatisporites mesozoicus* Klaus 1960.

**Diagnosis:** see Klaus (1960), p. 125.

*Conbaculatisporites mesozoicus* Klaus 1960

Pl. 5, fig. 11

1960 *Conbaculatisporites mesozoicus* sp. nov. in Klaus 1960, p. 125, pl. 29, fig. 15.

**Description:** see Klaus (1960), p. 125.

**Remarks:** *Conbaculatisporites mesozoicus* often possesses long spines up to 4 µm in length and has a triangular equatorial contour, unlike *Baculatisporites comaumensis*, which is circular to sub-circular.

#### 3.2.4.5 Dipteridaceae/Matoniaceae

##### Genus *Concavisporites* Pflug in Thomson and Pflug 1953 emend. Delcourt and Sprumont 1955

**Type species:** *Concavisporites rugulatus* Pflug in Thomson and Pflug 1953.

**Diagnosis:** see Delcourt and Sprumont (1955), p. 22.

**Remarks:** The present author follows Delcourt and Sprumont (1955) in restricting *Concavisporites* to refer to spores that are smooth, have a concavely triangular amb and possess a torus along the trilete mark.

*Concavisporites* sp. Delcourt and Sprumont 1955

Pl. 5, fig. 12

1993 *Concavisporites* spp. Pflug, 1952 in Boulter and Windle 1993, p. 131, pl. 137, figs. 33-43.

**Diagnosis:** see Delcourt and Sprumont (1955), p. 22.

**Remarks:** Differs from *Concavissimisporites punctatus* and *Concavissimisporites subgranulosus* in having a psilate surface.

*Concavisporites* sp. 1

Pl. 5, fig. 13

**Description:** Trilete, laevigate, amb triangular. Laesurae are straight with prominent labra that flare and extend across the margin of the amb. Labra are 1.5-2 times wider than the margin of the amb.

**Remarks:** Singular specimen. Differs from *Concavisporites* sp. in that labra flare and extend across the margin of the amb.

**Genus *Dictyophyllidites* Couper 1958**

**Type species:** *Dictyophyllidites harrisii* Couper 1958.

**Diagnosis:** see Couper (1958), p. 140.

*Dictyophyllidites (Matonisporites) equiexinus* (Couper 1958) Dettmann 1963

Pl. 5, fig. 14

1958 *Matonisporites equiexinus* n. gen. n. sp. Couper 1958, p. 140, pl. 20, figs. 13, 14.

1963 *Dictyophyllidites equiexinus* (Couper 1958) comb. nov. in Dettmann 1963, p. 27.

1975 *Harrispora equiexina* Couper 1958 in Dodd 1975, p. 140, pl. 20, figs. 13, 14.

1993 *Dictyophyllidites equiexinus* (Couper 1958) Dettmann 1963 in Hogg 1993, p. 71, pl. 4, fig. 1.

1993 *Deltoideospora equiexinus* (Couper 1958) Muir 1964 in Boulter and Windle 1993, p. 132, pl. 7, figs. 1-10.

2011 *Dictyophyllidites equiexinus* (Couper 1958) Dettmann 1963 in Srivastava 2011, p. 152, pl. 3, fig. 9.

**Description:** see Couper (1958), p. 140.

**Remarks:** The present author follows Dettmann (1963) in incorporating non-valvate spores of *Matonisporites* into *Dictyophyllidites*.

*Dictyophyllidites harrisii* Couper 1958

Pl. 5, fig. 15

- 1958 *Dictyophyllidites harrisii* n. sp. Couper 1958, p. 140, pl. 21, fig. 6.  
1975 *Deltoidospora harrisii* Couper 1958 in Dodd 1975, p. 22, pl. 1, figs. 8-10.  
1975 *Dictyophyllidites harrisii* Couper 1958 in Wilkinson 1975, p. 60, pl. 2, figs. 1-3.  
1979 *Dictyophyllidites harrisii* Couper 1958 in Al-Jubori 1979, p. 42, pl. 3, figs. 10, 12, 13.  
1979 *Dictyophyllidites harrisii* Couper 1958 in Cadman 1979, p. 34, pl. 1, figs. 7, 8.  
1980 *Dictyophyllidites harrisii* Couper 1958 in Fenton 1980, p. 84, pl. 1, fig. 8.  
1983 *Dictyophyllidites harrisii* Couper 1958 in Stronach 1983, p. 19, pl. 1, fig. 3.  
1993 *Dictyophyllidites harrisii* Couper 1958 in Hogg 1993, p. 71, pl. 4, fig. 2.  
1993 *Dictyophyllidites harrisii* Couper 1958 in Boulter and Windle 1993, p. 132, pl. 7, figs. 11-21.

**Description:** see Couper (1958), p. 140.

**Remarks:** Differs from *Deltoidospora minor* in having raised commissures and a distinct margo.

**3.2.4.6 Matoniaceae**

**Genus *Matonisorites* Couper 1958 emend. Dettmann 1963**

**Type species:** *Matonisorites phlebopteroides* Couper 1958.

**Diagnosis:** see Dettmann (1963), p. 58.

**Remarks:** The preset author follows Dettmann (1963) in restricting *Matonisorites* to include only smooth trilete spores with a valvae.

*Matonisorites phlebopteroides* Couper 1958

Pl. 5, fig. 16

- 1958 *Matonisorites phlebopteroides* n. sp. Couper 1958, p. 140, pl. 20, figs. 15-17.  
1993 *Matonisorites phlebopteroides* Couper 1958 in Hogg 1993, p. 73, pl. 4, fig. 3.  
2011 *Matonisorites phlebopteroides* Couper 1958 in Srivastava 2011, p. 156, pl. 5, fig. 8.

**Description:** see Couper (1958), p.140.

**Remarks:** Highly conspicuous species, recognised by the presence of elongated valvae.

*Matonisorites* cf. *phlebopteroides* Couper 1958

Pl. 5, fig. 17

**Description:** see Couper (1958), p.140.

**Remarks:** Differs from *Matonisorites phlebopteroides* in possessing a more prominent concave equatorial contour and a thicker exine.

### 3.2.4.7 Schizaeaceae

#### Genus *Contignisorites* Dettmann 1963

**Type species:** *Contignisorites glebulentus* Dettmann 1963.

**Diagnosis:** see Dettmann (1963), p. 73.

*Contignisorites* sp. Dettmann 1963

Pl. 5, fig. 18

1993 *Contignisorites* spp. Dettman 1963 in Boulter and Windle 1993, p. 131, pl. 3, figs. 59-64.

**Diagnosis:** see Dettmann (1963), p. 73.

**Remarks:** Differs from *Duplexisorites* in that parallel muri on the distal face arise directly from the cingulum, in *Duplexisorites* the outer murus is parallel to the spore equatorial contour.

#### Genus *Duplexisorites* Deák 1962

**Type species:** *Duplexisorites generalis* Deák 1962.

**Diagnosis:** see Deák (1962), p. 232.

*Duplexisorites* (*Cingulatisporites*) *problematicus* (Couper 1958) Playford and Dettmann

1965

Pl. 5, fig. 19

1958 *Cingulatisporites problematicus* n. sp. Couper 1958, p. 146, pl. 24, figs. 11-13.

1965 *Duplexisorites problematicus* (Couper 1958) comb. nov. in Playford and Dettmann 1965, p. 140.



- 1975 *Corrugatisporites amplexiformis* (Kara-Murza) Pocock 1970 in Dodd 1975, p. 55, pl. 6, figs. 1-2.
- 1975 *Duplexisporites problematicus* (Couper 1958) Playford and Dettmann 1965 in Wilkinson 1975, p. 102, pl. 4, fig. 15.
- 1979 *Duplexisporites problematicus* (Couper 1958) Playford and Dettmann 1965 in Cadman 1979, p. 52, pl. 2, fig. 10.
- 1980 *Duplexisporites problematicus* (Couper 1958) Playford and Dettmann 1965 in Fenton 1980, p. 117, pl. 5, fig. 8.
- 1983 *Duplexisporites problematicus* (Couper 1958) Playford and Dettmann 1965 in Stronach 1983, p. 25, pl. 2, figs. 7, 8.
- 1993 *Duplexisporites problematicus* (Couper 1958) Playford and Dettmann 1965 in Boulter and Windle 1993, p. 131, pl. 4, figs. 20-33.
- 2011 *Duplexisporites problematicus* (Couper 1958) Playford and Dettmann 1965 in Srivastava 2011, p. 152, pl. 4, fig. 2.

**Description:** see Couper (1958), p. 146.

**Remarks:** Differs from *Contignisporites* in that the outer murus is parallel to the spore equatorial contour in *Duplexisporites*.

### **Genus *Ischyosporites* Balme 1957**

- 1958 *Klukisporites* Couper 1958, p. 137.

**Type species:** *Ischyosporites crateris* Balme 1957.

**Diagnosis:** see Balme (1957), p. 23.

#### *Ischyosporites* sp. Balme 1957

Pl. 6, fig. 1

- 1993 *Ischyosporites* spp. Balme 1957 in Boulter and Windle 1993, p. 132, pl. 8, figs. 15-46.

**Diagnosis:** see Balme (1957), p. 23.

**Remarks:** Highly conspicuous genera recognised from the distinctive foveo-reticulate ornamentation. Numerous authors (e.g. Schulz 1967; Tralau 1968; Guy 1971) have considered *Ischyosporites* and *Klukisporites* to be synonymous based on their similar foveo-reticulate ornamentation.

### 3.2.4.8 Schizaeaceae/Cyatheaceae/Dicksoniaceae/Matoniaceae

#### Genus *Trilobosporites* Pant 1954 ex Potonié 1956

**Type species:** *Trilobosporites (Concavisporites) hannonicus* (Delcourt and Sprumont 1955) Potonié 1956 (designated Potonié 1956).

**Diagnosis:** see Potonié (1956), p. 55.

*Trilobosporites* sp. Pant 1954 ex Potonié 1956

Pl. 6, fig. 2

**Diagnosis:** see Potonié (1956), p. 55.

**Remarks:** Single specimen recovered. Distinguished from *Concavissimisporites* by possessing valvae.

### 3.2.4.9 Cyatheaceae/Dicksoniaceae/Gleicheniaceae

#### Genus *Cibotiumspora* (Maljavkina 1949) Chang 1965

**Type species:** *Cibotiumspora (Tripartina) paradoxa* (Maljavkina 1949) Chang 1965.

**Diagnosis:** see Chang (1965), p. 165.

*Cibotiumspora (Concavisporites) jurienensis* (Balme 1957) Filatoff 1975

Pl. 6, figs. 3, 4

1957 *Concavisporites jurienensis* Balme 1957, p. 20, pl. 2, fig. 30.

1975 *Cibotiumspora jurienensis* (Balme 1957) comb. nov. in Filatoff 1975, p. 61, pl. 10, figs. 8-13.

1975 *Concavisporites jurienensis* Balme 1957 in Dodd 1975, p. 28, pl. 3, fig. 1

1975 *Cibotiumspora jurienensis* (Balme 1957) Filatoff 1975 in Cadman 1979 p. 31, pl. 1, figs. 1, 2.

1980 *Cibotiumspora jurienensis* (Balme 1957) Filatoff 1975 in Fenton 1980, p. 87, pl. 1, fig. 5.

1993 *Cibotiumspora jurienensis* (Balme 1957) Filatoff 1975 in Hogg 1993, p. 67, pl. 3, fig. 5.

2011 *Obtusisporis jurienensis* (Balme 1957) Srivastava 1987 in Srivastava 2011, p. 157, pl. 6, figs. 2, 3.

**Description:** see Balme (1957), p. 20.

**Remarks:** Conspicuous species from folds across apices.

### 3.2.4.10 Dicksoniaceae

#### Genus *Obtusisporis* Krutzsch 1954

**Type species:** *Obtusisporis (Sporites) obtusangulus* (Potonié 1934) Krutzsch 1954.

**Diagnosis:** see Krutzsch (1954), p. 296.

#### *Obtusisporis canadensis* Pocock 1970

Pl. 6, fig. 5

1970 *Obtusisporis canadensis* n. sp. Pocock 1970, p. 35, pl. 5, figs. 22, 23.

1980 *Obtusisporis* cf. *canadensis* Pocock 1970 in Riding 1980, p. 118, not figured.

1993 *Obtusisporis canadensis* Fensome 1987 in Boulter and Windle 1993, p. 132, pl. 7, figs. 46-52.

**Description:** see Pocock (1970), p. 35.

**Remarks:** Conspicuous species, recognised by the unusual exine structure which produces anastomosing, bifurcating lines of thinned exine.

### 3.2.4.11 Cyatheaceae/Dicksoniaceae

#### Genus *Concavissimisorites* (Delcourt and Sprumont 1955) Delcourt *et al.*, 1963

**Type species:** *Concavissimisorites (Concavisporites) verrucosus* (Delcourt and Sprumont 1955) Delcourt *et al.*, 1963.

**Diagnosis:** see Delcourt *et al.*, (1963), p. 284.

#### *Concavissimisorites (Concavisporites) punctatus* (Delcourt and Sprumont 1955) Brenner

1963

Pl. 6, fig. 6

1955 *Concavisporites punctatus* Delcourt and Sprumont 1955, p. 25, pl. fig. 8, pl. 2, fig. 2.

1958 *Concavisporites punctatus* Delcourt and Sprumont 1955 in Couper 1958, p. 142, pl. 22, figs. 1-3.

1963 *Concavissimisorites punctatus* (Delcourt and Sprumont 1955) in Brenner 1963, p. 59, pl. 14, fig. 6.

**Description:** see Delcourt and Sprumont (1955), p. 25.

**Remarks:** Distinguished from *Concavissimisorites subgranulosus* by its strongly concave equatorial contour and less sculptured ornament.

*Concavissimisorites (Concavisporites) subgranulosus* (Couper 1958) Pocock 1970

Pl. 6, fig. 7

- 1958 *Concavisporites subgranulosus* n. sp. Couper 1958, p. 143, pl. 22, fig. 6.  
1970 *Concavissimisorites subgranulosus* (Couper 1958) n. comb. in Pocock 1970, p. 41, pl. 7, fig. 24.  
1975 *Concavissimisorites subgranulosus* (Couper 1958) Pocock 1970 in Dodd 1975, p. 53, pl. 4, fig. 4.  
1980 *Microreticulatisporites fuscus* (Nilsson 1958) Morbey 1975 in Fenton 1980, p. 112, pl. 4, fig. 10.  
1983 *Concavissimisorites subgranulosus* (Couper 1958) Pocock 1970 in Stronach 1983, p. 22, pl. 1, fig. 9.  
1993 *Granulatisporites subgranulosus* (Couper 1958) n. comb. in Hogg 1993, p. 86, pl. 7, fig. 15.

**Description:** see Couper (1958), p. 143.

**Remarks:** Distinguished from *Concavissimisorites punctatus* by its more triangular equatorial contour and highly sculptured granular ornament.

*Concavissimisorites (Concavisporites) variverrucatus* (Couper 1958) Brenner 1963

Pl. 6, figs. 8, 9

- 1958 *Concavisporites variverrucatus* n. sp. Couper 1958, p. 142, pl. 22, figs. 4, 5.  
1963 *Concavissimisorites variverrucatus* (Couper 1958) in Brenner 1963, p. 59, pl. 14, fig. 4.  
1975 *Concavissimisorites verrucosus* Delcourt and Sprumont 1955 in Dodd 1975, p. 52, pl. 4, figs. 1-3.  
1975 *Concavissimisorites verrucosus* (Delcourt and Sprumont 1955) Delcourt, Dettmann and Hughes 1963 in Wilkinson 1975, p. 66, pl. 2, figs. 12-16, pl. 3, figs. 1-3.  
1979 *Concavissimisorites verrucosus* Delcourt and Sprumont 1955 emend. Delcourt, Dettmann and Hughes 1963 in Al-Jubori 1979, p. 46, pl. 2, figs. 1-3.  
1979 *Concavissimisorites verrucosus* (Delcourt and Sprumont 1955) Delcourt *et al.*, 1963 in Cadman 1979, p. 38, pl. 1, fig. 14.  
1980 *Concavissimisorites verrucosus* Couper 1958 comb. nov. in Fenton 1980, p. 90, pl. 2, fig. 1.  
1983 *Concavissimisorites verrucosus* Delcourt and Sprumont 1955 in Stronach 1983, p. 22, pl. 1, figs. 10-12.  
1993 *Tuberositriteles variverrucatus* (Couper 1958) Döring 1964, in Hogg 1993, p. 88, pl. 8, fig. 7.  
1996 *Concavissimisorites variverrucatus* (Couper) Brenner 1963 in Trout 1996, p. 105, pl. 6, fig. 1.

**Description:** see Couper (1958), p. 142.

**Remarks:** Conspicuous species recognised from rounded verrucae present on proximal and distal surfaces. The overall spore size and distribution of verrucae is highly variable in this

species. None of the specimens found here had an equatorial diameter of over 68 µm, thus this species has not been synonymised with *Concavissimisporites verrucosus*, which is considerably larger (Delcourt *et al.*, 1963).

### **Genus *Deltoidospora* Miner 1935**

1953 *Cyathidites* Couper 1953, p. 27.

**Type species:** *Deltoidospora hallii* Miner 1935 (subsequent designation by Potonié 1956).

**Diagnosis:** see Miner (1935), p. 618.

#### *Deltoidospora (Cyathidites) australis* (Couper 1953) Pocock 1970

##### Pl. 6, fig. 10

1953 *Cyathidites australis* Couper 1953, p. 27, pl. 2, figs. 11, 12.

1958 *Cyathidites australis* Couper 1953 in Couper 1958, p. 138, pl. 20, fig. 8.

1970 *Deltoidospora australis* Couper var. *rimalis* Balme (n. comb.) in Pocock 1970, p. 28, pl. 5, fig. 28.

1975 *Deltoidospora australis* Couper 1953 in Dodd 1975, p. 23, pl. 1, fig. 1.

1975 *Deltoidospora australis* (Couper 1953) Pocock 1970 in Wilkinson 1975, p. 47, pl. 1, figs. 1, 2.

1979 *Cyathidites australis* Couper 1958 in Al-Jubori 1979, p. 35, pl. 1, fig. 3.

1979 *Cyathidites australis* Couper 1953 in Cadman 1979, p. 32, pl. 1, fig. 4.

1980 *Deltoidospora australis* (Couper 1953) Pocock 1970 in Fenton 1980, p. 82, pl. 1, fig. 1.

1983 *Cyathidites australis* Couper 1953 in Stronach 1983, p. 18, pl. 1, fig. 1.

1993 *Deltoidospora australis* (Couper 1953) Pocock 1970 in Hogg 1993, p. 66, pl. 3, fig. 4.

1993 *Deltoidospora australis* (Couper 1953) Pocock 1970 in Boulter and Windle 1993, p. 132, pl. 14-33.

2011 *Deltoidospora australis* (Couper 1953) Srivastava 1977 in Srivastava 2011, p. 151, pl. 3, fig. 5.

**Description:** see Couper (1953), p. 27.

**Remarks:** Differs from *Deltoidospora minor* by its larger size.

#### *Deltoidospora (Stenozonotriletes) concavus* (Bolkhovitina 1953) Dettmann 1963

##### Pl. 6, fig. 11

1953 *Stenozonotriletes concavus* Bolkhovitina 1953, p. 64, pl. 6, fig. 7.

1963 *Cyathidites concavus* (Bolkhovitina 1953) Dettman 1963, p. 24, pl. 1, fig. 17-19.

- 1975 *Deltoidospora concavus* (Bolkhovitina 1953) Dettman 1963 in Dodd 1975, p. 23, pl. 1, fig. 7
- 1980 *Deltoidospora concavus* Bolkhovitina 1953 comb. nov. in Fenton 1980, p. 83, pl. 1, fig. 4.
- 1979 *Cyathidites concavus* (Bolkhovitina 1953) Dettman 1963 in Al-Jubori 1979, p. 37, pl. 1, fig. 5.
- 1993 *Waltzisporea concava* (Bolkhovitina 1953) n. comb. in Hogg 1993, p. 70, pl. 3, fig. 11.
- 1993 *Deltoidospora concavus* Bolchovitina 1956 in Boulter and Windle 1993, p. 132, pl. 6, figs. 34-38.

**Description:** see Bolkhovitina (1953), p. 64.

**Remarks:** Differs from other *Deltoidospora* species in possessing a distinctive strongly concave triangular equatorial contour. Note that ‘Bolchovitina 1956’ from Boulter and Windle (1993) is an incorrect spelling of ‘Bolkhovitina (1956)’, in the reference list here, this is listed as Bolkhovitina (1956).

*Deltoidospora* (*Cyathidites*) *minor* (Couper 1953) Pocock 1970

Pl. 6, figs. 12, 13

- 1953 *Cyathidites minor* Couper 1953, p. 28, pl. 2, fig. 13.
- 1958 *Cyathidites minor* Couper 1953 in Couper 1958, p. 139, pl. 20, figs. 9, 10.
- 1970 *Deltoidospora minor* Couper 1953 in Pocock 1970, p. 28, pl. 5, fig. 3.
- 1975 *Deltoidospora minor* Couper 1953 in Dodd 1975, p. 22, pl. 1, figs. 2-4.
- 1975 *Deltoidospora minor* (Couper 1953) Pocock 1970 in Wilkinson 1975, p. 49, pl. 1, figs. 3-8.
- 1979 *Cyathidites minor* Couper 1953 in Al-Jubori 1979, p. 38, pl. 1, figs. 2, 6, 7, 9.
- 1979 *Cyathidites minor* Couper 1953 in Cadman 1979, p. 33, pl. 1, fig. 3.
- 1980 *Deltoidospora minor* (Couper 1953) Pocock 1970 in Fenton 1980, p. 83, pl. 1, figs. 2, 3.
- 1983 *Cyathidites minor* Couper 1953 in Stronach 1983, p. 18, pl. 1, fig. 2.
- 1993 *Deltoidospora minor* (Couper 1953) Pocock 1970 in Hogg 1993, p. 67, pl. 3, fig. 2 and 3.
- 2011 *Deltoidospora minor* (Couper 1953) Pocock 1970 in Srivastava 2011, p. 151, pl. 3, fig. 6.

**Description:** see Couper (1953), p. 28.

**Remarks:** Differs from *Deltoidospora australis* by its smaller size.

### 3.2.4.12 Fern spores of unknown affinity

#### Genus *Pilosisporites* Delcourt and Sprumont 1955

**Type species:** *Pilosisporites* (*Sporites*) *trichopapillosus* (Thiergart 1949) Delcourt and Sprumont 1955.

**Diagnosis:** see Delcourt and Sprumont (1955), p. 34.

*Pilosisorites brevipapillosus* Couper 1958

Pl. 7, fig. 1

1958 *Pilosisorites brevipapillosus* n. sp. Couper 1958, p. 144, pl. 22, figs. 11, 12.

1980 *Pilosisorites brevipapillosus* Couper 1958 in Fenton 1980, p. 99, pl. 3, fig 2.

1993 *Trachysporites brevipapillosus* (Couper 1958) n. comb. and emend. in Hogg 1993, p. 84, pl. 7, figs. 10, 11.

**Description:** see Couper (1958), p. 144.

**Remarks:** Conspicuous species recognised by the strongly concave equatorial contour and closely spaced, thick papillae (~1-1.5 µm in length) that cover the distal and proximal surfaces.

*Pilosisorites trichopapillosus* (Thiergart 1949) Delcourt and Sprumont 1955

Pl. 7, fig. 2

1949 *Sporites trichopapillosus* Thiergart 1949, p. 22, pl. 4, 5, fig. 18.

1955 *Pilosisorites trichopapillosus* (Thiergart) Delcourt and Sprumont 1955, p. 34, pl. 3, fig. 3.

1958 *Pilosisorites trichopapillosus* (Thiergart) Delcourt and Sprumont 1955 in Couper 1958, p. 144, pl. 23, figs. 1-3.

**Diagnosis:** see Delcourt and Sprumont (1955), p. 34.

**Remarks:** Many figured specimens in other studies (e.g. Baltes 1967) have spines confined to the corners of the spore. As mentioned by Couper (1958), specimens often have spines developed all over the spore. Specimens encountered in this study conform to this later form.

### 3.3 Gymnosperms

#### 3.3.1 Pteridospermophyta/Conifers

##### Genus *Alisporites* Daugherty 1941

**Type species:** *Alisporites opii* Daugherty 1941.

**Diagnosis:** see Daugherty (1941), p. 98.

*Alisporites (Abietinaepollenites) dunrobinensis* (Couper 1958) Orbell 1973

Pl. 8, fig. 1

1958 *Abietinaepollenites dunrobinensis* Couper 1958, p. 153, pl. 29, figs. 1, 2.

1973 *Alisporites dunrobinensis* (Couper 1958) in Orbell 1973, p. 14, pl. 1, fig. 10.

1975 *Abietinaepollenites dunrobinensis* Couper 1958 in Dodd 1975, p. 72, pl. 13, fig. 1.

1975 *Alisporites dunrobinensis* (Couper 1958) Orbell 1973 in Wilkinson 1975, p. 125, pl. 7, fig. 2.

1993 *Abietinaepollenites dunrobinensis* Couper 1958 in Hogg 1993, p. 103, pl. 15, fig. 15.

1993 *Alisporites dunrobinensis* (Couper 1958) Muir 1964 in Boulter and Windle 1993, p. 134, pl. 12, figs. 27-29.

**Description:** see Couper (1958), p. 153.

**Remarks:** Conspicuous species, significantly larger than all other bisaccate pollen in this study.

*Alisporites (Pteruchipollenites) microsaccus* (Couper 1958) Pocock 1962

Pl. 8, fig. 2

1958 *Pteruchipollenites microsaccus* n. sp. Couper 1958, p. 151, pl. 26, figs. 13, 14.

1962 *Alisporites microsaccus* (Couper 1958) comb. nov. Pocock 1962, p. 61, pl. 9, figs. 138-139.

1975 *Alisporites microsaccus* Couper 1958 in Dodd 1975, p. 74, pl. 13, fig. 10.

1979 *Alisporites microsaccus* (Couper 1958) Pocock 1962 in Al-Jubori 1979, p. 81, pl. 6, fig. 1.

1993 *Alisporites microsaccus* (Couper 1958) Pocock 1962 in Hogg 1993, p. 105, pl. 16, fig. 3.

1993 *Alisporites microsaccus* (Couper 1958) Nilsson 1958 in Boulter and Windle 1993, p. 134, pl. 12, figs. 30-34, pl. 13, figs. 1-9.

**Description:** see Couper (1958), p. 151.

**Remarks:** Conspicuous species, recognisable from the poorly developed sacci.



*Alisporites (Pteruchipollenites) thomasii* (Couper 1958) Nilsson 1958

Pl. 8, fig. 3

- 1958 *Pteruchipollenites thomasii* Couper 1958, p. 150, pl. 26, figs. 10-12.
- 1958 *Alisporites thomasii* (Couper 1958) comb. nov. in Nilsson 1958, p. 83-84, pl. 8, fig. 1.
- 1975 *Alisporites thomasii* (Couper 1958) Nilsson 1958 in Dodd 1975, p. 73, pl. 13, fig. 9.
- 1975 *Alisporites thomasii* (Couper 1958) Pocock 1962 in Wilkinson 1975, p. 123, pl. 6, figs. 11, 12.
- 1979 *Alisporites thomasii* (Couper 1958) Pocock 1962 in Al-Jubori 1979, p. 81, pl. 6, figs. 2, 3.
- 1979 *Alisporites bilateralis* Rouse 1959 in Cadman 1979, p. 60, pl. 3, fig. 5.
- 1983 *Alisporites thomasii* (Couper 1958) Pocock 1962 in Stronach 1983, p. 43, pl. 7, fig. 5.
- 1993 *Alisporites thomasii* (Couper 1958) Nilsson 1958 in Boulter and Windle 1993, p. 134, pl. 13, figs. 10-27.
- 2011 *Pteruchipollenites thomasii* Couper 1958 in Srivastava 2011, p. 165, pl. 9, figs. 13, 14.

**Description:** see Couper (1958), p. 150.

**Remarks:** Conspicuous species, recognisable from other *Alisporites* species in this study from its elliptical shape.

### 3.3.1.1 Caytoniales

#### Genus *Vitreisporites* (Leschik 1955) Jansonius 1962

**Type species:** *Vitreisporites signatus* Leschik 1955.

**Diagnosis:** see Jansonius (1962), p. 55.

*Vitreisporites (Pityopollenites) pallidus* (Reissinger 1950) Nilsson 1958

Pl. 8, fig. 4

- 1938 *Pityosporites pallidus* Reissinger 1938, p. 14, not figured.
- 1950 *Pityopollenites pallidus* (Reissinger) Reissinger 1950, p. 109, pl. 15, figs. 1-5.
- 1958 *Caytonipollenites pallidus* (Reissinger 1950) comb. nov. in Couper 1958, p. 150, pl. 26, figs. 7-8.
- 1958 *Vitreisporites pallidus* (Reissinger 1950) comb. nov. in Nilsson 1958, p. 77, pl. 7, figs. 12-14.
- 1975 *Vitreisporites pallidus* (Reissinger 1938) Nilsson 1958 in Dodd 1975, p. 75, pl. 13, fig. 7.
- 1975 *Vitreisporites pallidus* (Reissinger 1950) Nilsson 1958 in Wilkinson 1975, p. 132, pl. 7, fig. 8.
- 1979 *Vitreisporites pallidus* (Reissinger 1950) Nilsson 1958 in Al-Jubori 1979, p. 91, pl. 6, figs. 10, 11.
- 1979 *Vitreisporites pallidus* (Reissinger 1950) Nilsson 1958 in Cadman 1979, p. 62, pl. 3, fig. 7.

- 1993 *Vitreisporites pallidus* (Reissinger 1950) Nilsson 1958 in Hogg 1993, p. 107, pl. 16, fig. 6.
- 1993 *Vitreisporites pallidus* (Reissinger 1950) Nilsson 1958 in Boulter and Windle 1993, p. 133, pl. 12, figs. 9-11.
- 2011 *Vitreisporites pallidus* (Reissinger 1950) Nilsson 1958 in Srivastava 2011, p. 165, pl. 9, fig. 15.

**Description:** see Reissinger (1950), p. 109.

**Remarks:** Highly conspicuous species due to its relatively small size.

### 3.3.2 Conifers

#### 3.3.2.1 Pinaceae

##### Genus *Pityosporites* Seward 1914 emend. Manum 1960

**Type species:** *Pityosporites antarcticus* Seward 1914.

**Diagnosis:** see Manum (1960), p. 14.

*Pityosporites (Piceae-pollenites) microalatus* (Potonié 1931) Thomson and Pflug 1953

Pl. 8, fig. 5

- 1931 *Piceae-pollenites microalatus* Potonié 1931, p. 5, fig. 34.
- 1953 *Pityosporites microalatus* (Potonié 1931) Thomson and Pflug 1953, p. 67, pl. 5, figs. 51, 57.
- 1958 *Abietinaepollenites microalatus* Potonié in Couper 1958, p. 152, pl. 28, figs. 11-13.
- 1975 *Abietinaepollenites microalatus* Potonié 1951 in Dodd 1975, p. 71, pl. 12, figs. 8-9.
- 1975 *Pityosporites microalatus* (Potonié 1931) Thomson and Pflug 1953 in Wilkinson 1975, p. 129, pl. 7, fig. 6.
- 1979 *Abietinaepollenites microalatus* (Potonié 1931) Delcourt and Sprumont 1955 in Cadman 1979, p. 59, pl. 3, figs. 2, 3, 4.
- 1983 *Abietinaepollenites microalatus* Potonié 1951 in Stronach 1983, p. 42, pl. 7, fig. 6, pl. 8, fig. 1.
- 1993 *Pityosporites microalatus* Potonié 1931 in Boulter and Windle 1993, p. 134, pl. 14, figs. 6-13.

**Description:** see Potonié (1931), p. 34.

*Pityosporites (Abietinaepollenites) minimus* (Couper 1958) Ziaja 2006

Pl. 8, fig. 6

- 1958 *Abietinaepollenites minimus* sp. nov. Couper 1958, p. 153, pl. 28, figs. 14-15.

- 1975 *Abietineaepollenites minimus* Couper 1958 in Dodd 1975, p. 71, pl. 12, figs. 12-14.  
1993 *Pityosporites scaurus* (Nilsson) Schulz 1967 in Boulter and Windle 1993, p. 134, pl. 14, figs. 14-21.  
2006 *Pityosporites minimus* (Couper 1958) comb. nov. Ziaja 2006, p. 37, pl. 5, figs. 7-10, pl. 6, figs. 1-3.

**Description:** see Couper (1958), p. 153.

### 3.3.2.2 Podocarpaceae

#### Genus *Podocarpidites* Cookson 1947 ex Couper 1953

**Type species:** *Podocarpidites ellipticus* Cookson 1947 (designated Couper 1953).

**Diagnosis:** see Cookson (1947), p. 131.

#### *Podocarpidites ellipticus* Cookson 1947 ex Couper 1953

Pl. 8, fig. 7

- 1947 *Disaccites (Podocarpidites) elliptica* Cookson 1947, p. 131, pl. 13, figs. 5-7.  
1953 *Podocarpidites ellipticus* Cookson 1947 in Couper 1953, p. 35.  
1975 *Podocarpidites* cf. *P. ellipticus* (Cookson 1947) Couper 1953 in Wilkinson 1975, p. 134, pl. 7, fig. 9.  
1979 *Podocarpidites* cf. *P. ellipticus* (Cookson 1947) Couper 1953 in Cadman 1979, p. 61, pl. 3, fig. 6.  
1979 *Podocarpidites* cf. *P. ellipticus* (Cookson 1947) Couper 1953 in Al-Jubori 1979, p. 87, pl. 6, fig. 5.  
1979 *Podocarpidites* cf. *multesimus* (Bolkhovitina 1956) Pocock 1962 in Al-Jubori 1979, p. 88, pl. 6, fig. 7.  
1993 *Podocarpidites ellipticus* Cookson ex Couper 1953 in Hogg 1993, p. 107, pl. 16, fig. 2.  
2011 *Podocarpidites ellipticus* (Cookson 1947) Couper 1953 in Srivastava 2011, p. 164, pl. 9, figs. 10, 11.

**Description:** see Cookson (1947), p. 131.

**Remarks:** Differs from other bisaccate taxa in this study in that bladders are pendant shaped and longer than the central body.

#### Genus *Quadraeculina* Maljavkina 1949

**Type species:** *Quadraeculina anellaeformis* Maljavkina 1949 (designated Potonié 1960).

**Diagnosis:** see Srivastava (1987), p. 39.

#### *Quadraeculina anellaeformis* Maljavkina 1949

Pl. 8, fig. 8

- 1949 *Quadraeculina anellaeformis* Maljavkina 1949, p. 110, pl. 39, fig. 3.
- 1958 *Parvisaccites enigmatus* n. sp. Couper 1958, p. 154, pl. 30, figs. 3-5.
- 1975 *Quadraeculina anellaeformis* Maljavkina 1949 in Dodd 1975, p. 78, pl. 13, fig. 8.
- 1979 *Quadraeculina anellaeformis* Maljavkina 1949 in Al-Jubori 1979, p. 90, pl. 6, figs. 8, 9.
- 1993 *Ovalipollis limbata* (Maljavkina) Pocock and Jansonius 1969 in Hogg 1993, p. 106, pl. 16, fig. 8.
- 1993 *Parvisaccites enigmatus* Couper 1958 in Boulter and Windle 1993, p. 134, pl. 14, fig. 22-33.
- 2005 *Quadraeculina anellaeformis* Maljavkina 1949 in Butler *et al.*, 2005, p. 52, not figured.

**Description:** see Maljavkina (1949), p. 110.

**Remarks:** Conspicuous species, bladders tend to join at their ends so that they encircle the body.

### 3.3.2.3 Araucariaceae

#### Genus *Araucariacites* Cookson 1947 ex Couper 1953

**Type species:** *Araucariacites australis* Cookson 1947 (designated Couper 1953).

**Diagnosis:** see Cookson (1947), p. 130.

#### *Araucariacites australis* Cookson 1947

Pl. 9, fig. 1

- 1947 *Araucariacites australis* Cookson 1947, p. 130, pl. 13, fig. 3.
- 1958 *Araucariacites australis* Cookson 1947 in Couper 1958, p. 151, pl. 27, figs. 3-5.
- 1975 *Araucariacites australis* Cookson 1947 in Dodd 1975, p. 82, pl. 10, fig. 6.
- 1975 *Araucariacites australis* Cookson 1947 in Wilkinson 1975, p. 148, pl. 8, figs. 15, 16.
- 1979 *Araucariacites australis* Cookson 1947 in Al-Jubori 1979, p. 97, pl. 7, fig. 7.
- 1979 *Araucariacites australis* Cookson 1947 in Cadman 1979, p. 63, pl. 3, fig. 8.
- 1980 *Araucariacites australis* Cookson 1947 in Fenton 1980, p. 159, pl. 11, fig. 1.
- 1983 *Araucariacites australis* Cookson 1947 in Stronach 1983, p. 48, pl. 5, figs. 4, 7.
- 1993 *Araucariacites australis* Cookson 1947 in Hogg 1993, p. 98, pl. 11, fig. 9.
- 1993 *Inaperturopollenites australis* Fensome 1987 in Boulter and Windle 1993, p. 133, pl. 10, figs. 28-40, pl. 11, figs. 1-6.
- 2011 *Araucariacites australis* Cookson 1947 in Srivastava 2011, p. 161, pl. 7, fig. 11.

**Description:** see Cookson (1947), p. 130.

**Remarks:** Variable sculpture, often sub-granular, sub-papillate or scabrate. Recognised from its generally large size (typically about 70 µm in diameter) and lack of a germinal aperture.

**Genus *Callialasporites* Dev 1961**

**Holotype:** *Callialasporites (Zonalapollenites) trilobatus* (Balme 1957) Dev 1961.

**Diagnosis:** see Dev (1961), p. 48.

*Callialasporites (Zonalapollenites) dampieri* (Balme 1957) Dev 1961

Pl. 9, fig. 2

- 1957 *Zonalapollenites dampieri* Balme 1957, p. 32, pl. 8, figs. 88-90.
- 1961 *Callialasporites dampieri* (Balme 1957) in Dev 1961, p. 48, pl. 4, figs. 26, 27.
- 1975 *Callialasporites dampieri* (Balme 1957) Dev 1961 in Dodd 1975, p. 65, pl. 9, fig. 5.
- 1975 *Callialasporites dampieri* (Balme 1957) Norris 1969 in Wilkinson 1975, p. 108, pl. 5, fig. 6, 7, 8.
- 1979 *Callialasporites dampieri* (Balme 1957) Sukh-Dev 1961 in Al-Jubori 1979, p. 71, pl. 4, figs. 3-8.
- 1979 *Callialasporites dampieri* (Balme 1957) Sukh-Dev 1961 in Cadman 1979, p. 53, pl. 2, figs. 11, 12.
- 1980 *Callialasporites dampieri* (Balme 1957) Norris 1969 in Fenton 1980, p. 146, pl. 8, fig. 9.
- 1983 *Callialasporites dampieri* (Balme 1957) Sukh-Dev 1961 in Stronach 1983, p. 39, pl. 6, fig. 10.
- 1993 *Callialasporites dampieri* (Balme 1957) Dev 1961 in Hogg 1993, p. 99, pl. 11, fig. 4.
- 1993 *Callialasporites dampieri* (Balme 1957) Dev 1961 in Boulter and Windle 1993, p. 134, pl. 15, figs. 8-17.
- 2011 *Callialasporites dampieri* (Balme 1957) Dev 1961 in Srivastava 2011, p. 161, pl. 8, fig. 6, pl. 12, fig. 1.

**Description:** see Balme (1957), p. 32.

**Remarks:** Differs from *Callialasporites minus* and *C. segmentatus* in that the ratio of the corpus diameter to total diameter is smaller in *C. dampieri* (corpus diameter between ½ and ¾ of total diameter).

*Callialasporites (Tsugaepollenites) minus* (Tralau 1968) Guy 1971

Pl. 9, fig. 3

- 1968 *Tsugaepollenites minus* Tralau 1968, p. 96, pl. 13, fig. 4.
- 1971 *Callialasporites minus* (Tralau 1968) in Guy 1971, p. 61, pl. 4, figs. 17-18.

- 1975 *Callialasporites minus* (Tralau 1968) Guy 1971 in Cadman 1979, p. 54, pl. 2, fig. 13.  
 1980 *Callialasporites minus* (Tralau 1968) Guy 1971 in Fenton 1980, p. 148, pl. 9, fig. 9.  
 1993 *Callialasporites minus* (Tralau 1968) Guy 1971 in Hogg 1993, p. 99, pl. 11, fig. 6.

**Description:** see Tralau (1968), p. 96.

**Remarks:** *Callialasporites minus* is an intermediate between *C. segmentatus* and *C. dampieri* (corpus diameter between  $\frac{3}{4}$  and  $\frac{7}{8}$  of total diameter). Exoexine folding is less extensive than in *C. segmentatus*.

*Callialasporites (Zonalapollenites) segmentatus* (Balme 1957) Srivastava 1963

Pl. 9, fig. 4

- 1957 *Zonalapollenites segmentatus* Balme 1957, p. 33, pl. 9, figs. 93-94.  
 1963 *Callialasporites segmentatus* (Balme) in Srivastava 1963, p. 1323, fig. 3.  
 1975 *Callialasporites segmentatus* Balme 1957 in Dodd 1975, p. 66, pl. 9, figs. 4, 9.  
 1979 *Callialasporites segmentatus* (Balme 1957) Sukh-Dev 1961 in Al-Jubori, p. 75, pl. 5, figs. 2, 3.  
 1980 *Callialasporites segmentatus* (Balme 1957) Srivastava 1963 in Fenton 1980, p. 148, pl. 9, fig. 3.

**Description:** see Balme (1957), p. 33.

**Remarks:** The diameter of the corpus is only slightly smaller than the total diameter of *Callialasporites segmentatus* (corpus diameter approximately  $\frac{7}{8}$  of total diameter). The exoexine is convolutedly folded so that folding extends to the margin, distinguishing *C. segmentatus* from other *Callialasporites* species.

*Callialasporites (Zonalapollenites) trilobatus* (Balme 1957) Dev 1961

Pl. 9, fig. 5

- 1957 *Zonalapollenites trilobatus* Balme 1957, p. 33, pl. 8, figs. 91, 92.  
 1961 *Callialasporites trilobatus* (Balme) in Dev 1961, p. 48, pl. 4, figs. 28-29.  
 1975 *Callialasporites trilobatus* (Balme 1957) Dev 1961 in Dodd 1975, p. 66, pl. 9, figs. 7, 9, 10.  
 1975 *Callialasporites trilobatus* (Balme 1957) Sukh-Dev 1961 in Wilkinson 1975, p. 111, pl. 5, fig. 12, pl. 6, fig. 1-3.  
 1979 *Callialasporites trilobatus* (Balme 1957) Sukh-Dev 1961 in Al-Jubori 1979, p. 76, pl. 5, figs. 4-6.  
 1979 *Callialasporites trilobatus* (Balme 1957) Sukh-Dev 1961 in Cadman 1979, p. 55, pl. 2, fig. 14.

- 1980 *Callialasporites trilobatus* (Balme 1957) Sukh-Dev 1961 in Fenton 1980, p. 147, pl. 9, fig. 1.
- 1993 *Callialasporites trilobatus* (Balme 1957) Dev 1961 in Hogg 1993, p. 99, pl. 11, fig. 7.
- 1993 *Callialasporites trilobatus* (Balme 1957) Dev 1961 in Boulter and Windle 1993, p. 134, pl.16, figs. 1-3.
- 2011 *Callialasporites trilobatus* (Balme 1957) Dev 1961 in Srivastava 2011, p. 162, pl. 8, figs. 7, 8.

**Description:** see Balme (1957), p. 33.

**Remarks:** Differs from other *Callialasporites* species in possessing a strongly trilobite saccus and a generally darker triangular corpus.

*Callialasporites (Inaperturopollenites) turbatus* (Balme 1957) Schulz 1967

Pl. 9, fig. 6

- 1957 *Inaperturopollenites turbatus* Balme 1957, p. 31, pl. 7, fig. 85.
- 1967 *Callialasporites turbatus* (Balme) in Schulz 1967, p. 593, pl. 17, figs. 3, 4.
- 1975 *Inaperturopollenites turbatus* Balme 1957 in Dodd 1975, p. 79, pl. 10, figs. 7-8.
- 1979 *Inaperturopollenites turbatus* Balme 1957 in Al-Jubori 1979, p. 101, pl. 7, fig. 9.
- 1979 *Callialasporites turbatus* (Balme 1957) Schulz 1967 in Cadman 1979, p. 56, pl. 2, fig. 15.
- 1980 *Inaperturopollenites turbatus* Balme 1957 in Fenton 1980, p. 162, pl. 11, fig. 2
- 1983 *Callialasporites turbatus* (Balme 1957) Schulz 1967 in Stronach 1983, p. 40, pl. 7, figs. 1, 2.
- 1993 *Callialasporites turbatus* (Balme 1957) Schulz 1967 in Hogg 1993, p. 100, pl. 11, fig. 8.
- 1993 *Callialasporites turbatus* (Balme 1957) Dev 1961 in Boulter and Windle 1993, p. 134, pl. 15, figs. 1-3.
- 2011 *Balmeiopsis turbata* (Balme 1957) Srivastava 1987 in Srivastava 2011, p. 161, pl. 8, figs. 4, 5.

**Description:** see Balme (1957), p. 31.

**Remarks:** Differs from *Callialasporites dampieri* in that the exoexine is unfolded.

### 3.3.2.4 Cheirolepidiaceae

#### Genus *Classopollis* Pflug 1953 emend. Pocock and Jansonius 1961

**Type species:** *Classopollis torosus* (Reissinger 1950) Couper 1958.

**Diagnosis:** see Pocock and Jansonius (1961), p. 443.

*Classopollis (Pollenites) torosus* (Reissinger 1950) Couper 1958

Pl. 9, figs. 7, 8

- 1950 *Pollenites torosus* Reissinger 1950, p. 115, pl. 14, fig. 20.
- 1958 *Classopollis torosus* (Reissinger 1950) n. comb. in Couper 1958, p. 156, pl. 28, figs. 2-7
- 1975 *Classopollis torosus* (Reissinger 1950) Couper 1958 in Dodd 1975, p. 83, pl. 11, figs. 3-4.
- 1975 *Classopollis torosus* (Reissinger 1950) Couper 1958 emend. Morbey in Wilkinson 1975, p. 158, pl. 8, fig. 7-9, 13.
- 1979 *Classopollis torosus* (Reissinger 1950) Couper 1958 in Al-Jubori 1979, p. 95, pl. 5, figs. 11, 12.
- 1980 *Classopollis torosus* (Reissinger 1950) Balme 1957 in Fenton 1980, p. 164, pl. 11, fig. 14.
- 1993 *Corollina torosus* (Reissinger) Cornet and Traverse 1975 in Hogg 1993, p. 103, pl. 14, fig. 9.
- 1993 *Classopollis torosus* (Reissinger 1950) Balme 1957 in Boulter and Windle 1993, p. 133, pl. 10, figs. 1-27.

**Diagnosis:** see Couper (1958), p. 156.

**Remarks:** Pollen grains are originally spherical but are frequently distorted. In some specimens annular bands are present forming a zone approximately 5 to 8  $\mu\text{m}$  wide. Specimens are occasionally preserved in tetrads.

### 3.3.2.5 Taxodiaceae

#### Genus *Cerebropollenites* Nilsson 1958

**Type species:** *Cerebropollenites (Tsugaepollenites) mesozoicus* (Couper 1958) Nilsson 1958.

**Diagnosis:** see Nilsson (1958), p. 72.

*Cerebropollenites (Tsugaepollenites) mesozoicus* (Couper 1958) Nilsson 1958

Pl. 9, fig. 9

- 1958 *Tsugaepollenites mesozoicus* n. sp. Couper 1958, p. 155, pl. 30, figs. 8-10
- 1958 *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958, p. 72, pl. 6, figs. 10 and 12.
- 1975 *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958 in Dodd 1975, p. 69, pl. 11, fig. 10.
- 1975 *Tsugaepollenites mesozoicus* Couper 1958 in Wilkinson 1975, p. 105, pl. 5, figs. 1-5.
- 1979 *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958 in Al-Jubori 1979, p. 78, pl. 5, figs. 7-10.
- 1979 *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958 in Cadman 1979, p. 57, pl. 3, fig. 1.
- 1980 *Cerebropollenites macroserratus* Fenton 1980, p. 153, pl. 10, fig. 2.
- 1980 *Cerebropollenites macroverrucosus* (Thiergart 1949) Schulz 1967 in Fenton 1980, p. 153, pl. 10, fig. 2.



- 1983 *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958 in Stronach 1983, p. 38, pl. 8, figs. 8, 9.
- 1993 *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958 in Hogg 1993, p. 110, pl. 15, fig. 9.
- 1993 *Cerebropollenites macroverrucosus* Nilsson 1958 in Boulter and Windle 1993, p. 135, pl. 16, figs. 14-24.

**Description:** see Couper (1958), p. 155.

**Remarks:** Conspicuous species, recognisable from the equatorial fringe consisting of numerous twisted saccate protrusions.

### **Genus *Spheripollenites* Couper 1958**

**Type species:** *Spheripollenites scabratus* Couper 1958.

**Diagnosis:** see Couper (1958), p. 158.

#### *Spheripollenites psilatus* Couper 1958

Pl. 10, fig. 1

- 1958 *Spheripollenites psilatus* Couper 1958, p. 159, pl. 31, figs. 4-8.
- 1980 *Spheripollenites psilatus* Couper 1958 in Fenton 1980, p. 161, pl. 11, fig. 6.
- 1993 *Spheripollenites psilatus* Couper 1958 in Boulter and Windle 1993, p. 134, pl. 12, figs. 12-26.

**Description:** see Couper (1958), p. 159.

**Remarks:** Differs from *Spheripollenites scabratus* and *S. subgranulosus* in possessing smooth ornamentation.

#### *Spheripollenites scabratus* Couper 1958

Pl. 10, fig. 2

- 1958 *Spheripollenites scabratus* Couper 1958, p. 158, pl. 31, figs. 12-14.
- 1980 *Spheripollenites scabratus* Couper 1958 in Fenton 1980, p. 160, pl. 11, fig. 7.
- 1993 *Spheripollenites scabratus* Couper 1958 in Boulter and Windle 1993, p. 133, not figured.

**Description:** see Couper (1958), p. 158.

**Remarks:** Differs from *Spheripollenites subgranulosus* in possessing scabrate ornamentation.

*Spheripollenites subgranulatus* Couper 1958

Pl. 10, fig. 3

1958 *Spheripollenites subgranulatus* sp. nov. Couper 1958, p. 158, pl. 31, figs. 9-11.

1980 *Spheripollenites subgranulatus* Couper 1958 in Fenton 1980, p. 161, pl. 11, fig. 8.

**Description:** see Couper (1958), p. 158.

**Remarks:** Differs from *Spheripollenites scabratus* in possessing subgranulate ornamentation.

**Genus *Perinopollenites* Couper 1958**

**Type species:** *Perinopollenites elatoides* Couper 1958.

**Diagnosis:** see Couper (1958), p. 152.

*Perinopollenites elatoides* Couper 1958

Pl. 10, fig. 4

1958 *Perinopollenites elatoides* n. gen. n. sp. Couper 1958, p. 152, pl. 24, figs. 9-11.

1975 *Perinopollenites elatoides* Couper 1958 in Dodd 1975, p. 84, pl. 27, fig. 9.

1975 *Perinopollenites elatoides* Couper 1958 in Wilkinson 1975, p. 119, pl. 6, figs. 7-9.

1979 *Perinopollenites elatoides* Couper 1958 in Al-Jubori 1979, p. 103, pl. 8, figs. 2, 3.

1979 *Perinopollenites elatoides* Couper 1958 in Cadman 1979, p. 65, pl. 3, figs. 10, 11.

1980 *Perinopollenites elatoides* Couper 1958 in Fenton 1980, p. 152, pl. 10, fig. 1.

1983 *Perinopollenites elatoides* Couper 1958 in Stronach 1983, p. 41, pl. 6, figs. 7-9.

1993 *Perinopollenites elatoides* Couper 1958 in Hogg 1993, p. 102, pl. 15, fig. 1.

1993 *Perinopollenites elatoides* Couper 1958 in Boulter and Windle 1993, p. 135, pl. 16, figs. 25-36.

**Description:** see Couper (1958), p. 152.

**Remarks:** Conspicuous species from the loosely fitting outer wall layer.

**3.3.3 Cycadophytes/Ginkgophytes**

**Genus *Chamatosporites* (Nilsson 1958) Pocock and Jansonius 1969**

**Type species:** *Chamatosporites major* (Nilsson 1958) Pocock and Jansonius 1969.

**Diagnosis:** see Pocock and Jansonius (1969), p. 157.

*Chasmatosporites (Pollenites) apertus* (Rogalska 1954) Nilsson 1958

Pl. 10, fig. 5

- 1954 *Pollenites apertus* sp. nov. Rogalska 1954, p. 45, pl. 12, figs. 13-15.  
1958 *Chasmatosporites apertus* (Rogalska 1954) comb. nov. Nilsson 1958, p. 56, pl. 4, figs. 5-6.  
1975 *Chasmatosporites apertus* (Rogalska 1954) Nilsson 1958 in Dodd 1975, p. 87, pl. 11, fig. 11.  
1975 *Chasmatosporites apertus* (Rogalska 1954) Nilsson 1958 in Wilkinson 1975, p. 144, pl. 8, fig. 6.  
1983 *Chasmatosporites apertus* (Rogalska 1954) Nilsson 1958 in Stronach 1983, p. 50, pl. 5, figs. 1, 2.  
1993 *Chasmatosporites apertus* (Rogalska 1954) Nilsson 1958 in Hogg 1993, p. 108, pl. 15, figs. 4 and 5.

**Description:** see Rogalska (1954), p. 45.

**Remarks:** Differs from *Chasmatosporites hians* in possessing a circular to sub-circular shape and differs from *C. major* by its smaller size.

*Chasmatosporites hians* Nilsson 1958

Pl. 10, fig. 6

- 1958 *Chasmatosporites hians* sp. nov. Nilsson 1958, p. 55, pl. 4, figs. 3-4.  
1993 *Chasmatosporites hians* Nilsson 1958 in Hogg 1993, p. 108, pl. 15, fig. 6.

**Description:** see Nilsson (1958), p. 55.

**Remarks:** Differs from *Chasmatosporites apertus* in possessing an elongated oval shaped equatorial outline and sulcus.

*Chasmatosporites major* (Nilsson 1958) Pocock and Jansonius 1969

Pl. 10, fig. 7

- 1958 *Chasmatosporites major* sp. nov. Nilsson 1958, p. 54, pl. 3, figs. 10-15.  
1969 *Chasmatosporites major* Nilsson 1958, emend., Pocock and Jansonius 1969, p. 157, pl 2, figs. 44, 45.

**Description:** see Pocock and Jansonius (1969), p. 157.

**Remarks:** Differs from *Chasmatosporites apertus* by its larger size.

**Genus *Cycadopites* Wodehouse 1933 ex Wilson and Webster 1946**

**Type species:** *Cycadopites follicularis* Wilson and Webster 1946.

**Diagnosis:** see Wilson and Webster (1946), p. 274.

*Cycadopites (Monosulcites) minimus* (Cookson 1947) Pocock 1970

Pl. 10, figs. 8, 9

- 1947 *Monosulcites minimus* Cookson 1947, p. 135, pl. 15, figs. 47-50.  
1958 *Monosulcites minimus* Cookson 1947 in Couper 1958, p. 157, pl. 26, fig 23-25.  
1970 *Cycadopites minimus* (Cookson 1947) n. comb. Pocock 1970, p. 108, pl. 26, figs. 21-24, 26-28.  
1975 *Cycadopites minimus* (Cookson 1947) Muir 1963 in Dodd 1975, p. 88, pl. 12, fig. 5.  
1979 *Cycadopites minimus* (Cookson 1947) Pocock 1970 in Al-Jubori 1979, p. 93, pl. 7, figs. 3, 4.  
1979 *Monosulcites minimus* Cookson 1947 in Cadman 1979, p. 66, pl. 3, fig. 13.  
1980 *Cycadopites minimus* (Cookson 1947) Pocock 1970 in Fenton 1980, p. 154, pl. 10, fig. 4.  
1993 *Cycadopites minimus* (Cookson 1947) Pocock 1970 in Hogg 1993, p. 108, pl. 15, fig. 3.  
1993 *Cycadopites minimus* (Cookson 1947) Muir 1963 in Boulter and Windle 1993, p. 133, pl. 11, figs. 18-30.

**Description:** see Cookson (1947), p. 135.

**Remarks:** Differs from *Cycadopites carpentieri* and *C. subgranulosus* by its smaller size and smooth exine.

### 3.3.3.1 ?Bennettitales

*Cycadopites (Monosulcites) carpentieri* (Delcourt and Sprumont 1955) Singh 1964

Pl. 10, fig. 10

- 1955 *Monosulcites carpentieri* Delcourt and Sprumont 1955, p. 54, pl. 3, fig. 14.  
1958 *Monosulcites carpentieri* Delcourt and Sprumont 1955 in Couper 1958, p. 158, pl. 26, figs. 26, 27.  
1964 *Cycadopites carpentieri* (Delcourt and Sprumont 1955) n. comb. Singh 1964, p. 104, pl. 14, fig. 3.  
1975 *Cycadopites carpentieri* (Delcourt and Sprumont 1955) Muir 1963 in Dodd 1975, p. 89, pl. 12, fig. 6.  
1979 *Monosulcites carpentieri* Delcourt and Sprumont 1955 in Cadman 1979, p. 66, pl. 3, fig. 12.  
1980 *Cycadopites carpentieri* Delcourt and Sprumont 1955 comb. nov. in Fenton 1980, p. 154, pl. 10, fig. 3.  
1983 *Cycadopites carpentieri* (Delcourt and Sprumont 1955) Singh 1964 in Stronach 1983, p. 51, pl. 5, figs. 5, 6.  
1993 *Cycadopites carpentieri* (Delcourt and Sprumont 1955) Singh 1964 in Hogg 1993, p. 108, pl. 15, fig. 2.

1993 *Cycadopites carpenteri* (Delcourt and Sprumont 1955) Muir 1963 in Boulter and Windle 1993, p. 133, pl. 11, fig. 31.

**Description:** see Delcourt and Sprumont (1955), p. 54.

**Remarks:** Distinguished from *Cycadopites subgranulosus* by the absence of granulate ornamentation.

*Cycadopites (Monosulcites) subgranulosus* (Couper 1958) Clarke 1965

Pl. 10, fig. 11

1958 *Monosulcites subgranulosus* n. sp. Couper 1958, p. 158, pl. 26, figs. 28-30.

1965 *Cycadopites subgranulosus* (Couper) comb. nov. Clarke 1965, p. 312, pl. 39, figs. 16, 17.

1975 *Cycadopites subgranulosus* Couper 1958 in Dodd 1975, p. 89, pl. 12, fig. 7.

1980 *Cycadopites subgranulosus* Couper 1958 comb. nov. in Fenton 1980, p. 155, pl. 10, fig. 5.

1993 *Cycadopites subgranulosus* (Couper 1958) Clark 1965 in Boulter and Windle 1993, p. 133, not figured.

**Description:** see Couper (1958), p. 158.

**Remarks:** Distinguished from *Cycadopites carpentieri* by the presence of granulate ornamentation.

### 3.3.4 Erdtmanithecales

#### Genus *Eucommiidites* (Erdtman 1948) Potonié 1958 emend. Hughes 1961

**Type species:** *Eucommiidites (Tricolpites) troedssonii* (Erdtman 1948) Potonié 1958 emend. Hughes 1961.

**Diagnosis:** see Hughes (1961), p. 292.

*Eucommiidites (Tricolpites) troedssonii* (Erdtman 1948) Potonié 1958 emend. Hughes 1961

Pl. 10, fig. 12

1948 *Tricolpites troedssonii* Erdtman 1948, p. 267, figs. 5-10, 13-15.

1958 *Eucommiidites troedssonii* Erdtman 1948 in Potonié 1958, p. 87, pl. 10, fig. 117.

1958 *Eucommiidites troedssonii* Erdtman 1948 in Couper 1958, p. 160, pl. 31, figs. 23-27.

1961 *Eucommiidites troedssonii* (Erdtman 1948) Couper 1958 emend. Hughes 1961, p. 292, pl. 37, figs. 1-16.

1975 *Eucommiidites troedssonii* Erdtman 1948 in Dodd 1975, p. 85, pl. 12, figs. 3-4.

- 1979 *Eucommiidites troedssonii* Erdtman 1948 in Cadman 1979, p. 67, pl. 3, fig. 14.
- 1980 *Eucommiidites troedssonii* Erdtman 1948 in Fenton 1980, p. 158, pl. 11, fig. 3.
- 1993 *Eucommiidites troedssonii* Erdtman 1948 ex Couper 1958, in Hogg 1993, p. 109, pl. 15, fig. 8.
- 2011 *Eucommiidites troedssonii* (Erdtman 1948) Potonié 1958 emend. Hughes 1961 in Srivastava 2011, p. 163, pl. 9, figs. 2, 3.

**Description:** see Erdtman (1948), p. 267.

**Remarks:** Conspicuous species recognised by the presence of two distal furrows that run parallel with the sulcus.

### 3.3.5 Pollen of unknown affinity

#### Striate bisaccate sp.

Pl. 10, fig. 13, 14

**Diagnosis:** Refers to all bisaccate pollen with taeniae extending across the corpus.

**Remarks:** Striate bisaccate pollen is common in Permian and Triassic palynofloras (e.g. Hart 1966; Awatar *et al.*, 2014). Mander *et al.*, (2010) reported on *Lunatisporites rhaeticus* and *Protohaploxylinus hercynicus* from the lowermost Hettangian of East Greenland. Two specimens of striate bisaccate pollen have been recovered from Aalenian samples from Hasty Bank. These grains are potentially reworked from older strata.

#### Trisaccate sp. 1

Pl. 10, fig. 15

**Diagnosis:** Trisaccate, central body rounded to sub-triangular, sacci rounded, fine reticulation on sacci. Overall maximum diameter (including sacci) 65  $\mu\text{m}$ , inner maximum diameter (excluding sacci) 35  $\mu\text{m}$ .

**Remarks:** Single specimen. Dodd (1975) described similar specimens and named them cf. *Crustaesporites* sp. A on account of their monosaccate morphology. The specimen discussed here is considered to be trisaccate. The specimen could potentially belong to one of the following genera: *Microcachryidites*, *Dacrycarpites* or *Podosporites*, however the general shape and arrangement of sacci have proved difficult to assign the specimen to generic level.

The specimen could be an abnormal *Alisporites*. Similar such specimens are recorded by Foster and Afonin (2005). Abnormal trisaccate pollen occurs as a result of intraspecific variation (Lindström *et al.*, 1997) or environmental stress (Foster and Afonin 2005). Lindström *et al.*, (1997) recovered pollen from intact glossopterid sporangia and recovered sporadic monosaccate and trisaccate grains in sporangia dominated by bisaccate specimens.

Plate 1

Scale bar represents 20 µm

Figure 1. *Foveosporites moretonensis*, slide JP2/2ii (England finder D44/C).

Figure 2. *Nevesisporites bigranulatus*, slide SS06/04ii (England finder G43/C).

Figure 3. *Rogalskaisporites cicatricosus*, slide HB39i (England finder M38/2).

Figure 4. *Stereisporites* sp., slide JP2/1iii (England finder E30/2).

Figure 5. *Anapiculatisporites* sp., slide SS06/04ii (England finder R29/C).

Figure 6. *Densoisporites circumundulatus*, slide JP1/5i (England finder X25/2).

Figure 7. *Densoisporites velatus*, slide JP2/11ii (England finder V44/3).

Figure 8. *Densoisporites* cf. *velatus*, slide HB10i (England finder O36/C).

Figure 9. *Kraeuselisporites whitfordensis*, slide JP2/1iii (England finder X23/1).

Figure 10. *Kraeuselisporites* sp. 1, slide JP2/3iii (England finder W36/C).



Plate 1

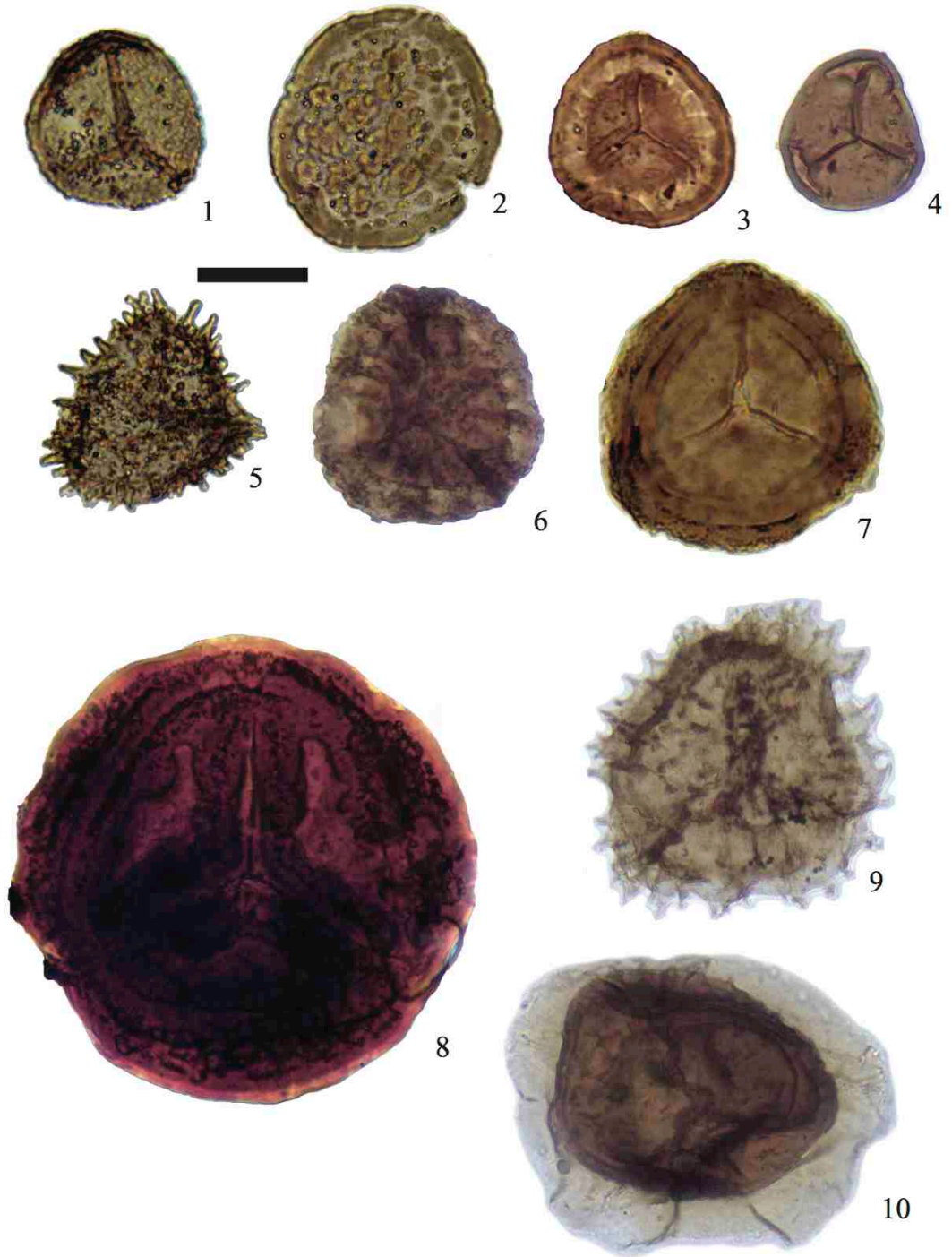


Plate 2

Scale bar represents 20  $\mu\text{m}$

Figure 1. *Lycopodiacidites cerniidites*, slide JP2/3iii (England finder C29/3).

Figure 2. *Lycopodiacidites rugulatus*, slide HB32i (England finder C49/4).

Figure 3. *Neoraistrickia truncates*, slide JP2/3ii (England finder P47/1).

Figure 4. *Retitriletes austroclavatidites*, slide JP2/5iii (England finder J42/3).

Figure 5. *Retitriletes clavatoides*, slide EW P3(2)EM (England finder G43/1).

Figure 6. *Retitriletes semimuris*, slide HB44i (England finder T34/4).

Figure 7. *Retitriletes singhii*, slide SS06/04i (England finder R46/C).

Figure 8. *Leptolepidites bossus*, slide HB34ii (England finder J37/4).

Figure 9. *Leptolepidites crassibalteus*, slide HB30i (England finder N37/2).

Figure 10. *Leptolepidites equatibossus*, slide HB40ii (England finder F34/3).

Figure 11. *Leptolepidites major*, slide JP2/1iv (England finder P31/4).

Figure 12. *Sestrosporites pseudoalveolatus*, slide JP1/3viii (T19/C).

Figure 13. *Staplinisporites* sp., slide HB40ii (England finder H22/4).

Figure 14. *Staplinisporites mathurii*, slide JP1/5i (England finder A44/4).

Figure 15. *Uvaesporites argenteaformis*, slide HB34ii (England finder N44/1).

Plate 2

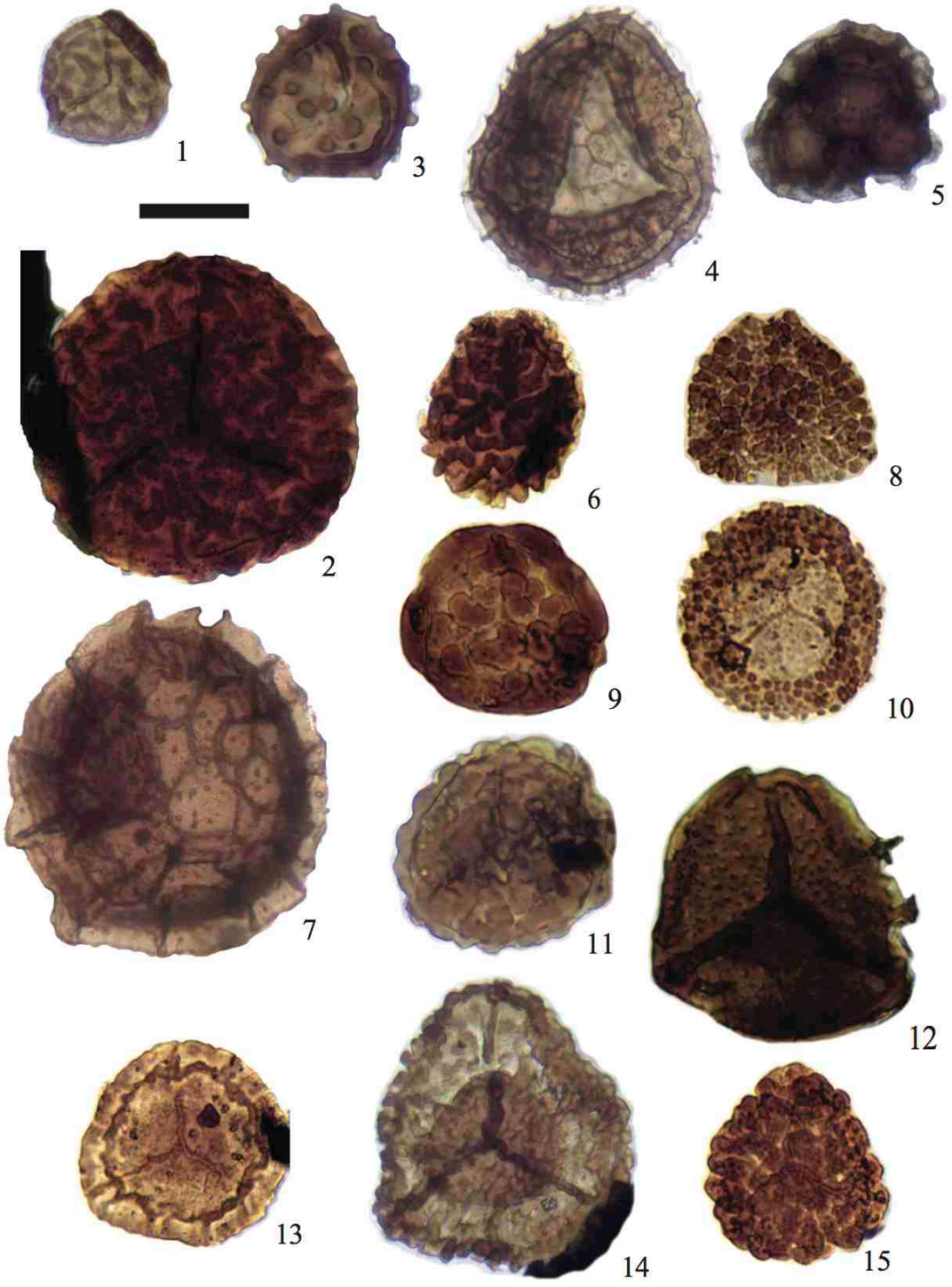


Plate 3

Scale bar represents 100  $\mu\text{m}$

Figure 1. *Paxillitriletes phyllicus*, slide JP2/3iv (England finder N35/4).

Figure 2. *Paxillitriletes phyllicus*, slide JP2/3iii (England finder O26/1).

Figure 3. *Paxillitriletes phyllicus*, slide JP2/3i (England finder U35/4).

Figure 4. *Paxillitriletes phyllicus*, slide JP2/5ii (England finder Q46/2).

Figure 5. *Paxillitriletes phyllicus*, slide JP2/3ii (England finder G24/3).

Figure 6. *Paxillitriletes phyllicus*, slide JP2/3iii (England finder H22/1).

Plate 3



1.



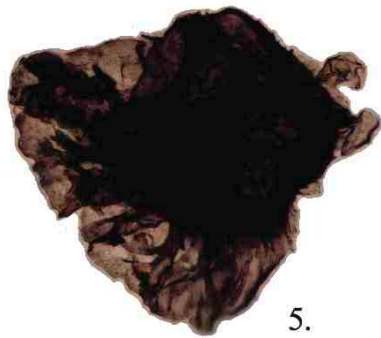
2.



3.



4.



5.



6.

Plate 4

All scale bars represent 100  $\mu\text{m}$

Figure 1. *Paxillitriletes phyllicus*, sample JP2/2, stub SS06.

Figure 2. *Paxillitriletes phyllicus*, sample JP2/2, stub SS09.

Figure 3. *Paxillitriletes phyllicus*, sample JP2/4, stub SSJP02.

Figure 4. *Paxillitriletes phyllicus*, sample JP2/3, stub SS10.

Figure 5. *Paxillitriletes phyllicus*, sample JP2/3, stub SS12.

Figure 6. *Paxillitriletes phyllicus*, sample JP2/2, stub SS06.

Plate 4

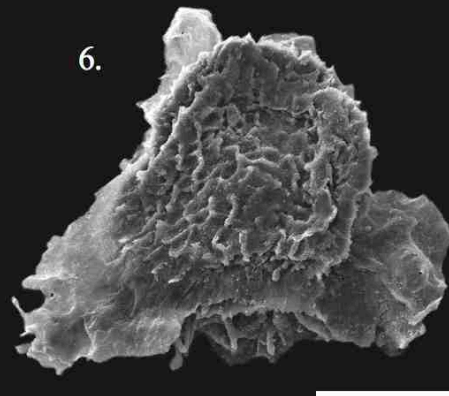
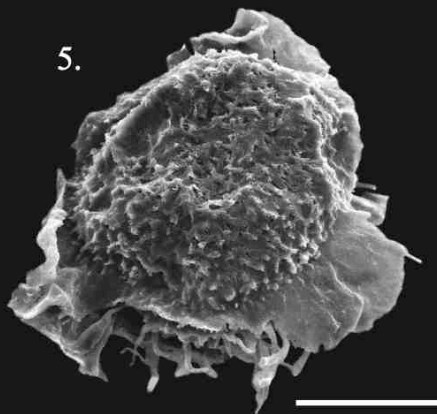
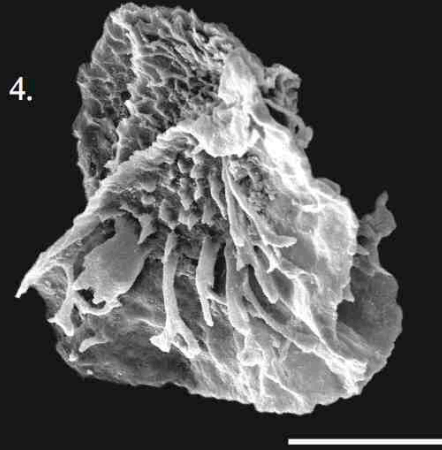
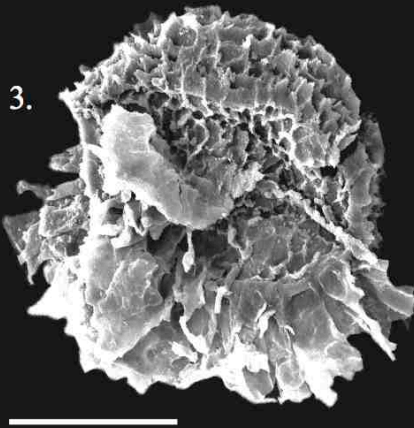
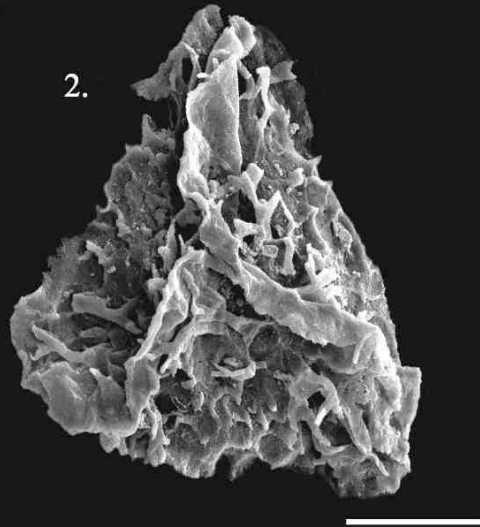
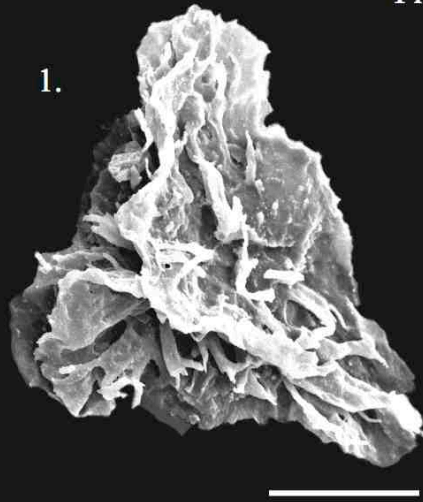


Plate 5

Scale bar represents 20 µm

Figure 1. *Calamospora mesozoica*, slide SS06/05i (England finder T37/1).

Figure 2. *Laevigatosporites* sp., slide JP2/6Aii (England finder C41/4).

Figure 3. *Marattisporites scabratus*, slide HB11ii (England finder P34/3).

Figure 4. *Baculatisporites comaumensis*, slide JP2/8ii (England finder B28/C).

Figure 5. *Osmundacidites wellmanii*, slide JP1/3vii (England finder P51/1).

Figure 6. *Todisporites major*, slide 10320i (England finder J31/4).

Figure 7. *Todisporites major*, slide JP2/11ii (England finder B36/C).

Figure 8. *Todisporites minor*, slide JP2/11i (England finder C52/2).

Figure 9. *Todisporites minor*, slide JP2/11i (England finder G33/3).

Figure 10. *Gleicheniidites senonicus*, slide JP2/1i (England finder Q36/3).

Figure 11. *Conbaculatisporites mesozoicus*, slide JP2/3i (England finder K30/2).

Figure 12. *Concavisporites* sp., slide HB6ii (T36/1).

Figure 13. *Concavisporites* sp. 1, slide JP2/11i (C47/C).

Figure 14. *Dictyophyllidites equiexinus*, slide HB8i (England finder X47/1).

Figure 15. *Dictyophyllidites harrisii*, slide JP2/2iii (England finder J30/3).

Figure 16. *Matonisorites phlebopteroides*, slide SS06/04i (England finder U39/2).

Figure 17. *Matonisorites* cf. *phlebopteroides*, slide HB40ii (England finder S43/4).

Figure 18. *Contignisorites* sp., slide JP2/11i (England finder O40/3).

Figure 19. *Duplexisorites problematicus*, slide JP2/11i (England finder H49/C).



Plate 5

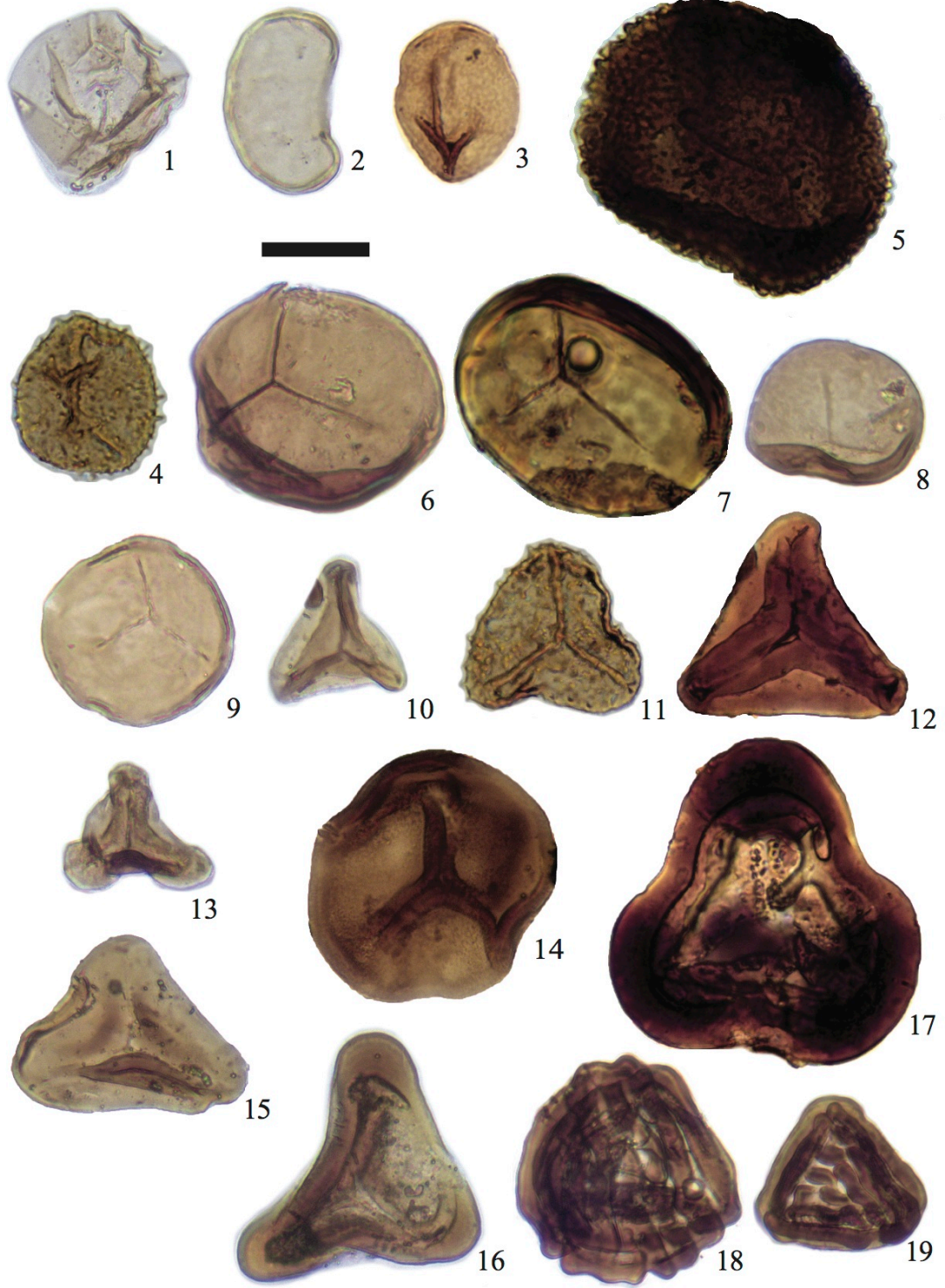


Plate 6

Scale bar represents 20 µm

Figure 1. *Ischyosporites* sp., slide HB26i (England finder M36/C).

Figure 2. *Trilobosporites* sp., slide JP2/1i (England finder J42/C).

Figure 3. *Cibotiumspora jurienensis*, slide JP2/3i (England finder L40/4).

Figure 4. *Cibotiumspora jurienensis*, slide JP2/8ii (England finder F43/C).

Figure 5. *Obtusisporis canadensis*, slide HB13i (England finder C20/3).

Figure 6. *Concavissimiporites punctatus*, slide JP1/7iv (England finder D38/4).

Figure 7. *Concavissimiporites subgranulosus*, slide JP1/3viii (England finder T20/1).

Figure 8. *Concavissimiporites variverrucosus*, slide JP2/1ii (England finder G33/3).

Figure 9. *Concavissimiporites variverrucosus*, slide HB11ii (England finder Y20/1).

Figure 10. *Deltoidospora australis*, slide (England finder JP1/3i E35/C).

Figure 11. *Deltoidospora concavus*, slide JP1/10iv (England finder N23/C).

Figure 12. *Deltoidospora minor*, slide JP1/7i (England finder E20/1).

Figure 13. *Deltoidospora minor*, slide JP1/7i (England finder G37/4).

Plate 6



Plate 7

Scale bar represents 20  $\mu\text{m}$

Figure 1. *Pilosisorites brevipapillosus*, slide HB29iii (England finder O43/1).

Figure 2. *Pilosisorites trichopapillosus*, slide SS06/05i (England finder E53/C).

Plate 7

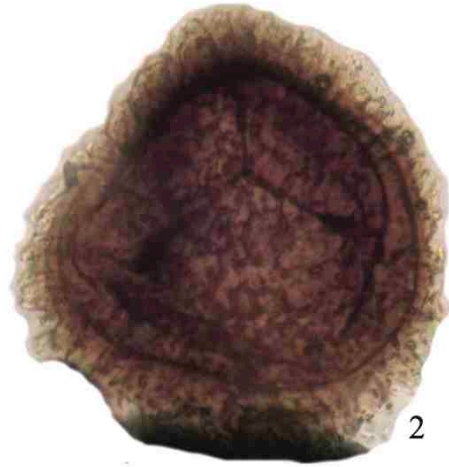
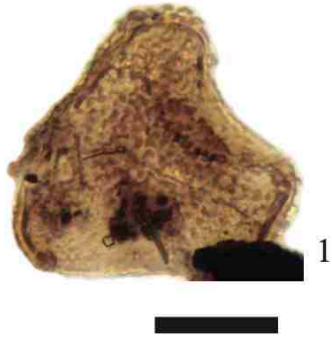


Plate 8

Scale bar represents 20  $\mu\text{m}$

Figure 1. *Alisporites dunrobinensis*, slide HB46i (England finder T39/C).

Figure 2. *Alisporites microsaccus*, slide JP1/3vii (England finder P22/1).

Figure 3. *Alisporites thomasii*, slide JP2/11i (England finder S28/3).

Figure 4. *Vitreisporites pallidus*, slide HB8i (O32/2).

Figure 5. *Pityosporites microalatus*, slide JP2/3iv (England finder E39/1).

Figure 6. *Pityosporites minimus*, slide JP1/3iii (England finder C27/4).

Figure 7. *Podocarpidites ellipticus*, slide HB12i (England finder X38/1).

Figure 8. *Quadraeculina anellaeformis*, slide HB23i (England finder R24/3).

Plate 8

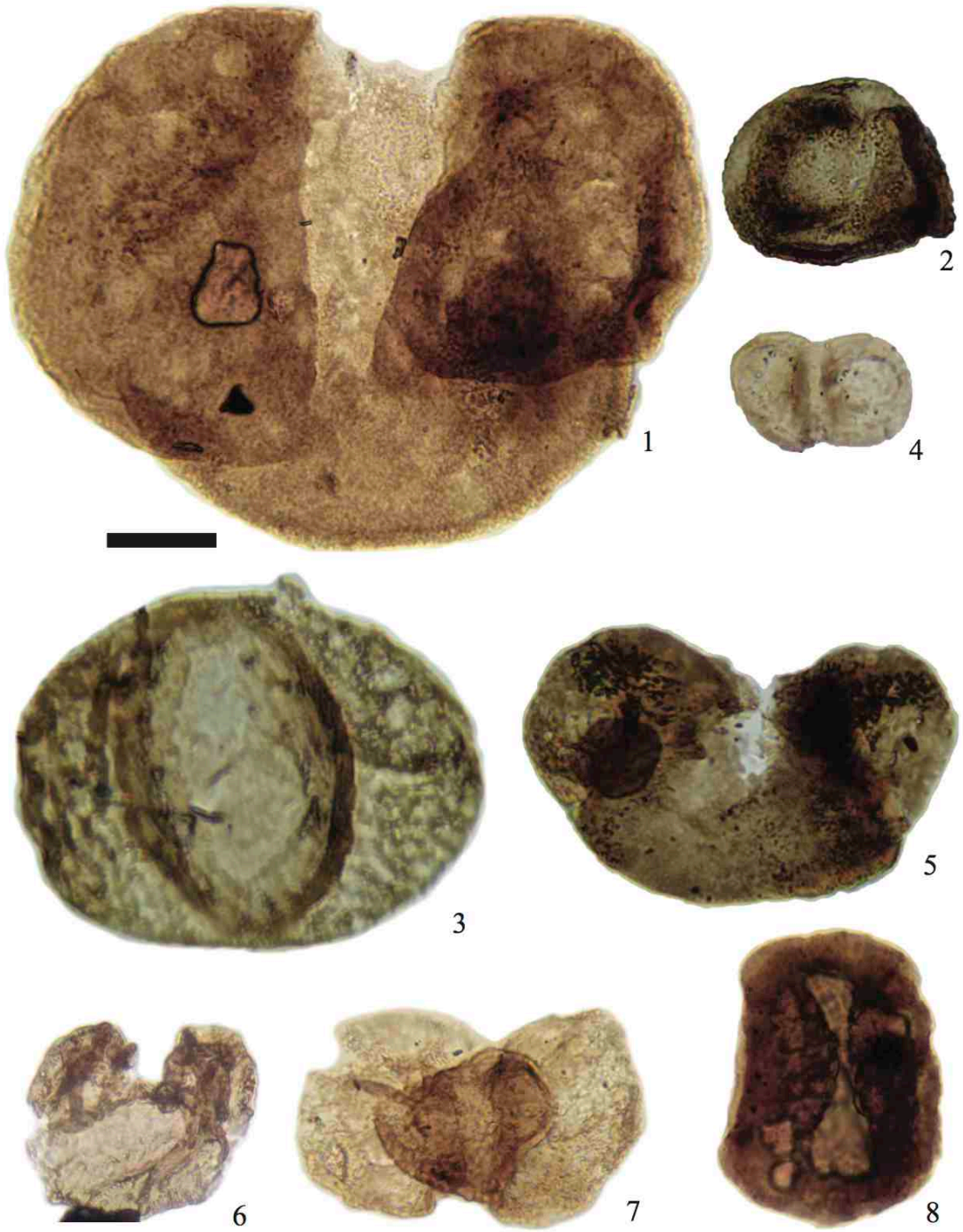


Plate 9

Scale bar represents 20  $\mu\text{m}$

Figure 1. *Araucariacites australis*, slide JP2/9ii (England finder P33/4).

Figure 2. *Callialasporites dampieri*, slide JP2/11ii (England finder B35/4).

Figure 3. *Callialasporites minus*, slide JP1/3i (England finder K40/C).

Figure 4. *Callialasporites segmentatus*, slide HB28i (England finder J40/3).

Figure 5. *Callialasporites trilobatus*, slide JP2/11i (England finder R43/1).

Figure 6. *Callialasporites turbatus*, slide HB6ii (England finder T36/1).

Figure 7. *Classopollis torosus*, slide JP1/5i (England finder E35/2).

Figure 8. Tetrad of *Classopollis torosus*, slide JP2/11ii (England finder B41/C).

Figure 9. *Cerebropollenites mesozoicus*, slide HB8i (England finder J52/2).



Plate 9

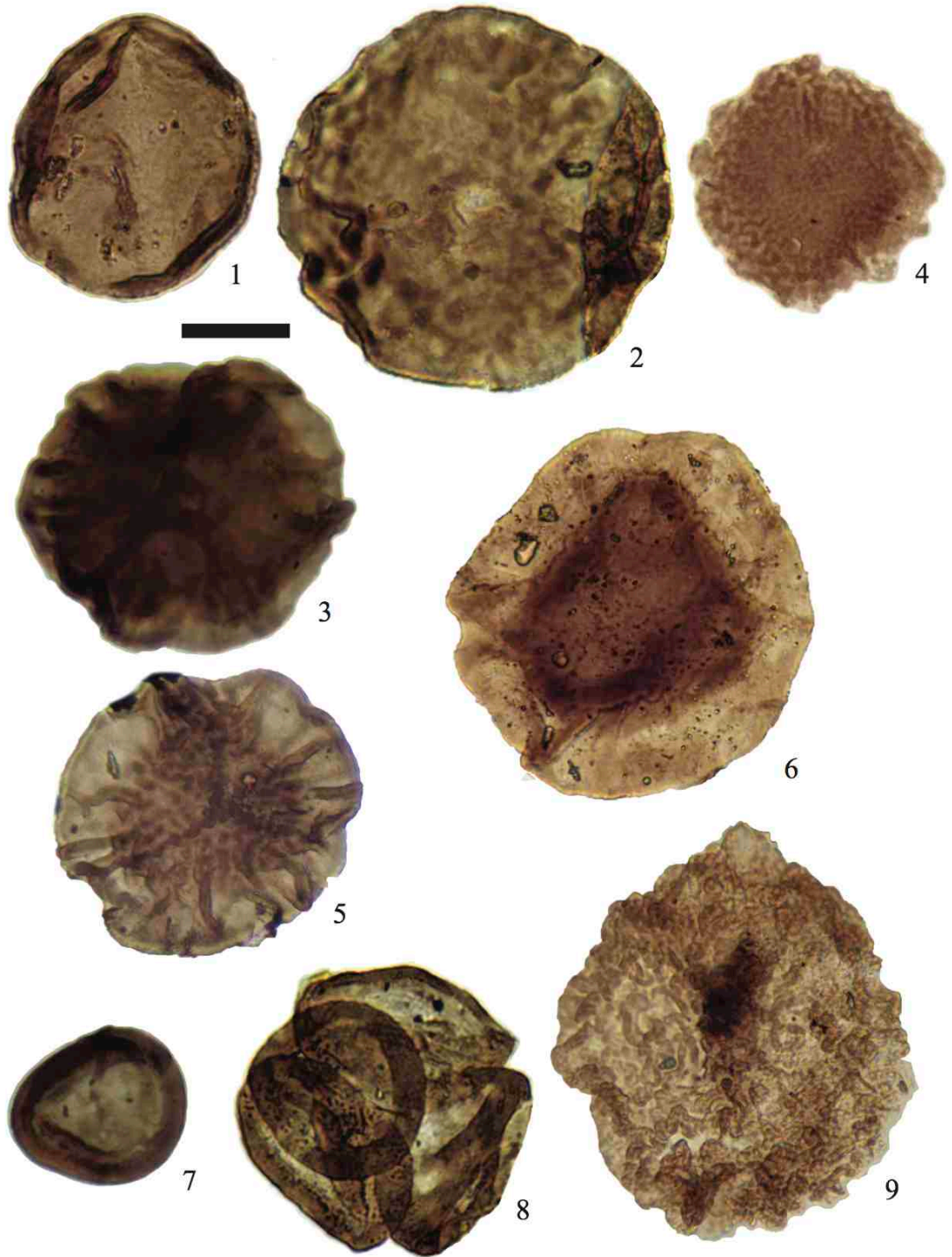


Plate 10

Scale bar represents 20  $\mu\text{m}$

Figure 1. *Spheripollenites psilatus*, slide JP2/11ii (England finder B37/2).

Figure 2. *Spheripollenites scabratus*, slide JP2/2ii (England finder U47/2).

Figure 3. *Spheripollenites subgranulatus*, slide JP2/3i (England finder F24/C).

Figure 4. *Perinopollenites elatoides*, slide JP1/3ii (England finder L22/3).

Figure 5. *Chasmatosporites apertus*, slide HB8i (England finder O41/4).

Figure 6. *Chasmatosporites hians*, slide HB8i (England finder H32/1).

Figure 7. *Chasmatosporites major*, slide HB9i (England finder E51/3).

Figure 8. *Cycadopites minimus*, slide JP2/11i (England finder L27/3).

Figure 9. *Cycadopites minimus*, slide JP2/11i (England finder F46/2).

Figure 10. *Cycadopites carpentieri*, slide SS06/01iii (England finder S28/2).

Figure 11. *Cycadopites subgranulosus*, slide JP2/11ii (England finder G46/2).

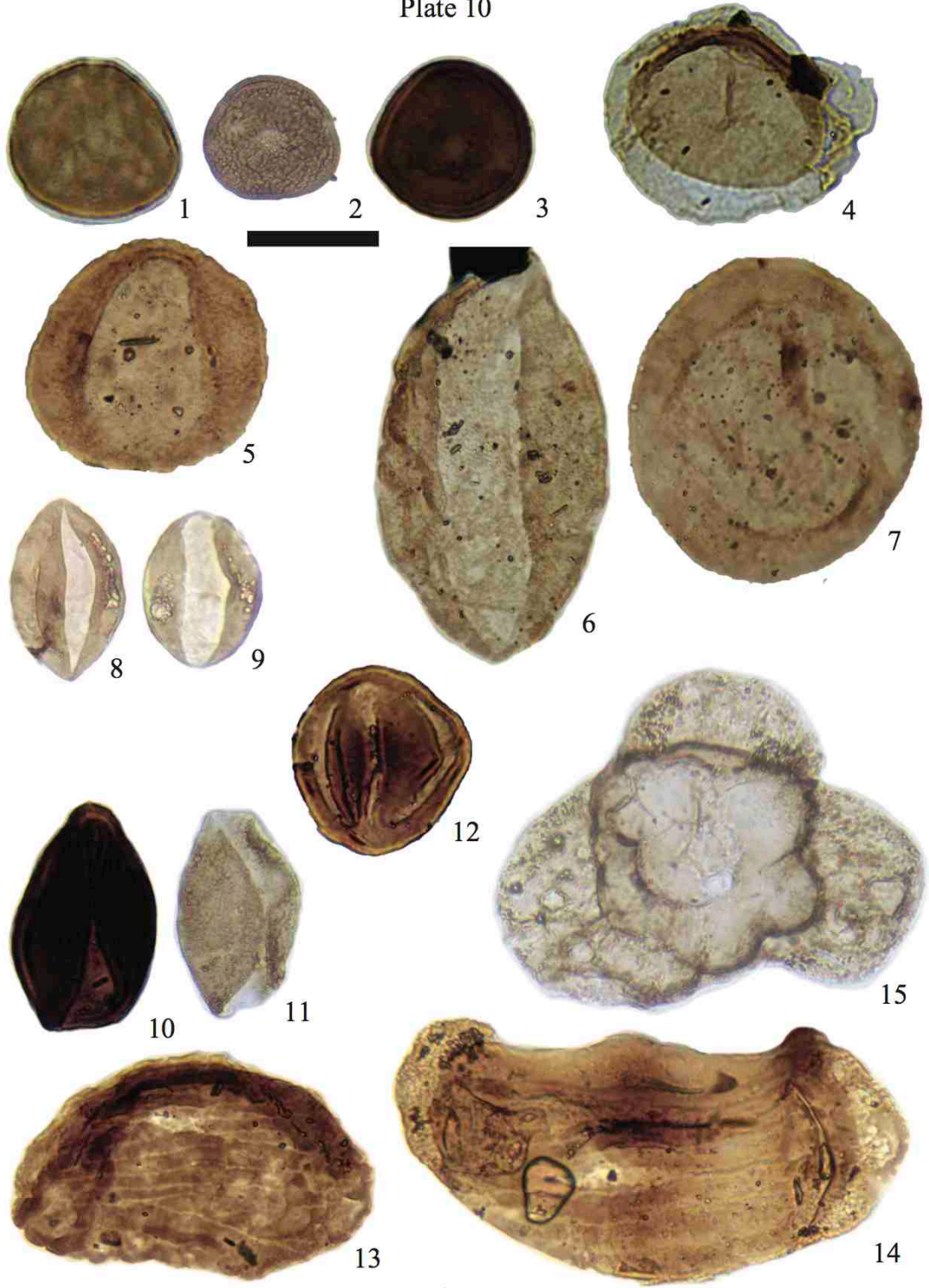
Figure 12. *Eucommiidites troedssonii*, slide HB9i (England finder O29/C).

Figure 13. Striate bisaccate sp., slide HB13i (England finder T36/1).

Figure 14. Striate bisaccate sp., slide HB27i (England finder K32/4).

Figure 15. Trisaccate sp. 1, slide 10311i (England finder M36/4).

Plate 10



## CHAPTER 4: MIDDLE JURASSIC VEGETATION DYNAMICS BASED ON QUANTITATIVE ANALYSIS OF SPORE/POLLEN ASSEMBLAGES FROM THE RAVENSCAR GROUP, NORTH YORKSHIRE, UK

A manuscript version of this chapter has been accepted for publication in the journal *Palaeontology* (Slater and Wellman in press). The experiment was devised by SMS and CHW, conducted by SMS, and the chapter/manuscript was written by SMS under the guidance of CHW.

### 4.1 Introduction

This chapter assesses temporal changes in the dispersed sporomorph record of the Middle Jurassic Ravenscar Group by using modern quantitative methods. The aim is to build upon previous studies into the Jurassic palaeoflora of Yorkshire based on the dispersed sporomorph record (e.g. Boulter and Windle 1993) to improve vegetation reconstructions and explain the causes of potential variations in sporomorph assemblages through time.

One of the major problems with vegetation reconstructions based on dispersed spore/pollen data has been that it was often difficult to link parent plants/parent plant groups with sporomorphs with confidence as many taxa were not known from in situ material and some plant species produce spores/pollen that appear superficially indistinguishable, particularly when only using light microscopy (Frederiksen 1980; Mander and Punyasena 2014). However, extensive investigations into the rare occurrences where spores/pollen are preserved in situ (e.g. van Konijnenburg-van Cittert 1968, 1971, 1978, 1981, 1989, 1993, 2000, 2010; Pedersen *et al.*, 1989; Hill 1990; Osborn and Taylor 1993; Balme 1995; Friis and Pedersen 1996; Yang *et al.*, 2008) now means that the majority of Middle Jurassic sporomorphs can be assigned at least to family level plant classification. In addition, TEM studies of the spore/pollen wall ultrastructure have been used to refine parent plant affinities of dispersed taxa without the need for rare in situ preservation (e.g. Batten and Dutta 1997; Slater *et al.*, 2015). Thus, dispersed spore/pollen assemblages from the Jurassic of Yorkshire

offer important insight into vegetation dynamics of this time period, and when integrated with the plant megafossil record, these data sets can be used to improve local and regional-scale palaeoenvironmental reconstructions.

## **4.2 Material and Methods**

### ***4.2.1 Collection***

A total of 114 samples were collected through the Ravenscar Group from a combination of coastal outcrop successions and one inland outcrop locality (Figure 4.1A). Sampling focussed on: (i) exposures with fine grained and reduced sediments likely to yield rich palynomorph assemblages; (ii) non-marine deposits that are known for their plant megafossil contents (i.e. plant beds) to allow comparison plant megafossil and dispersed sporomorph assemblages. The sampling distribution thus reflects these focus areas. Rock samples represent approximately 1–5 cm in vertical section from individual horizons (i.e. none were composite samples). All sample points and depositional environments for each part of the section are provided in Figures 4.1B–4.3. Aalenian samples were collected from the Hasty Bank (section 1) (see Spicer and Hill 1979; Slater and Wellman 2015) and Hayburn Wyke (section 2) plant beds (discussed in van Konijnenburg-van Cittert and Morgans 1999). Bajocian samples were collected from Cloughton Wyke (section 3), Cayton Bay and Yons Nab (section 4). A number of samples from Cloughton Wyke were collected and analysed by Cadman (1979), the slides have been reassessed here for taxonomic consistency. Bathonian samples were collected from sections at Burniston Bay (section 5), through which dinosaur footprints are common (Rawson and Wright 2000). Twelve coal samples were collected; these originated from thin, laterally discontinuous deposits (typically <10 m in lateral-section). Soft clay horizons that contained rootlets were present beneath the coals at Hayburn Wyke and Cloughton Wyke.

#### ***4.2.2 Processing***

Dry rock samples were weighed at 20 g before being dissolved in 40 % hydrochloric acid for at least 24 hours to remove carbonates followed by two-week maceration in 40 % hydrofluoric acid to remove silicates. Samples were agitated every two days to ensure full break down of rock material. Samples were then decanted and fresh water added, repeating the process until neutral before sieving at 10 or 20  $\mu\text{m}$ ; no sporomorphs were found less than 20  $\mu\text{m}$  in diameter in samples that were sieved at 10  $\mu\text{m}$ , thus it was deemed adequate to sieve further samples at 20  $\mu\text{m}$ . One day was left between decants to ensure minimal loss of palynomorphs. Centrifuging residues in zinc chloride was then undertaken to remove heavy minerals. Residues were then sieved again at 10 or 20  $\mu\text{m}$  to remove the heavy liquid and final residues were spread across cover slips and gently heated on a hot plate to remove excess water. Cover slips were then mounted onto slides using epoxy resin on a hot plate. Five of the 12 coal samples were processed using Schulze solution overnight, before being neutralised with water and sieved at 20  $\mu\text{m}$ . The remainder of the processing method followed the same procedure as all other samples. A number of excess residues were sieved at 100  $\mu\text{m}$  for megaspores and larger floral components. Specimens were picked using a fine paint brush and mounted on SEM stubs, gold coated using an Edwards Coater 5250B for 3 minutes, and examined under a Philips XL20 field emission SEM at 15 kV. Processing details for all samples are provided in Appendix 2. All materials (rock samples and slides) are housed in the collections of the Centre for Palynology at the University of Sheffield, UK.

#### ***4.2.3 Counting***

Slides were examined under a Meiji Techno (MA151/35/50) light microscope. A minimum of 200 sporomorphs were counted from each sample. Counts were carried out in systematic traverses to ensure no grains were missed. The remainder of the slide was then examined in the same fashion to identify rare species that were not present in the count data. The complete sporomorph raw data set is provided in Appendix 3.

#### **4.2.4 Palynofacies Analysis**

Basic palynofacies analysis was undertaken on all samples to assess differences in depositional environments between samples. The term palynofacies typically refers to all of the visible organic particles (usually between 2–250 µm in size) that occur within palynological maceration residues (Traverse 2007). Palynofacies analysis is commonly used to assess depositional environments (e.g. Parry *et al.*, 1981; Boulter and Riddick 1986; Van der Zwan 1990; Brugman *et al.*, 1994; Oboh-Ikuenobe and Yepes 1997; Oboh-Ikuenobe *et al.*, 2005; Carvalho *et al.*, 2006). Categories for palynofacies debris are: spores, pollen, algae, dinoflagellate cysts, acritarchs, humic debris, amorphous organic matter (AOM), *Botryococcus*, structured vitrinite, unstructured vitrinite, cuticle and inertinite. For comprehensive descriptions and figures of palynofacies categories, see Tyson (1995) and Batten and Stead (2005). In the classification scheme used here ‘spores’ refers to trilete spores; ‘pollen’ refers to all pollen morphotypes; ‘algae’ refers to all algal forms that are not *Botryococcus*; ‘dinoflagellate cysts’ and ‘acritarchs’ represent marine palynomorphs which belong to these groups; ‘humic debris’ refers to yellow–brown humic material exhibiting little structure; ‘AOM’ refers to unstructured, amorphous organic matter; ‘*Botryococcus*’ represent fresh/brackish water algal colonies; ‘structured vitrinite’ refers to translucent–brown, lath-shaped to blocky woody particles that exhibit longitudinal structural thickenings; ‘unstructured vitrinite’ refers to brown woody material that has undergone extensive degradation; ‘cuticle’ refers to transparent to yellow epidermal fragments; and ‘inertinite’ refers to black woody material. Counts of 200 palynodebris based on point counts were carried out on all samples, the complete palynofacies raw data set is provided in Appendix 4.

#### **4.2.5 Data analysis**

Individual and sample-based rarefaction analysis were undertaken to assess changes in richness through the sequence. Individual-based rarefaction calculates the expected richness of a sample at a lower count total so that different count sizes can be compared more fairly (e.g. Gotelli and Colwell 2001). Sample-based rarefaction is used on groups of samples to

calculate the expected richness at lower numbers of pooled samples (e.g. Jardine and Harrington 2008). Individual-based rarefaction curves were calculated for each sample and plotted for each stage to compare richness between stages. Count data was also rarefied at 200 specimens per sample to construct a rarefied richness plot through the sequence. A problem with individual-based rarefaction is that when a small number of taxa are highly abundant, as is the case in many samples here, a large portion of the richness data (taxa that are present in slides but not in counts) is excluded from the analysis. Thus, raw richness data is also provided as this includes all taxa that were present in each sample. Richness patterns present in both plots are therefore potentially more reliable. Sample-based rarefaction, using presence–absence data was also carried out on grouped samples from the Aalenian, Bajocian and Bathonian to assess broad changes in richness between stages. Rarefaction analysis was carried out using PAST (Hammer *et al.*, 2001).

The ordination technique nonmetric multidimensional scaling (NMDS) was used to assess compositional change between sporomorph samples. NMDS is a non-parametric ordination method that uses ranked distances between samples to assess the degree of similarity between samples. This enables complex multivariate data to be plotted onto a minimal number of axes (e.g. Jardine *et al.*, 2012). In NMDS ordinations, samples that are compositionally similar plot close together, whereas samples that are compositionally dissimilar plot far apart. The Bray-Curtis dissimilarity metric was used to generate distances between samples as this method is considered to perform well in ecological studies (e.g. Harrington 2008). Repeated runs were carried out for two dimensions until a convergent solution was established. Principal components rotation and centring was then carried out to the final ordination. NMDS was carried out using R, version 3.1.2 (R Core Team 2014), within the package ‘vegan’, version 2.2–1 (Oksanen *et al.*, 2015). Ordinations displayed here were performed on sporomorph relative abundance and presence–absence data sets (e.g. Harrington 2008). Unlike ordination of relative abundance data, which can be strongly controlled by the most abundant taxa, ordination of presence–absence data is not affected by this problem, as all taxa within a sample are equally weighted in the ordination. For the



relative abundance data matrix, species that were present in samples but not in counts and singletons in the count data (samples present in one sample) were removed from the data set to reduce statistical noise. For the presence–absence matrix all taxa were included; taxa that were present were scored as ‘1’ and taxa that were absent were scored as ‘0’. NMDS ordinations were also carried out on sporomorph data sets following logarithmically transforming relative abundances (e.g. Slater and Wellman 2015) and the Wisconsin double standardisation method (e.g. Jardine and Harrington 2008; Mander *et al.*, 2010). The ordinations and stress values from these plots were highly similar to the unaltered relative abundance NMDS plot, thus it was deemed unnecessary to manipulate abundances and so unaltered relative abundances are presented here. The high degree of similarity between NMDS plots using different data manipulation techniques demonstrates that the results are robust.

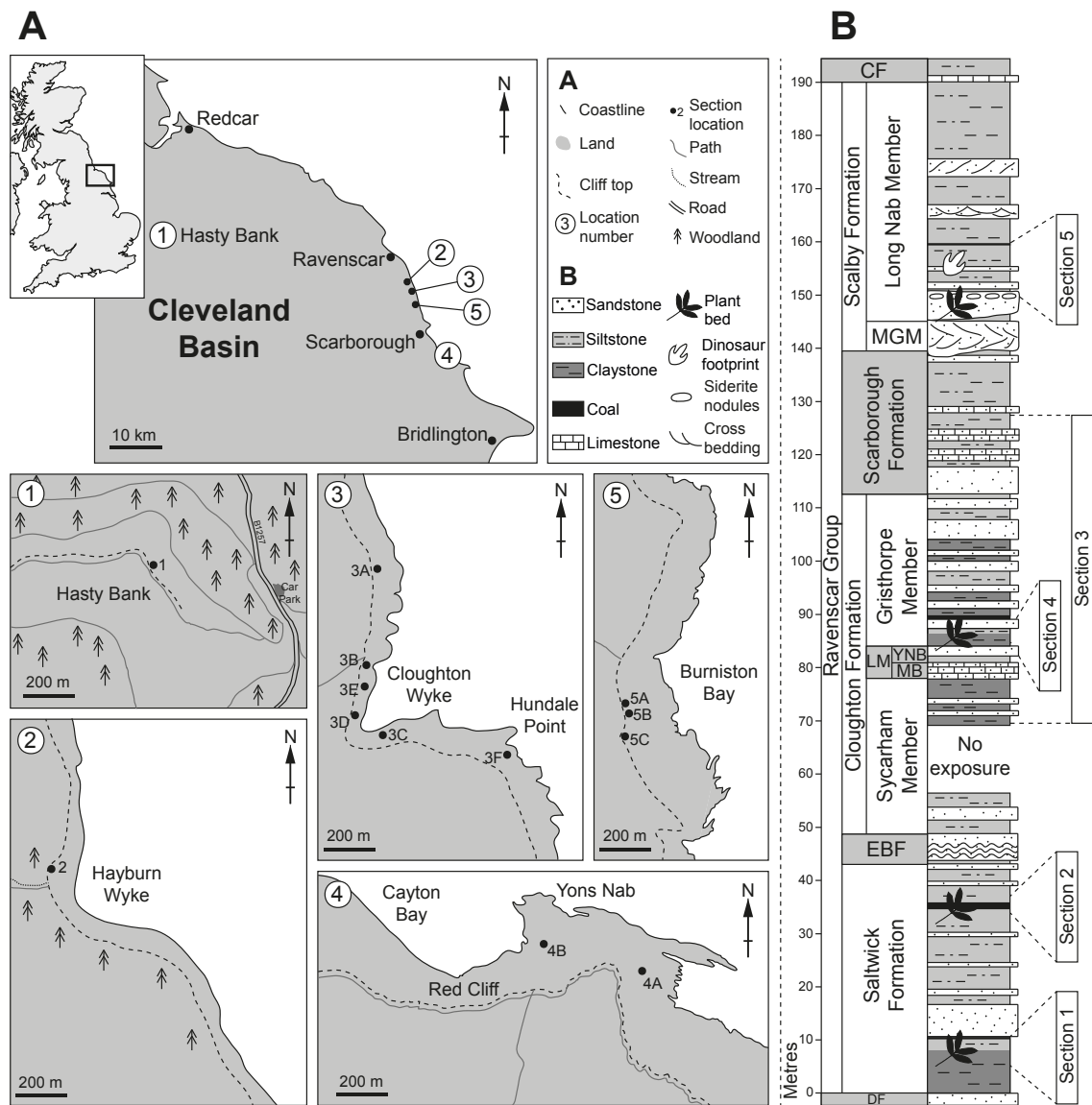


Figure 4.1: Localities and sampling points through the Middle Jurassic of Yorkshire. A, locations of all sections with detailed maps of individual section locations. B, composite sedimentary log of the Middle Jurassic of Yorkshire with the stratigraphic positions of sections 1–5. Shaded text regions represent marine units, DF = Dogger Formation, EBF = Eller Beck Formation, LM = Leberston Member, MB = Millepore Bed, YNB = Yons Nab Beds, MGM = Moor Grit Member, CF = Cornbrash Formation. Maps 1, 2 and 4 modified from van Konijnenburg-van Cittert and Morgans (1999).

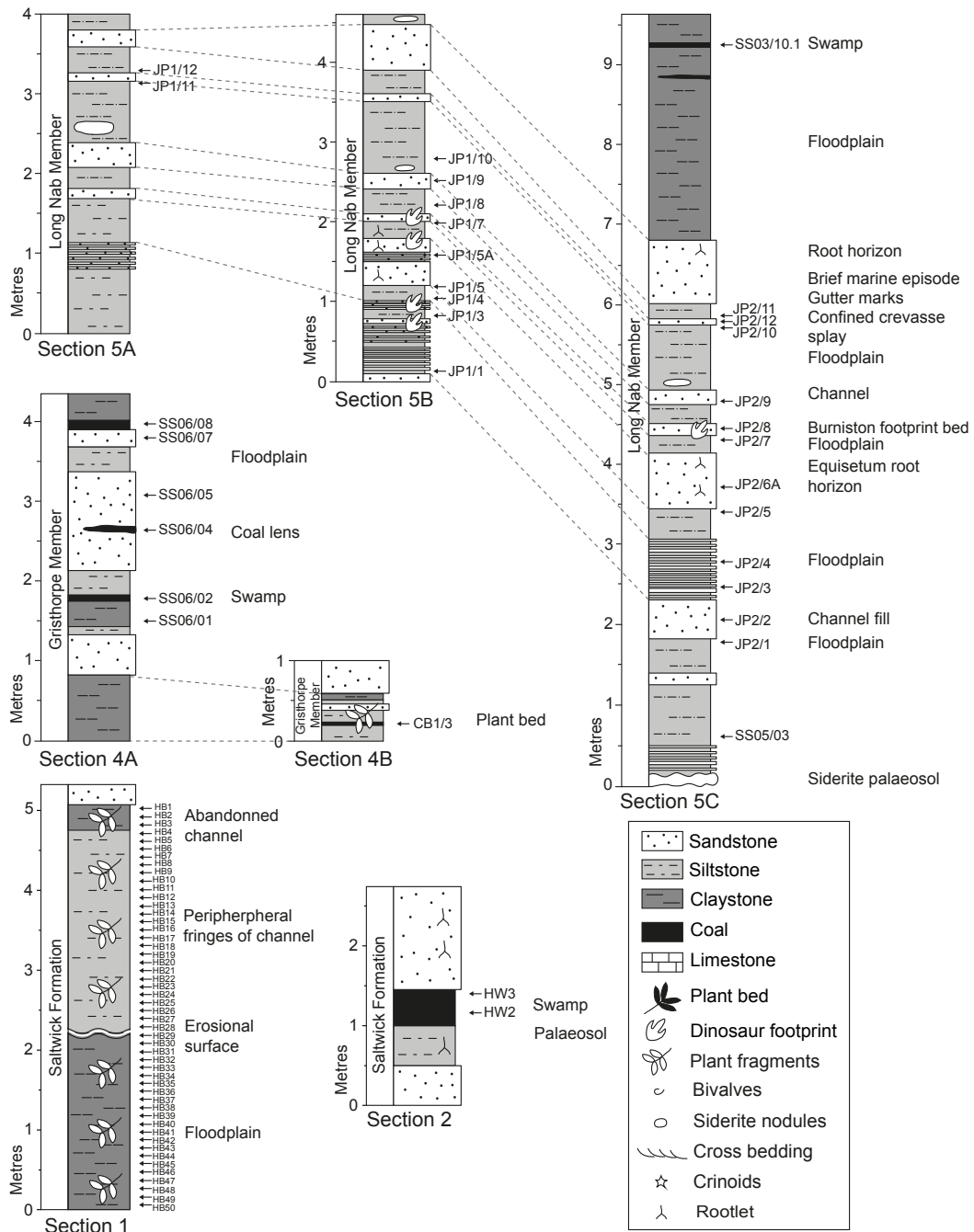


Figure 4.2: Detailed sedimentary logs of sections 1, 2, 4, and 5 with sample points and palaeoenvironmental interpretations.

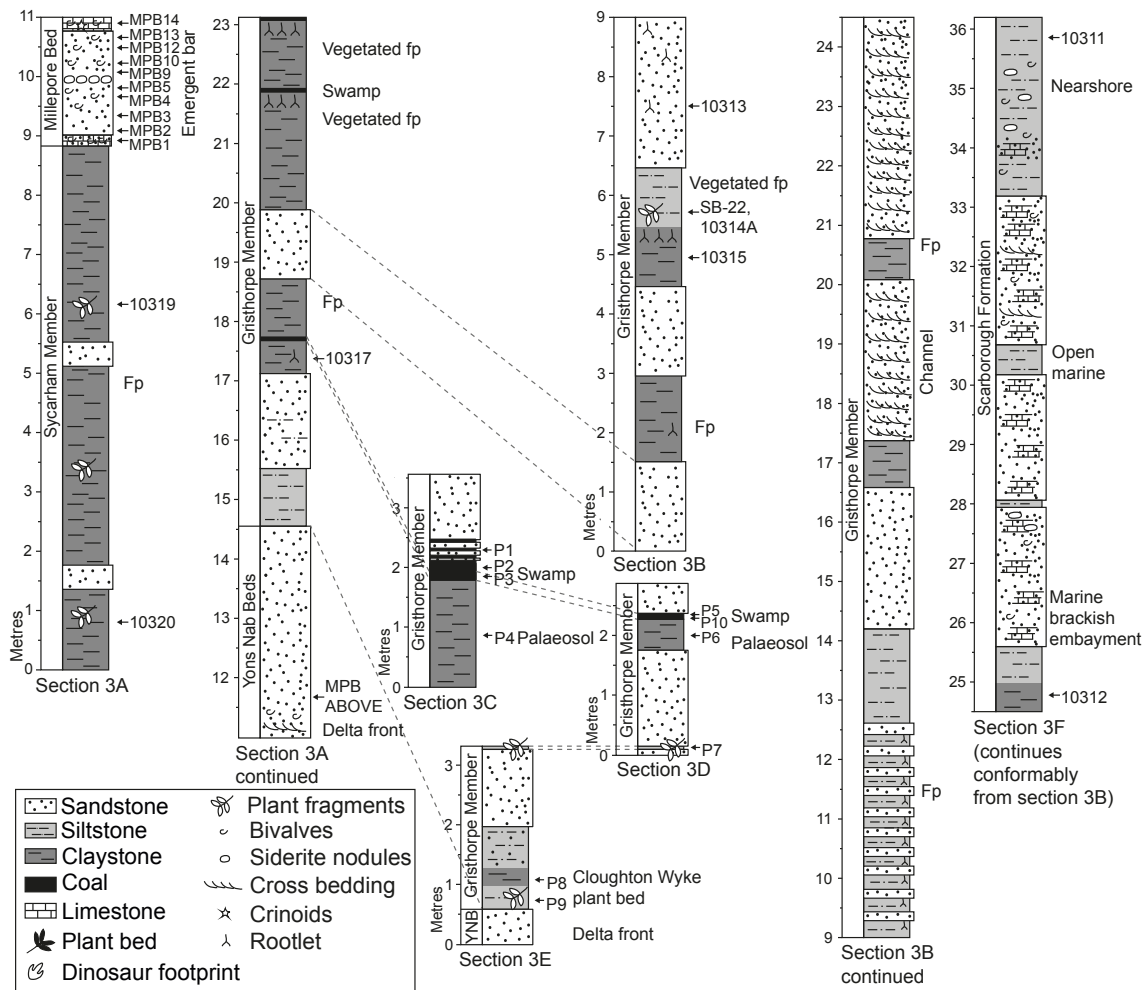


Figure 4.3: Detailed sedimentary logs of section 3 with sample points and palaeoenvironmental interpretations. Fp and fp = Floodplain, YNB = Yons Nab Beds.

## 4.3 Results

### 4.3.1 Temporal sporomorph variation and vegetation reconstruction

A total of 85 sporomorph taxa were identified from 114 palynological samples; the entire taxonomic list with sporomorph botanical affinities is provided in Appendix 1. These associations are mostly based on the relatively rare situations where spores/pollen are preserved in situ (e.g. van Konijnenburg-van Cittert 1981). Figure 4.4 displays an example of in situ spores from a fern sporangium recovered from sample JP2/2. The spores are smooth walled and trilete, however assigning these to a genus confidence is difficult due to their orientation and lack of obvious defining features.

The commonly used Chao2 species richness estimator with bias correction (e.g. Gotelli and Colwell 2011) gave a species estimate of 91.94 taxa (standard deviation = 7.07) for the entire data set, which suggests the data was not severely undersampled. Relative abundances of the ten most abundant species are provided in Figure 4.5A, with richness data for every sample provided in Figure 4.5B–C. Sporomorphs have been grouped into their respective botanical affinities in Figure 4.6A to assess large-scale vegetation change through the Ravenscar Group. Figures 4.5–4.6 reveal that the Aalenian, Bajocian and Bathonian samples have relatively distinct sporomorph assemblages regarding the overall abundances of certain species and plant groups. Section 4 and the lower part of the Gristhorpe Member in section 3 are roughly synchronous, however it is difficult to correlate samples from these sections with certainty, thus section 4 has been excluded from the composite sporomorph abundance/richness plots and is shown below them (Figures 4.5–4.6).

Regarding sporomorph groupings, the ‘Monosulcate producers’ group (Figure 4.6A) refers to simple monosulcate pollen of the genera *Chasmatosporites* and *Cycadopites*. *Chasmatosporites* is known to have botanical affinities within the Cycadales and Ginkgoales and *Cycadopites* has broad botanical affinities within the Cycadales, Ginkgoales, Peltaspermales and Bennettitales (e.g. Townrow 1960; Balme 1995; Mander 2011). Plant megafossil studies (e.g. Spicer and Hill 1979) demonstrate that Cycadales, Ginkgoales and Bennettitales are common from the Yorkshire Jurassic, thus these

sporomorphs probably originate from a mixture of these groups. The ‘Pteridosperms/Conifers’ group (Figure 4.6A) refers to species of *Alisporites*. These are considered to have both pteridosperm and/or coniferous origins (Mander 2011).

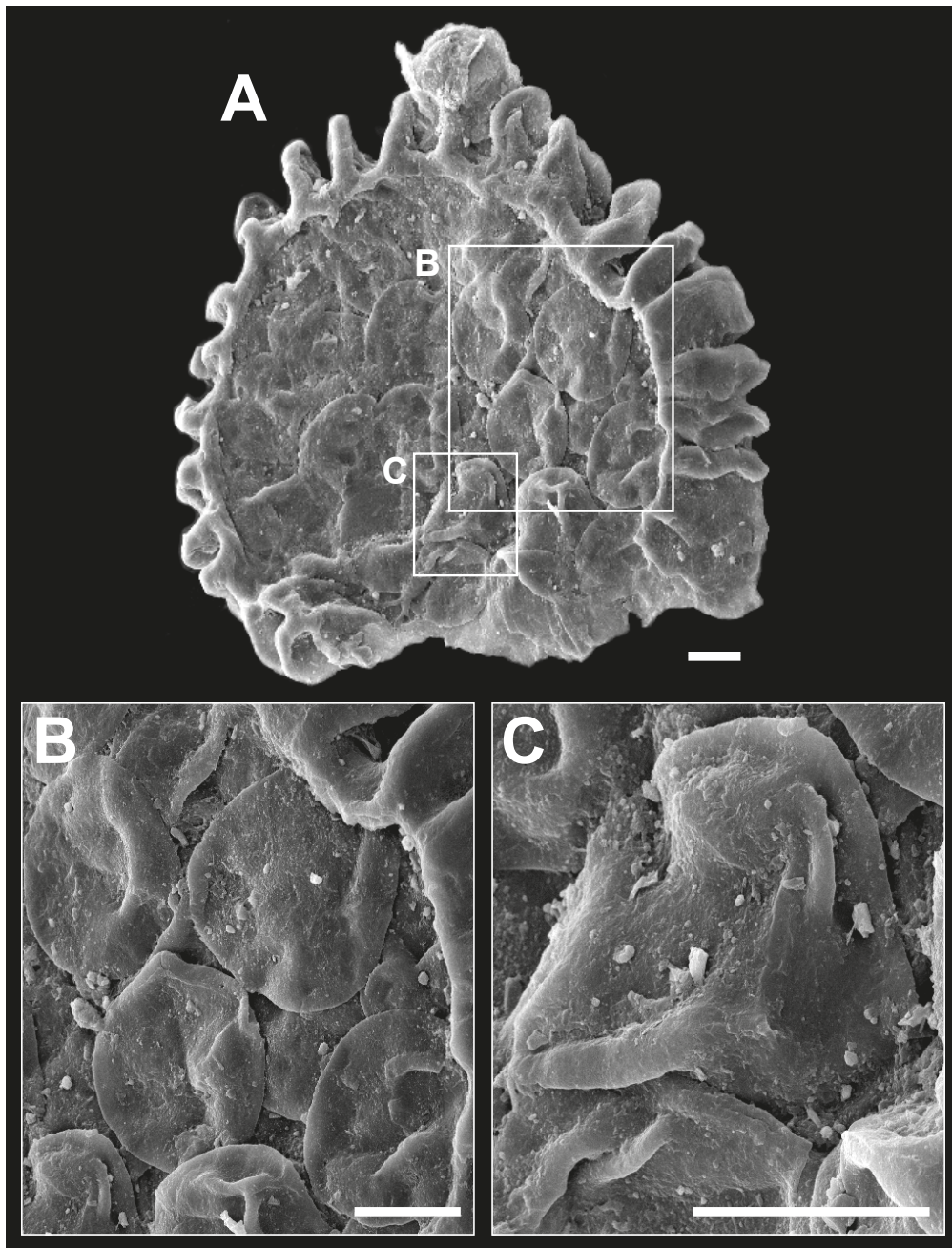


Figure 4.4: Fern sporangium with in situ spores, from sample JP2/2. A, overview of sporangium. B, close-up of A showing smooth walled spores within sporangium. C, close-up of A showing smooth walled spore with probable trilete mark. All scale bars represent 25  $\mu\text{m}$ .

#### 4.3.1.1 Aalenian

Sporomorph assemblages from the lower Saltwick Formation at Hasty Bank (section 1) contain abundant *Araucariacites australis*, *Calamospora mesozoica*, *Classopollis torosus*, *Dictyophyllidites harrisii*, and *Perinopollenites elatoides* with higher abundances of *Cycadopites*, *Marattisporites scabratus* and *Spheripollenites* and lower abundances of *Deltoidospora minor* compared to the rest of the section (Figure 4.5A). Assemblages from the lower part of section 1 (claystone) differ from the upper part (siltstone and grey clay) in that abundances of *Callialasporites turbatus*, *C. torosus* and *P. elatoides* are higher and abundances of *A. australis* and *Deltoidospora* are lower in the claystone. Assemblages from section 2 contain abundant *D. minor* with low abundances of all other taxa.

In general, Aalenian samples are co-dominated by conifers and ferns (conifers are more abundant than ferns) and have considerably more simple monosulcates and sphenophytes with moderately more Caytoniales and Erdtmanithecales pollen compared to the Bajocian and Bathonian samples (Figure 4.6A). Fern spores are considerably less abundant within Hasty Bank samples compared to the Bajocian and Bathonian counterparts. The low abundances of *M. scabratus* (Figure 4.5A) demonstrate that Marattiaceae ferns contrast the general abundance pattern of the ferns through the Ravenscar Group and are abundant within the Aalenian, but become considerably less abundant in the Bajocian and Bathonian. Abundant *C. mesozoica* suggests that sphenophytes were more common in the Aalenian compared to the Bajocian and Bathonian (Figure 4.6A).

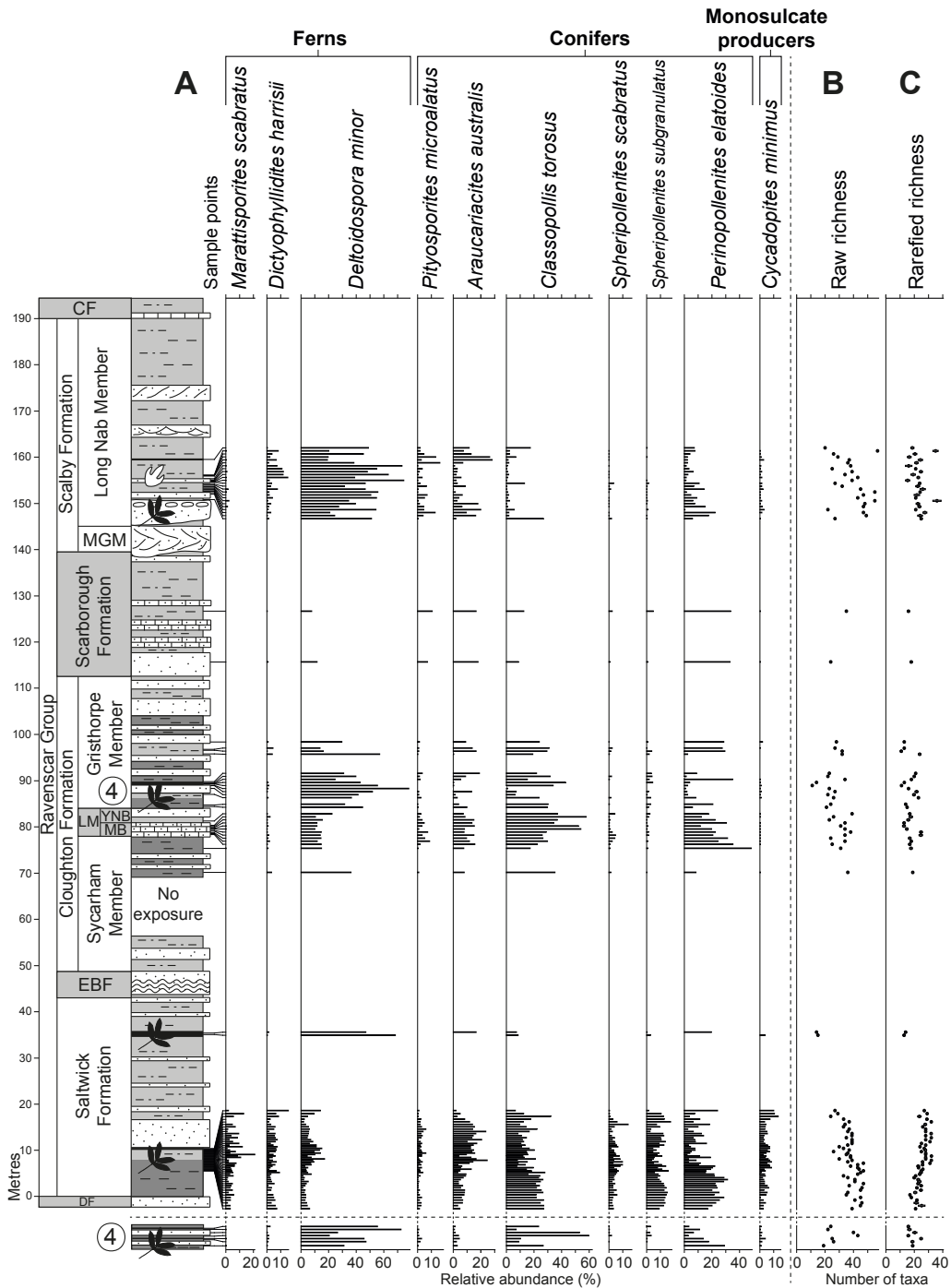


Figure 4.5: Sporomorph abundance and richness charts. Shaded text regions in the log represent marine units, DF = Dogger Formation, EBF = Eller Beck Formation, LM = Lebberton Member, MB = Millepore Bed, YNB = Yons Nab Beds, MGM = Moor Grit Member, CF = Cornbrash Formation. A, relative abundances of the ten most abundant sporomorph taxa. B, raw richness for all samples. C, rarefied richness (at 200 specimens) for all samples, horizontal bars across sample points represent 95 % confidence intervals. In the composite log '4' refers to the stratigraphic position of section 4.



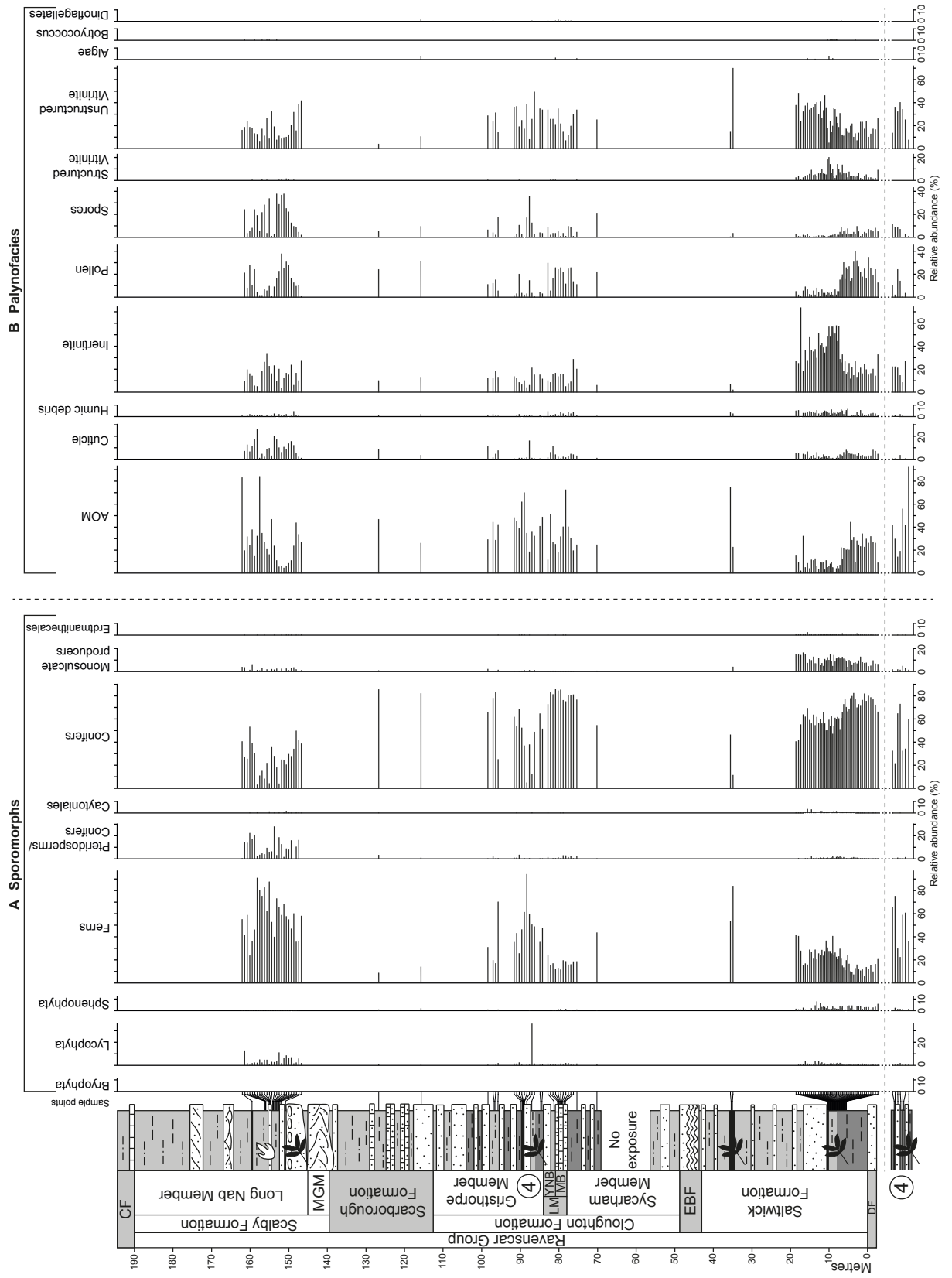


Figure 4.6 (previous page): Sporomorph and palynofacies abundance charts. Shaded text regions in the log represent marine units, DF = Dogger Formation, EBF = Eller Beck Formation, LM = Lebberston Member, MB = Millepore Bed, YNB = Yons Nab Beds, MGM = Moor Grit Member, CF = Cornbrash Formation. A, relative abundances of sporomorphs grouped into their respective affinities. B, relative abundances of palynofacies categories. In the composite log '4' refers to the stratigraphic position of section 4.

#### 4.3.1.2 Bajocian

Assemblages from the Sycarham Member contain abundant *C. torosus*, *D. minor* and *P. elatoides* (Figure 4.5A) with generally low abundances of all other taxa. Assemblages from the Lebberston Member possess abundant *C. torosus* and *P. elatoides* with moderate abundances of *A. australis* and low abundances of *D. minor* (Figure 4.5A). The Gristhorpe Member contains abundant *C. torosus* and *D. minor* with moderately abundant *A. australis* and relatively low abundances of *P. elatoides* in the lower samples of the Gristhorpe Member, which increases in abundance within samples from the middle part of the Gristhorpe Member (Figure 4.5A). Assemblages from the Scarborough Formation are predominantly composed of abundant *A. australis*, *Cerebropollenites mesozoicus*, *P. elatoides*, *Pityosporites microalatus* and low abundances of *C. torosus* and *D. minor* (Figure 4.5A).

Bajocian palynofloras are unsurprisingly intermediate in terms of plant group abundances (Figure 4.6A) between the Aalenian and Bathonian assemblages. Similarly to the Aalenian samples, conifers dominate abundances and lycophytes and pteridosperms/conifers are low in abundance. However, unlike the Aalenian assemblages, fern spores are considerably more abundant in the Bajocian and monosulcate producers and sphenophytes are notably less abundant in the Bajocian (Figure 4.6A).

#### 4.3.1.3 Bathonian

Assemblages of the Long-Nab Member are composed of abundant *Alisporites*, *A. australis*, *D. minor*, *Dictyophyllidites harrisii* and *P. microalatus* with low abundances of *C. torosus* and *P. elatoides* (Figure 4.5A). In contrast to the Aalenian and Bajocian assemblages, conifers are less abundant than ferns in the Bathonian (Figure 4.6A). In particular, abundances of Cheirolepidiaceae pollen (*C. torosus*) and Taxodiaceae pollen (*P. elatoides*, *Spheripollenites scabratus* and *Spheripollenites subgranulatus*) are considerably lower in Bathonian samples compared to Bajocian and Aalenian samples (Figure 4.5A). The large trees of the Cheirolepidiaceae are typical of dry floodplain environments, whereas the Taxodiaceae trees are typical of swamp/poorly drained floodplain environments (Stukins *et al.*, 2013). A reduction in both plant groups, which reflect quite different environmental conditions suggests perhaps, (i) an increased dominance of low-standing vegetation types, including ferns and lycophytes over large, coniferous varieties, and/or (ii) a reduction in geographical catchment area from which sporomorphs are being supplied from, perhaps due to depositional change. Similarly to the Bajocian palynofloras, abundances of monosulcate producers and sphenophyte sporomorphs remain low into the Bathonian (Figure 4.6A). However, abundances of lycophytes and pteridosperms/conifers increase markedly in the Bathonian from the Bajocian and Aalenian (Figure 4.6A).

Several of the major temporal abundance changes seen here agree with the findings of Couper (1958). Specifically, *Classopollis torosus* and *C. mesozoica* are more abundant in the Saltwick (Lower Deltaic Series in Couper 1958) and Cloughton (Middle Deltaic Series in Couper 1958) formations compared to the Scalby Formation (Upper Deltaic Series in Couper 1958); *D. minor* (*Cyathidites minor* in Couper 1958) is notably less abundant in the Saltwick Formation compared to the Cloughton and Scalby formations; and *Pityosporites microalatus* (*Abietineaepollenites microalatus* in Couper 1958) is more abundant in the Scalby Formation. The major abundance changes recognized in Figures 4.5–4.6A loosely correlate with the Aalenian, Bajocian and Bathonian boundaries respectively. The timing of these changes potentially indicates (i) extensive floral turnover between these three stages and/or

(ii) substantial changes in taphonomic biases to preserve quite different sporomorph assemblages between stages.

#### 4.3.2 Richness changes

Similarly to abundance patterns, richness data appears to vary distinctly between the Aalenian, Bajocian and Bathonian stages. Raw richness for every sample (Figure 4.5B) is moderately high in the Aalenian and decreases into the Bajocian, raw richness then increases to its highest levels in the Bathonian. When counts are rarefied at 200 specimens (Figure 4.5C), broad temporal patterns are similar to the raw richness changes. Rarefied richness is high in the Aalenian, this decreases into the Bajocian and then increases to its highest levels in the Bathonian. Individual-based rarefaction curves for all samples (Figure 4.7) agree with the overall raw and rarefied richness patterns seen in Figures 4.5B–C, although the curves reveal that there is substantial overlap between samples of different stages. Figure 4.7 suggests that Aalenian samples are typically richer than Bajocian samples and Bathonian samples display extensive variation, but possess the two richest samples (JP1/3 and JP2/11). Interestingly, in the Hasty Bank plant bed (section 1) raw and rarefied richness data in Figures 4.5B–C display conflicting temporal records. Specifically, raw richness is consistently higher in the lower part of the section compared to the upper part, but the opposite pattern is recorded by the rarefied richness data. This highlights a weakness when rarefying counts; samples from the lower part of the section contain higher abundances of conifer pollen, in particular *Classopollis* and *Perinopollenites*, thus rarefied values are ‘artificially’ reduced due to the high conifer abundances as a substantial portion of the richness data is not contained within the count data. The raw richness values are therefore almost certainly more representative of ‘true’ richness changes in this part of the section.

Coal samples often display low richness levels within individual-based rarefaction plots (Figure 4.7). For example, the Aalenian Hayburn Wyke coals are markedly less rich than all other Aalenian samples. This potentially reflects the probable small representative source areas for these deposits. Some coals however display relatively high richness levels

(e.g. SS06/02 in the Bajocian). The variation in richness levels between coals suggests that the source areas and potentially time periods represented by these samples varied between deposits, hence the depositional settings and formation processes may have varied.

Sample-based rarefaction (Figure 4.8) demonstrates that Bathonian samples are richer than Aalenian and Bajocian samples and unlike individual-based rarefaction suggests that richness between Aalenian and Bajocian samples is very similar. Sample-based rarefaction is potentially a more reliable method than individual-based rarefaction here as sample-based rarefaction includes all species that are present in each slide; therefore the method is not affected by highly abundant taxa, as is the case with individual-based rarefaction. However, the results may indicate that the same species are reoccurring in the Aalenian samples and thus with additional samples, sample-based rarefaction curves do not display a large increase in richness. Conversely, in Bajocian samples the among-sample richness may be higher even though within-sample richness is lower, for example different taxa may be present within different samples, even though the total number of taxa within each sample may be low, thus with additional samples, sample-based rarefaction curves appear markedly richer than individual-based rarefaction curves.

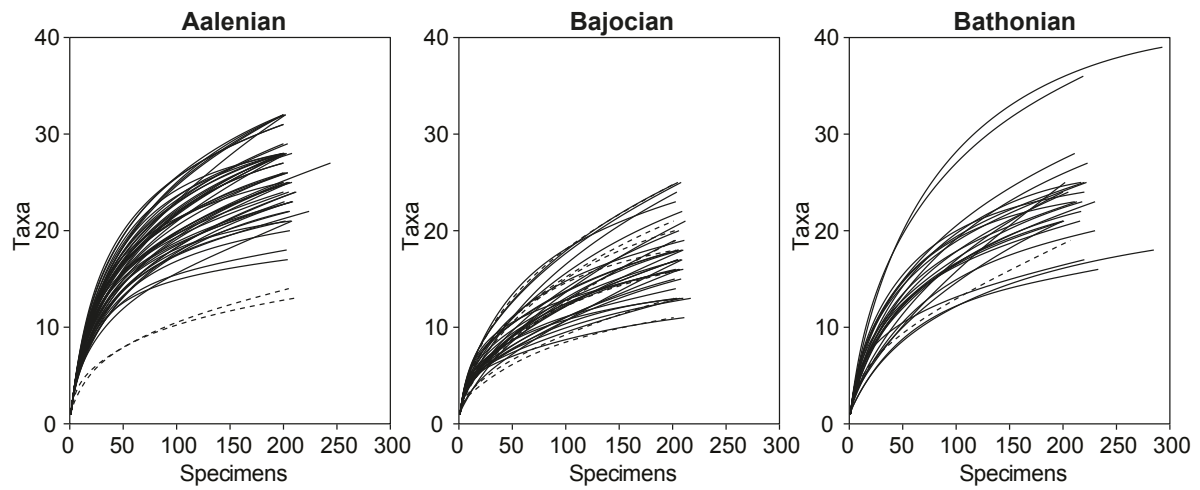


Figure 4.7: Individual-based rarefaction curves for all samples separated into the Aalenian, Bajocian and Bathonian stages. Dashed lines represent coal samples. The 95 % confidence interval lines have been removed for clarity.

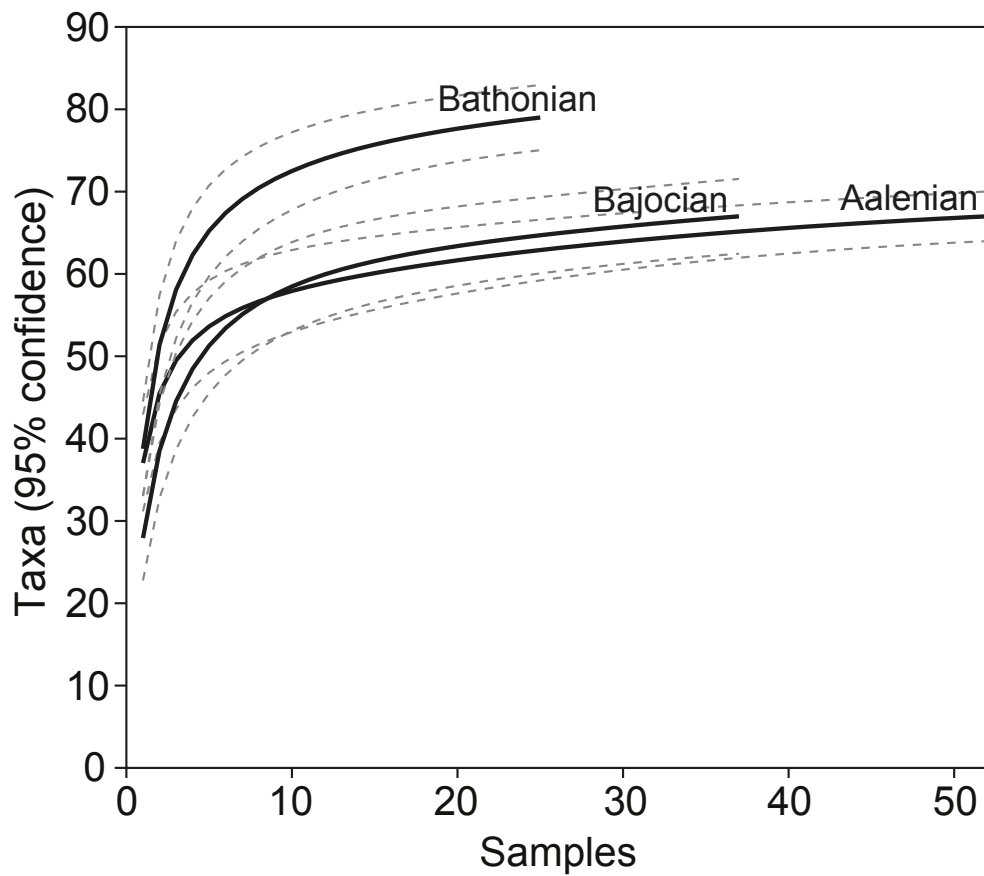


Figure 4.8: Sample-based rarefaction curves for Aalenian, Bajocian and Bathonian samples. Dashed grey lines represent 95 % confidence intervals.

### ***4.3.3 Sample ordination***

NMDS of relative abundance data (Figure 4.9A) and presence–absence data (Figure 4.9B) reveals that samples from the Aalenian, Bajocian and Bathonian stages are well separated in ordination space, with only minimal overlap. This demonstrates a clear change in sporomorph assemblage composition through time and, similarly to abundance plots (Figures 4.5A–4.6A) suggests that the Aalenian, Bajocian and Bathonian stages possessed relatively distinct floras, both in terms of species abundances and the presence/absence of taxa. It should be noted that the presence–absence NMDS shows a less clear separation of stages than the relative abundance NMDS. This suggests that the relative abundance shifts in range through taxa are more important than differences in composition (i.e. which taxa are present or absent) among the three stages. In both ordinations (Figure 4.9) samples primarily cluster according to their age, regardless of lithology, indicating that the stratigraphic position of a sample is more important than its lithology/local depositional environment through the Ravenscar Group. However, there are groupings of similar lithologies and coal samples are more scattered across plots, this potentially reflects the generally low richness of coals due to their small representative source areas. Thus composition varies to a measurable degree regarding the lithology of a sample, which potentially reflects different vegetation and/or different depositional processes to preserve different assemblages. This is however secondary to the temporal position of a sample, which, with the exception of coals, is evident in ordinations regardless of lithology. Axis scores for Figure 4.9 are provided in Appendices 5 and 6.

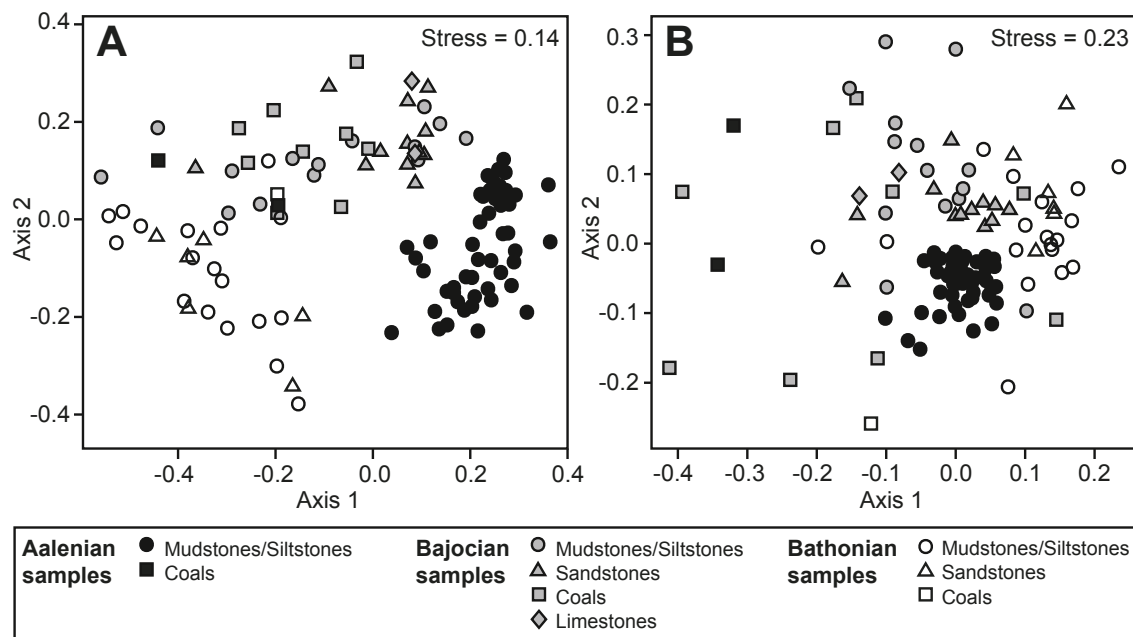


Figure 4.9: Nonmetric multidimensional scaling plots of sporomorph data. A, relative abundance data, and B, presence–absence data.

#### 4.3.4 Palynofacies Analysis

Abundances of organic debris are provided in Figure 4.6B. Most samples are composed of a heterogeneous mixture of organic debris, co-dominated by AOM, inertinite, unstructured vitrinite, pollen and spores. Abundant AOM throughout the Ravenscar Group suggests relatively low oxygen and high nutrient levels within the original water during deposition (Tyson 1995; Roncaglia 2004; Traverse 2007; Paction *et al.*, 2011). Similarly to sporomorph assemblages, stratigraphic variation is visible in palynofacies assemblages between the Aalenian, Bajocian and Bathonian stages, which potentially reflect long-term depositional and/or vegetation change through time. Short-term variations in assemblages are also present between stratigraphically adjacent samples from individual sections, which roughly correlate with lithological variation. Aalenian samples are composed of high abundances of inertinite, structured vitrinite and low abundances of spores compared to Bajocian and Bathonian samples. Bajocian samples contain considerably more spores, slightly more cuticle and less structured vitrinite and inertinite compared to Aalenian samples, and Bathonian samples contain high abundances of cuticle and spores compared to Aalenian and Bajocian samples.



Unsurprisingly, samples from the Leberston Member and the Scarborough Formation contain occasional dinoflagellates and marine algae, which reflect the marine environments of these units.

#### **4.4 Discussion**

##### ***4.4.1 Short-term vs. long-term variation in sporomorph assemblages***

Comparing variation in sporomorph and palynofacies assemblages with lithology and more generally with time can help to extract information on respective short-term and long-term changes in vegetation and depositional environments. Such comparisons can assist to determine whether temporal variation in these fossil assemblages represents ‘true’ variation in parent vegetation, or is simply the result of variable taphonomic processes through time. Abundance/richness plots and ordinations (Figures 4.5–4.9) demonstrate that variation between sporomorph and palynofacies assemblages correlates with lithology/depositional setting within individual sections. This is particularly apparent at Hasty Bank, where assemblage composition differs considerably between the lower and upper parts of the section, between which there is a change in depositional setting. Thus a change in parent vegetation and/or taphonomic processes, which shape sporomorph assemblages, is not particularly surprising (Slater and Wellman 2015). Furthermore, within individual sections there are often considerable abundance variations of taxa from samples that are stratigraphically very close to one another. Hence, relatively short-term depositional change within individual sections has a measurable impact on (i) parent vegetation and resultant sporomorph assemblages, and/or (ii) preferential preservation of certain sporomorphs due to taphonomic processes.

Within individual sections (e.g. section 5) samples taken from similar lithologies generally have similar palynofloral compositions. Broadly speaking, within individual sections, overbank deposits are characteristically composed of highly diverse palynofloras with abundant conifer pollen, channel sediments are routinely composed of diverse assemblages with abundant ferns and conifers, and coals and other confined deposits (e.g.

abandoned channels) are typically composed of abundant fern assemblages with very low overall diversities. The reasons for this correlation between sporomorph assemblages and lithology/depositional setting is due to a combination of both, (i) similar vegetation, and (ii) similar depositional/taphonomic processes occurring within these parallel environments. Specifically, the high overall diversities and abundant conifer pollen in floodplain samples is probably a result of the large source areas supplying such deposits (Behrensmeyer and Kidwell 1985; Behrensmeyer *et al.*, 2000), with multiple river channels potentially feeding hinterland taxa into these settings, thus increasing overall diversities and abundances of coniferous pollen. The relatively diverse sporomorph assemblages recognized within channel sediments are, similarly to floodplain deposits, but to a lesser extent, the result of relatively large source areas. Multiple tributaries would have potentially flowed into these channels, hence source area size is increased and abundances of coniferous hinterland taxa and overall diversities are increased alike. The high abundances of ferns, low abundances of conifers and low overall diversities within coal and abandoned channel deposits are likely a result of the confined source areas that supplied these deposits. Hence, coals and abandoned channel deposits sampled within this study are more representative of the parent vegetation close to the site of deposition compared to most other lithologies/depositional environments, which are generally more representative of the regional flora. The results here indicate that with decreased source area size, there is a decrease in the ratio of coniferous pollen compared to other sporomorphs. This suggests that abundant coniferous parent vegetation did not occupy the interior of the sedimentary basin, but instead, conifers were typical of extrabasinal/hinterland environments, whereas coal and abandoned channel samples demonstrate that primarily ferns dominated the interior of the basin.

Chaloner and Muir (1968) compared Jurassic sporomorph assemblages from Yorkshire from different lithologies and demonstrated that, when sporomorphs were grouped morphologically, assemblages were compositionally more similar to each other according to their respective lithologies than they were according to their sampled stratigraphic position. This relationship was attributed to changes in base level, which altered the relative areas of

different communities and their proximity to sampling sites (Chaloner 1968; Chaloner and Muir 1968). Similar results are apparent in this study, however ordination of samples (Figure 4.9) based on individual taxa (i.e. where sporomorphs have not been grouped as in Chaloner and Muir (1968)) reveal that samples cluster primarily according to their stratigraphic position and secondarily according to their lithology, thus samples appear more similar to one another in terms of their age than their lithology/depositional setting. Therefore, as postulated by Chaloner and Muir (1968), long-term changes in sporomorph assemblages are seemingly more apparent when taxa are analysed individually and are probably more important than short-term assemblage variations through individual sections (e.g. Hasty Bank). Coal samples are an exception to this rule, as sporomorph assemblages from coals sampled here are more similar to each other according to their lithology than they are according to their sampled stratigraphic position, presumably due their very localized catchment areas. The pattern described by Chaloner and Muir (1968) was more extreme in their study because the lithologies/depositional environments sampled were more varied than the environments sampled in this study. For example, they analysed samples ranging from marine black shales to terrestrial coals, thus there was high compositional variation between these highly different depositional environments even when samples were synchronous. The depositional environments sampled in this study are less varied, thus helping to explain why, with the exception of coals, variation between samples appears to be primarily stratigraphic and secondarily lithological/depositional.

Figures 4.5–4.9 reveal a dynamic long-term palynofloral history for the Ravenscar Group in which fern spores gradually become dominant over conifer pollen from the Aalenian into the Bathonian. Lycophytes and pteridosperms/conifers become markedly more abundant in the Bathonian, and conversely monosulcate producers and sphenophytes become considerably less abundant in the Bajocian and Bathonian. Although short-term taphonomic controls are highly important, such controls are superimposed on long-term variations in sporomorph assemblages, which are more apparent when taxa are analysed individually and are considered to be representative of long-term variations in depositional environments

through time, which influence depositional taphonomic processes and parent vegetation, thus giving rise to temporal variations in sporomorph assemblages.

#### ***4.4.2 Biases in the sporomorph record***

Extracting true changes in parent vegetation through time using the sporomorph record is often problematic as ecological and taphonomic biases can dramatically affect the composition of assemblages (e.g. Chaloner and Muir 1968).

Perhaps the most important biological factor in shaping assemblage composition is the variation in spore/pollen production levels between plant groups as a result of different reproductive strategies. For example, sporomorph production in wholly wind-dispersed taxa, such as the conifers and ferns is typically very high, thus such plant groups are overrepresented compared to reproductively specialized taxa (e.g. Mander *et al.*, 2010). Therefore, abundances of sporomorph plant groups almost certainly do not accurately reflect the abundances of parent plant groups within the palaeofloristic community. However, all factors being equal, temporal changes in sporomorph abundances often do fairly reflect regional scale abundance change within a particular plant group, as sporomorph production levels presumably do not vary greatly within plant groups through time.

The proximity of parent plants in relation to their depositional setting plays an important role in governing assemblage composition. An example of this is visible in this study; sample P4 contains exceptionally high abundances of the lycophyte spore *Densoisporites velatus*, which is typically rare in all other samples. This deposit presumably represents a confined source area, which was occupied by the lycophyte parent plant, hence, this sample almost certainly does not accurately reflect the regional flora, but provides insight into the parent vegetation close to the site of deposition. Determining information on the relative proximity of parent plants to their depositional setting is potentially possible regarding some of the reproductively specialized taxa such as the cycads. Kono and Tobe (2007) demonstrated that the pollen of the modern cycad, *Cycas revoluta*, occurs only in abundance within close proximity to the parent plant, thus if Jurassic equivalents share this

characteristic, deposits that are abundant in cycad pollen potentially formed within close proximity to the cycad parent plants.

The differential physical durability of taxa plays an important role in influencing assemblage composition. For example, many fern spores possess relatively thick spore walls (e.g. *Deltoidospora*) and are thus reasonably resistant to taphonomic processes such as transportation and corrosion. Conversely, some spores, such as *C. mesozoica* possess a thin spore wall and contain little sporopollenin (Traverse 2007; Grauvogel-Stamm and Lugardon 2009) and are resultantly comparatively underrepresented.

A further problem with the sporomorph record is that many parent plants produce sporomorph taxa that appear superficially indistinguishable from one another, particularly when using only light microscopy (Mander and Punyasena 2014). This is particularly apparent within the Jurassic cycads and ginkgos, which typically produce simple, monosulcate pollen that display no obvious distinguishing features under light microscopy (e.g. Frederiksen 1980). Thus, when using sporomorphs to make palaeofloristic reconstructions, it is sensible to group sporomorphs at a relatively high taxonomic level, preferably at family-level or higher.

Depositional environment is a fundamental factor controlling the composition of parent vegetation and resultant sporomorph assemblages. Additionally, different depositional environments often display considerable variation regarding the geographic catchment areas that supply deposits. This relationship is particularly apparent regarding the low richness levels visible in a number of coal samples. The associated rootlet beds present below the coals at Hayburn Wyke and Cloughton Wyke suggest that these deposits formed in situ. These coals potentially represent small, confined swamps that have formed above a soil horizon. All coals sampled here are considerably less extensive than the prominent drifted coal seam present at Brora, Scotland, which has yielded excellent palynomorphs (e.g. Couper 1958; Hughes and Couper 1958; Lam and Porter 1977; Riding 2005). Presumably, the coals sampled here were supplied by relatively small geographical catchment areas, thus input into these coal-forming environments is reduced and sporomorph richness is reduced

accordingly. Conversely, high richness within the Aalenian samples at Hasty Bank reflects the depositional environments there; samples originate from a probable floodplain and fluvial channel environment (Slater and Wellman 2015). Such depositional environments were potentially supplied by very large geographical catchment areas compared to confined coal-forming swamps, resultantly richness is considerably higher in these deposits.

Variable transportation processes and distances also influence sporomorph assemblage composition. Spores and pollen can be considered as sedimentary particles during transport and depositional processes. Hence, differences in factors such as particle size, shape and density influence whether certain sporomorphs are preserved in a particular depositional setting. Evidence for these variable processes is visible here; samples from the marine Leberston Member contain low numbers of fern spores and high numbers of conifer pollen; this pattern is mirrored in the overlying non-marine Gristhorpe Member. This almost certainly does not reflect genuine parent vegetation change, but is the result of variable taphonomic processes between these units comparable to the 'Neves effect' (Chaloner and Muir 1968). Specifically, the reduced clastic input/fluvial connection in the Leberston Member means that 'light' conifer pollen is more likely to reach these environments via water and air transport compared to 'heavy' fern spores that predominantly require fluvial action to be transported into the marine system. Similar patterns are visible in the Long-Nab Member; the high abundances of cuticle and spores relative to pollen in the Long-Nab Member potentially indicate less extensive and/or lower energy transportation distances and processes for Bathonian samples as fragile cuticle is likely to be destroyed during extensive transportation (Cross *et al.*, 1966; Muller 1959) and a high percentage of spores compared to pollen typically indicates that assemblages are derived from a relatively close proximity to parent vegetation (e.g. Habib 1982).

Spatial variations in depositional environments can have large consequences on sporomorph assemblages (e.g. Chaloner and Muir 1968). Samples from section 4 and the lower part of the Gristhorpe Member from section 3 are roughly synchronous; these samples display high compositional similarity suggesting little spatial floral variation between these

localities. Minimal variation was also noticed between synchronous samples from Burniston Bay. The similar sporomorph assemblages between these synchronous deposits with slightly different depositional settings suggest that temporal variations in assemblages are representative of potentially substantial changes in depositional processes and/or accompanying parent vegetation and indicate that spatial variations in local floras of the examples discussed are relatively minor.

#### ***4.4.3 Comparison with the plant mega/mesofossil record***

Changes in composition between plant megafossil assemblages through the Ravenscar Group are generally well-documented following extensive collection and description of specimens from numerous palaeobotanical studies over the past century (see van Konijnenburg-van Cittert and Morgans 1999). Harris (1952) discussed ranges of plant megafossil taxa through the Middle Jurassic of Yorkshire. He observed that unlike underlying and overlying strata, the plant megafossil assemblages of the Cloughton Formation were dominated by conifer cuticle and some ginkophytes and cycadophytes were absent. The spore and pollen record in this study agrees with these observations in that samples from the Cloughton Formation are dominated by conifer pollen and simple monosulcate pollen is markedly less abundant compared to underlying Aalenian samples and moderately less abundant than overlying Bathonian samples (Figure 4.6A). Hence, both sporomorph and plant megafossil records suggest that cycad and ginkgo parent vegetation was less abundant and diverse in the Bajocian compared to the Aalenian and Bathonian.

Van Konijnenburg-van Cittert and Morgans (1999) demonstrate that the plant megafossil *Equisetum* is markedly more abundant within the Aalenian plant beds of the Ravenscar Group. The sporomorph record agrees with this observation; *Calamospora* is also more abundant within the Aalenian. As both fossil assemblages record the same temporal abundance patterns this potentially reflects a ‘true’ vegetation change and suggests that *Equisetum* was more abundant in the Aalenian.

Slater and Wellman (2015) compared plant megafossil (Spicer and Hill 1979) and dispersed sporomorph assemblages through the Hasty Bank plant bed and recognized notable discrepancies between assemblages regarding the nature of parent vegetation. Specifically, conifers and ferns were underrepresented in plant megafossil assemblages, bryophytes and lycopsids were represented only in sporomorph assemblages, and sphenophytes, pteridosperms, Caytoniales, Cycadales, Ginkgoales and Bennettitales were comparatively underrepresented in sporomorph assemblages. The major causes for these discrepancies were attributed to a multitude of biological and taphonomic biases including, variation in sporomorph production levels between parent plants, depositional environment, variation in sporomorph and parent plant durability and the proximity of parent plants in relation to the site of deposition. Similar results were identified from Triassic–Jurassic sequences of East Greenland (Mander *et al.*, 2010) and from Lower Jurassic deposits of Odrowąż, central Poland (Ziaja 2006), suggesting that the taphonomic/ecological causes for the discrepancies between the sporomorph and plant megafossil assemblages occur across a range of different depositional environments and localities.

#### ***4.4.4 Comparison with climatic changes and regional-scale vegetation***

Diverse parent vegetation and favourable taphonomic conditions means that the total diversity of the Yorkshire Jurassic flora is high, however excellent sedimentary exposures and extensive investigations into these deposits means that overall diversity is relatively well represented compared to other contemporaneous regional deposits. Synchronous deposits from Gloucestershire and Oxfordshire are generally less diverse in terms of their sporomorph and megafossil assemblages (e.g. Riding 1983; Cleal and Rees 2003; Srivastava 2011) due to these taphonomic and collection biases, however despite these factors floral compositions do appear to display some consistencies and provincialism with regional deposits (e.g. Boulter and Windle 1993).

Determining the causes of vegetation change in the fossil record is frequently problematic as there are numerous possible variables that can influence floral communities



through time. Such variables include climatic, ecological, geographical and depositional factors. Chaloner (1968) and Chaloner and Muir (1968) postulated that changing sporomorph assemblages through the Jurassic of Yorkshire could be the result of changing base level, under a constant climate, however they emphasize that climatic changes could also be involved. More recent climatic interpretations through the Middle Jurassic of Yorkshire suggest multiple changes through these sequences. Based on fossil wood material collected through the Ravenscar Group, Hesselbo *et al.*, (2003) recorded a negative  $\delta^{13}\text{C}$  isotope excursion at the Aalenian–Bajocian boundary, across which the dominant preservation mode of fossil wood changed from charcoal to coal, suggesting a shift to a more continuously humid climate in the early Bajocian. Their findings were also indicative of a seasonally arid environment in the middle Bajocian marked by an increase in charcoal preservation mode. Hesselbo *et al.*, (2003) stated that the megafloral record, based on findings by Harris (1961, 1964, 1969, 1979) and Harris *et al.*, (1974) appeared to contradict the C-isotope results in that vegetation change apparently suggested a change from ‘wetter’ to ‘drier’ environments with a decrease in diversity from the Aalenian into the early Bajocian.

Boulter and Windle (1993) used dispersed sporomorph data in combination with megafloral records from Yorkshire and across the UK to reconstruct Middle Jurassic vegetation. Their findings suggested three distinct floral communities through the Middle Jurassic: (i) ‘Mesozoic gymnosperms’ in the Aalenian, (ii) ‘fern prairies’ in the middle Bathonian and (iii) ‘conifer forests’ in the late Bathonian. Both Bathonian floras were however dominated by conifer pollen and these two communities were considerably more similar to each other than they were compared to Aalenian palynofloras. The three communities described by Boulter and Windle (1993) are analogous to the vegetation reconstructions in this study. Specifically, ‘Mesozoic gymnosperm’ communities are highly similar in composition to the Aalenian Hasty Bank samples in this study and the Bathonian ‘fern prairies’ and ‘conifer forests’ from Oxfordshire and Northamptonshire are similar to the palynofloras of the Bathonian Long Nab Member in this study. This suggests high floral

compositional similarity between these localities and/or similar taphonomic processes were acting on assemblages to preserve similar fossil records. Boulter and Windle (1993) suggested that the change from ‘Mesozoic gymnosperm’ communities in the Aalenian to conifer dominated palynofloras in the Bajocian and Bathonian could be indicative of (i) conifers occupying niches left by other plants and/or (ii) increased aridity in the Bajocian and Bathonian. Equally, the ‘Mesozoic gymnosperm’ communities of the Aalenian are potentially suggestive of more humid conditions compared to the Bathonian (Boulter and Windle 1993).

Based on sporomorph assemblages from multiple localities across Europe (including the Jurassic of Yorkshire) and Australia, Hubbard and Boulter (1997) used groupings of climate indicative taxa to reconstruct climatic variation through parts of the Mesozoic. Their findings suggested overall temperatures decreased slightly near to the Aalenian–Bajocian boundary, temperatures then rose gradually towards the Bathonian–Callovian boundary. Hubbard and Boulter (1997) demonstrated that sporomorph groupings at Hasty Bank were dominated by cold adapted taxa, indicating relatively cold climatic conditions in the Aalenian. Bajocian assemblages from Cloughton Wyke and Yons Nab were co-dominated by cold–intermediate climatically adapted taxa and Bathonian assemblages from Scalby Ness and Gristhorpe were composed of a mixture of warm, intermediate and cold adapted taxa, thus suggesting a rise in temperatures from the Aalenian to the Bathonian.

Sporomorph evidence in this study concurs with previous megafloreal (Harris 1961, 1964, 1969, 1979; Harris *et al.*, 1974) and sporomorph investigations (Boulter and Windle 1993; Hubbard and Boulter 1997) from the Middle Jurassic of Yorkshire. Specifically, the megafloreal record agrees with the sporomorph record in that overall diversities here decrease from the Aalenian into the Bajocian and floral abundances shift from a heterogeneous mixture of conifers, ferns, monosulcate producers, sphenophytes and Caytoniales to a more homogeneous assemblage, co-dominated by conifers and ferns. Similarly to previous sporomorph investigations (Boulter and Windle 1993), assemblages here display a marked decrease in monosulcate producers at the end of the Aalenian.

Cleal and Rees (2003) investigated the Middle Jurassic fossil flora of Stonesfield, Oxfordshire. This is considered to represent mostly coastal vegetation with abundant Cheirolepidiaceae. The marine depositional setting at Stonesfield undoubtedly influences the taphonomy of the assemblages; despite this, terrestrial vegetation appears to be somewhat different to that of the Yorkshire Jurassic. Floras of Stonesfield are less diverse and possess no horsetails and ferns and Ginkgoalean foliage are poorly represented. Cleal and Rees (2003) suggest that the Stonesfield flora represents a seasonally dry climate; whilst Yorkshire and Araucariaceae dominated floras from the Isle of Skye (Bateman *et al.*, 2000; Cleal *et al.*, 2001) represent warm-temperate climatic conditions.

Although climatic interpretations display some general consistencies, it is difficult to state with certainty whether the apparent changes in vegetation recorded in this study are definitely related to climatic events, as there are numerous factors that could cause such changes to occur. The majority of temporal changes seen in sporomorph assemblages here are interpreted to be due to long-term changes in depositional environments through the Ravenscar Group which result in differences in depositional taphonomic processes and parent vegetation through time. For example, the variation in assemblages seen between non-marine and marine units, particularly regarding the ratios fern spores to conifer pollen is greatly affected by changes in depositional taphonomy, but changes in the proximity of the coastline to the basin interior (i.e. the palaeogeographic position of the coastline) will also influence parent vegetation, as numerous environmental factors (e.g. salinity, water supply and ground disturbance) will change with distance from the shoreline.

#### ***4.4.5 Emerging reconstruction***

Despite the numerous biases within the sporomorph record, it is clear that this fossil data can be useful in the assessment of palaeovegetation change through time, particularly when depositional context is taken into account. Integrating the sporomorph record with multiple fossil assemblages (e.g. plant megafossils) and geochemical proxies (e.g. C-isotope data) is an important task in refining palaeoenvironmental reconstructions. The emerging picture

from this study compliments previous palaeoenvironmental (e.g. Alexander 1989) and palaeogeographical (e.g. Rawson and Wright 2000) reconstructions for the Cleveland Basin. The general consensus in the literature is indicative of a lowland coastal plain basin interior that was periodically flooded by seawater (e.g. Ielpi and Ghinassi 2014), surrounded by upland environments (Rawson and Wright 2000). This study suggests the basin interior was occupied mostly by low-standing, lush species and the extrabasinal vegetation was dominated by coniferous taxa. Interestingly, samples from the dinosaur footprint bed at Burniston Bay (JP1/7 and JP2/8) contained highly abundant fern spores (*D. minor* and *D. harrisii*), with low abundances of conifer pollen and diverse lycophyte assemblages. The co-occurrence of abundant footprints (e.g. Whyte *et al.*, 2007) with low-standing, relatively lush vegetation within the basin interior is indirect evidence to suggest herbivorous species were visiting this area to feed.

#### **4.5 Conclusions**

The Aalenian, Bajocian and Bathonian stages possess relatively distinct sporomorph assemblages, which potentially reflect a dynamic history for the nature of parent vegetation through the Middle Jurassic of Yorkshire. Specifically, Aalenian floras were composed of a heterogeneous mixture of conifers (conifers dominate), ferns, monosulcate producers, sphenophytes and Caytoniales. Bajocian floras were more homogeneous in composition than Aalenian and Bathonian counterparts and were co-dominated by conifers (conifers dominate) and ferns with low abundances of all other plant groups. Bathonian communities were highly rich and composed of abundant ferns (ferns dominate), conifers, lycophytes, pteridosperms/conifers and Caytoniales. Vegetation reconstructions from this study combined with previous palaeogeographical reconstructions for the Cleveland Basin (e.g. Rawson and Wright 2000) suggest that the basin interior was occupied by low-standing, lush species and extrabasinal vegetation was dominated by coniferous taxa. Long-term changes in composition are probably a result of depositional and/or climatic changes, which altered depositional taphonomic processes and parent vegetation. Comparisons of the dispersed

sporomorph and plant megafossil records through the Ravenscar Group indicate that both fossil assemblages reflect different aspects of the parent vegetation due to a multitude of taphonomic and ecological biases. Such biases include, variation in spore/pollen production levels between plant groups, differences in transportation and depositional processes, variation in spore/pollen and parent plant durability and the proximity of parent plants in relation to the site of deposition.

**CHAPTER 5: A QUANTITATIVE COMPARISON OF DISPERSED  
SPORES/POLLEN AND PLANT MEGAFOSSIL ASSEMBLAGES FROM A  
MIDDLE JURASSIC PLANT BED FROM YORKSHIRE, UK**

A manuscript version of this chapter has been published in the journal *Paleobiology* (Slater and Wellman 2015). The experiment was devised by SMS and CHW, conducted by SMS, and the chapter/manuscript was written by SMS under the guidance of CHW. See Appendix 14 for the published paper.

### **5.1 Introduction**

Understanding the causes of temporal variation in palaeofloras is a fundamental objective of palaeobotany. Extracting these causes is, however, frequently problematic as it is often difficult to determine the dominant controls on the constituents of fossil assemblages. Such controls include ecological, climatic, depositional and preservational factors. Establishing the causes of palaeofloristic temporal variation is clearly enhanced when a multidisciplinary approach is used, as the overreliance on singular lines of evidence can often lead to over interpretation. Comparing data from the plant megafossil and terrestrial palynological records can provide important insight into ecological and preservational biases that can shape diversity (richness) and abundance patterns of these fossil assemblages. Thus, such comparisons can help to determine the reliability of palaeofloristic interpretations based on the sporomorph and plant megafossil records in isolation.

The sequences of North Yorkshire, UK offer a rare example of extensive Middle Jurassic terrestrial deposits. The sedimentary successions have previously been studied in detail for their palaeontological significance (e.g. Romano and Whyte 2003) and particularly for the famous plant beds that are scattered throughout these sequences (e.g. Black 1929; van Konijnenburg-van Cittert 1968, 1975, 1996, 2008; Crane and Herendeen 2009; Spicer and Hill 1979; van Konijnenburg-van Cittert and Morgans 1999). Although plant megafossil studies from these deposits are common in the literature (e.g. Harris 1941, 1944, 1952, 1953,

1961a, 1961b, 1964, 1969, 1978, 1979; van Konijnenburg-van Cittert 1972, 1975, 1978, 1981, 1989, 1996, 2008; Harris *et al.*, 1974; Spicer and Hill 1979; Hill 1990; Morgans 1999; van Konijnenburg-van Cittert and Morgans 1999), published dispersed spore and pollen investigations remain comparatively sparse (e.g. Couper 1958; Chaloner, 1968; Chaloner and Muir 1968; Riding 1984; Riding and Wright 1989; Gowland and Riding 1991; Boulter and Windle 1993; Hubbard and Boulter 1997; Butler *et al.*, 2005; Srivastava 2011).

This chapter provides a detailed palynological assessment of a plant bed from Hasty Bank, North Yorkshire, UK that was previously analyzed for its plant megafossil contents. Spicer and Hill (1979) carried out a comprehensive quantitative study of this plant bed in which they sampled contiguous plant megafossil census counts through a through a 5 m outcrop section. Plant megafossil counts were carried out on rock blocks of either 50 or 25 cm<sup>2</sup> parallel to bedding and 10 or 20 cm in depth, perpendicular to bedding. Counts were then multiplied accordingly so that all abundances correspond to a 50 × 50 × 20 cm<sup>3</sup> block of sediment. The histogram of their results is provided in Appendix 7. Sporomorph quantitative data was analyzed here from the same section discussed in Spicer and Hill (1979) in order to compare this with the quantitative plant megafossil data. Palynofacies analysis was also carried out in order to aid environmental reconstructions (Tyson 1995). Palaeofloristic comparisons of sporomorph and plant megafossil data are possible due to comprehensive in situ spore/pollen (e.g. van Konijnenburg-van Cittert 1968, 1971, 1978, 1981, 1989, 1993, 2000; Pedersen *et al.*, 1989; Hill 1990; Osborn and Taylor 1993; Balme 1995; Friis and Pedersen 1996; Yang *et al.*, 2008) and ultrastructural transmission electron microscope (TEM) studies (e.g. Batten and Dutta 1997) which means that the majority of Middle Jurassic sporomorphs can now be assigned at least to family level plant classification.

By comparing dispersed spore/pollen assemblages with plant megafossil data in association with palynofacies analysis it was anticipated that a more realistic palaeofloristic and palaeoenvironmental interpretation would be possible and potential discrepancies in data sets would help to explain preservational biases between sporomorph and plant megafossil records. Since sporomorph and plant megafossil assemblages undergo different

transportation and depositional processes, it was expected that the respective fossil assemblages would be notably dissimilar in composition (e.g. Bercovici *et al.*, 2008, 2009), with the anticipation that our analyses may shed light on the reasons behind these differences.

The plant bed under investigation is located on the northern slope of Hasty Bank (NZ 567 037), situated within the northwest region of the North York Moors National Park, northeast England. The plant bed occurs at the base of the Aalenian Saltwick Formation, stratigraphically located at the base of the Ravenscar Group (Figure 2.6) and lies unconformably above the marine Dogger Formation. The bed is approximately 7 m thick and has previously yielded a varied flora of 90 species (Hill and van Konijnenburg-van Cittert 1973; Hill 1974; Spicer and Hill 1979). Two lithologies dominate the plant bed (Figure 5.1), a claystone that forms the lower part of the section and a siltstone that occupies the majority of the upper part of the section. An erosional surface is present between the claystone and the siltstone. A thin lens of dark grey clay is also present at the top of the section (Hill and van Konijnenburg-van Cittert 1973; Hill 1974).

The claystone is uniform dark grey in color. Grain size is homogeneous through the unit and thin (1–3 mm scale) horizontal laminae are abundant. The rock is relatively soft and breaks apart easily along laminae, which often reveal highly abundant fragmentary plant megafossils.

The siltstone is a homogeneous medium grey color. Grain size is uniform through the unit and larger, more prominent horizontal laminae (5–10 mm scale) are present. The rock is harder than the claystone and fragmentary plant megafossils are abundant, although less so than in the claystone. Horizontal roots occur in low abundance within the basal ~1 m of the siltstone, these are typically less than 2 cm in length and ~2 mm in width.

The grey clay at the top of the section is a homogeneous very dark grey color. Grain size is uniform through the unit and no sedimentary structures are visible. The rock is very soft and not fully lithified. Plant megafossils are less common in the grey clay than in the claystone and siltstone.



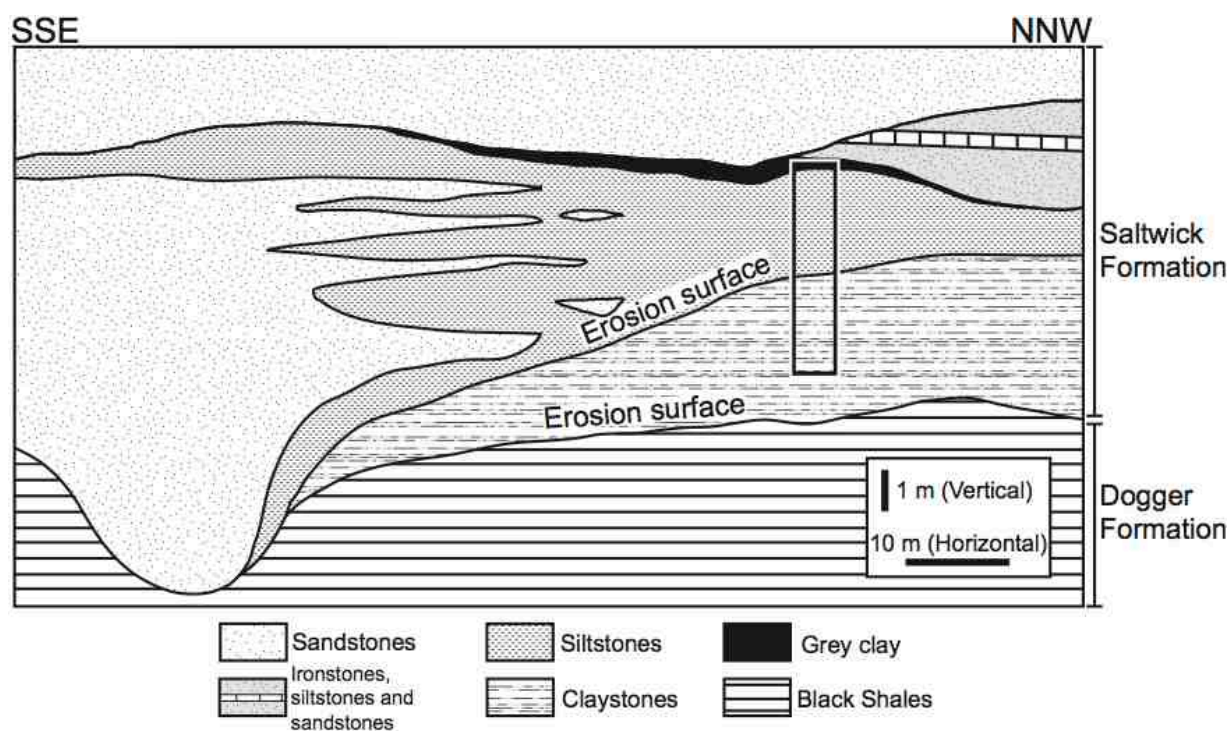


Figure 5.1: Cross-section of the geology of the main plant bed at Hasty Bank. Vertical and horizontal scales provided (vertical scale exaggerated four times). The section discussed is shown by the rectangle. Adapted from Hill and van Konijnenburg-van Cittert (1973); Spicer and Hill (1979); van Konijnenburg-van Cittert and Morgans (1999).

### 5.1.1 Previous Interpretations of the Depositional Environments at Hasty Bank

The Hasty Bank plant bed was first recognized as an important fossil locality by Black (1929). Subsequent palaeobotanical and palaeoecological studies have commented on possible environments of deposition for the plant bed, most notably by Harris (1964), Hill and van Konijnenburg-van Cittert (1973), Hill (1974) and van Konijnenburg-van Cittert and Morgans (1999).

Harris (1964) postulated that the claystone at the base of the plant bed (Figure 5.1) was deposited in a coastal environment periodically flooded by seawater. These interpretations were based on the occurrence of the pteridosperm *Pachypteris papillosa* in association with rare marine microfossils thought to be derived from marine flooding events.

Harris (1983) reconstructed *P. papillosa* as a large shrub that formed mangrove-like thickets along tidal rivers. Spicer and Hill (1979) showed that *P. papillosa* is markedly more abundant within the claystone deposit compared to the rest of the section.

The siltstone is interpreted as the peripheral fringes of a large channel sandstone deposit immediately adjacent to the southeast of the plant bed (Figure 5.1). Hill and van Konijnenburg-van Cittert (1973) concluded that the siltstone was deposited in the slower flowing region of the channel. It is possible that the siltstone could however represent a levee or floodplain deposit peripheral to the sandstone. The channel has cut into the underlying sediments forming an erosional surface between the claystone and the siltstone and thus there is a time gap between these deposits.

Previous depositional environmental interpretations for the grey clay are lacking. However, sedimentological, sporomorph and palynofacies evidence from this study suggests that this deposit represents a swamp or an abandoned channel.

## **5.2 Materials and Methods**

### **5.2.1 Collection**

A total of 50 samples (HB1-HB50, numbered in reverse stratigraphic order, i.e., HB1 is at the top of the section) were collected at 10 cm vertical intervals from the main Hasty Bank plant bed (NZ 567 037) for palynological processing. Samples were taken from the identical section of that discussed by Spicer and Hill (1979), shown in Figure 5.1. Christopher R. Hill (of Spicer and Hill [1979]) was present during collection of samples to ensure the exact position of the section was located. Sampling required the excavation of approximately 50 cm of modern deposits to access the outcrop. The exterior of the outcrop was weathered between 5 and 20 cm deep into the rock. The section was therefore excavated a further ~30 cm into the outcrop to ensure fresh exposure. Samples HB1-HB3 are from the grey clay at the top of the section; HB4-HB28 are from the siltstone unit; and HB29-HB50 are from the claystone unit.

### **5.2.2 Processing**

Dry rock samples were weighed at 20 g before being dissolved in 40 % hydrochloric acid for at least 24 hours to remove carbonates, followed by two week maceration in 40 % hydrofluoric acid to remove silicates. Samples were agitated every two days to ensure full break down of rock material. Samples were then decanted and fresh water added, repeating the process until neutral. One day was left between decants to ensure minimal loss of palynomorphs. Two *Lycopodium* tablets (produced by the University of Lund, Sweden; batch 1031) were added before sieving at 10  $\mu\text{m}$ . Centrifuging residues in zinc chloride was then undertaken to remove heavy minerals. Residues were then sieved again at 10  $\mu\text{m}$  to remove the heavy liquid and final residues were spread across cover slips and gently heated on a hot plate to remove excess water. Cover slips were then mounted onto slides using epoxy resin on a hot plate. All materials (rock samples and slides) are housed in the collections of the Centre for Palynology at the University of Sheffield, U.K.

### **5.2.3 Counting**

Slides were examined under a Meiji Techno (MA151/35/50) light microscope. A minimum of 200 indigenous Jurassic sporomorphs were counted from each sample in addition to any *Lycopodium* spores from tablets in order to assess the relative organic richness of samples. The *Lycopodium* tablets contain a known quantity of spores ( $20,848 \pm 1546$  spores per tablet). This allows the palynomorph productivity of each sample to be assessed when counting sporomorphs, as numbers of *Lycopodium* spores can be compared with numbers of indigenous Jurassic sporomorphs to assess the palynomorph richness of samples. In this study, increased numbers of *Lycopodium* correspond to a decrease in palynomorph productivity per unit of sediment. Counts were carried out in systematic traverses across slides to ensure no grains were missed. For presence–absence data, the remainder of the slide was then examined in the same fashion to identify species that were not present in the count data. The complete raw data set is provided in Appendix 3.

#### **5.2.4 Palynofacies Analysis**

The term palynofacies typically refers to all of the visible organic particles (usually between 2–250 µm in size) that occur within palynological maceration residues (Traverse 2007).

Palynofacies analysis is commonly used to assess depositional environments (e.g. Parry *et al.*, 1981; Boulter and Riddick 1986; Van der Zwan 1990; Brugman *et al.*, 1994; Oboh-Ikuenobe and Yepes 1997; Oboh-Ikuenobe *et al.*, 2005; Carvalho *et al.*, 2006). In this study, palynofacies analysis attempts to provide a more in depth interpretation of the depositional environments at Hasty Bank. Categories for palynofacies debris are: spores, pollen, algae, dinoflagellate cysts, acritarchs, humic debris, amorphous organic matter (AOM), *Botryococcus*, structured vitrinite, unstructured vitrinite, cuticle and inertinite. For comprehensive descriptions and figures of palynofacies categories, see Tyson (1995) and Batten and Stead (2005). In the classification scheme used here ‘spores’ refers to trilete spores; ‘pollen’ refers to all pollen morphotypes; ‘algae’ refers to all algal forms that are not *Botryococcus*; ‘dinoflagellate cysts’ and ‘acritarchs’ represent marine palynomorphs which belong to these groups; ‘humic debris’ refers to yellow–brown humic material exhibiting little structure; ‘AOM’ refers to unstructured, amorphous organic matter; ‘*Botryococcus*’ represent fresh/brackish water algal colonies; ‘structured vitrinite’ refers to translucent–brown, lath-shaped to blocky woody particles that exhibit longitudinal structural thickenings; ‘unstructured vitrinite’ refers to brown woody material that has undergone extensive degradation; ‘cuticle’ refers to transparent to yellow epidermal fragments; and ‘inertinite’ refers to black woody material. Counts of 200 palynodebris based on point counts were carried out on all samples, the complete palynofacies raw data set is provided in Appendix 4.

#### **5.2.5 Statistical Analysis**

Correspondence analysis (CA) and nonmetric multidimensional scaling (NMDS) were performed on sporomorph data sets to further understand the causes of floral variation through the Hasty Bank plant bed. CA and NMDS are ordination methods that plot complex multivariate data onto a minimal number of axes (e.g. Jardine *et al.*, 2012). CA is an

eigenvector method of ordination that produces a graphical representation of a contingency table (Spicer and Hill 1979). NMDS is a nonparametric ordination technique that uses ranked distances between samples to assess the degree of similarities between samples (Chatfield and Collins 1980; ter Braak 1995; Legendre and Legendre 2012; Hammer and Harper 2006; Jardine *et al.*, 2012), hence clustering of samples in ordination space indicates high compositional similarity between those samples. For comprehensive descriptions of CA and NMDS see Greenacre (2007) and Cox and Cox (2001) respectively. CA and NMDS are becoming increasingly used in palynological analysis of quantitative palaeoecological studies (e.g. Kovach 1989, 1993; Wing and Harrington 2001; Hammer and Harper 2006; Bonis and Kürschner 2012; Jardine *et al.*, 2012; Stukins *et al.*, 2013) as such methods allow the user to extract information on the major causes of variation from complex data sets. CA was chosen over detrended correspondence analysis (DCA) as this method was employed by Spicer and Hill (1979) on megafossil data, thus to allow comparison of ordinations we used the same technique here. Both CA and NMDS are used here to assess abundance and presence–absence data. For NMDS ordinations, the Bray-Curtis dissimilarity metric was used to generate distances between samples as this method is considered to perform well in ecological analyses (e.g. Minchin 1987; Harrington 2008; Bowman *et al.*, 2014). Repeated runs were carried out for two dimensions until a convergent solution was established. Principal components rotation and centering was then applied to the final ordination. NMDS ordinations were performed using R, version 3.1.2 (R Core Team 2014), within the package “vegan”, version 2.2–1 (Oksanen *et al.*, 2015). Sporomorph relative abundances have been transformed logarithmically for CA and NMDS. This procedure condenses the differences in scores between abundant and rare species between samples, thus reducing the impact of highly abundant taxa on the data set and also reducing statistical noise. Spicer and Hill (1979) suggested that the most effective way to assess megafossil data in ordinations was to logarithmically transform abundances. Species that are present in samples but not in counts have been excluded from logarithmically transformed relative abundance ordinations. For taxonomic CA the same data has been used with the exclusion of species that contribute less

than 1 % of the total count to eliminate statistical noise. Presence–absence CA and NMDS were performed to assess co-occurrence and compositional variation between samples. For presence–absence analyses all species are included; species that are present are scored as ‘1’, species that absent are scored as ‘0’. Spiked *Lycopodium* data has been excluded from all ordinations. The statistical program PAST (Hammer *et al.*, 2001) was used to create CA plots.

## 5.3 Results

### 5.3.1 Sporomorph Diversity (Richness) and Abundance Variation

A total of 67 sporomorph taxa were recognized from 50 samples; the entire taxonomic list with associations between sporomorphs and parent plant groups is provided in Appendix 1. The commonly used Chao2 species richness estimator (Colwell and Coddington 1994) gave a species estimate of 69.94 taxa (standard deviation = 3.36) for the entire data set, which suggests the data set was not severely undersampled. Diversities (richness) for all samples (Figure 5.2B) show an increased level of compositional heterogeneity within claystone samples; diversity (richness) is slightly lower within the siltstone assemblage and lower again in grey clay samples. This indicates that the claystone was deposited at a time of increased floral diversity and/or claystone samples are capturing more sporomorph taxa due to preservational biases.

Relative abundances of all taxa are displayed graphically in Appendix 8. Relative abundances of the ten most abundant sporomorph taxa are provided in Figure 5.2A. Sporomorphs have been grouped into their botanical affinities in Figure 5.3A to extract information on higher taxonomic level temporal floral variations. Spiked *Lycopodium* spores exhibit the most prominent abundance variation through the sequence. Abundant spiked *Lycopodium* in grey clay (HB1-3) and siltstone (HB4-HB28) samples indicates that claystone samples (HB29-HB50) preserve far greater numbers of indigenous Jurassic sporomorphs.

Bryophytes (Figure 5.3A) are represented by two species and are in low abundance throughout the section. Lycopods are highly diverse (16 taxa) and abundances are low throughout the plant bed, but slightly higher in the siltstone compared to the claystone and grey clay. Sphenophytes are represented by *Calamospora mesozoica* and abundances are low and relatively constant throughout the section. Ferns are the most diverse group (23 taxa) and are highly abundant through the plant bed. Abundances increase from the claystone into the siltstone and increase again into the grey clay. Pteridosperms are represented by two species of *Alisporites*; diversity and abundances are low throughout the section, but slightly higher in the siltstone compared to the claystone and grey clay. Caytoniales are represented by the single species *Vitreisporites pallidus*; similarly to pteridosperms, abundances are low throughout the section, but slightly higher in the siltstone compared to the claystone and grey clay. Conifers constitute the most abundant group and are highly diverse (14 taxa). Abundances decrease markedly from the claystone into the siltstone and decrease again within the grey clay. Relative abundance variation within the conifers is most apparent within the three most abundant species: *Classopollis torosus*, *Perinopollenites elatoides* and *Araucariacites australis* (Figure 5.2A). *Classopollis torosus* and *P. elatoides* are considerably more abundant within claystone samples, whereas *A. australis* contrasts the overall abundance pattern of the conifers and is more abundant within siltstone samples. Cycadopsida/Ginkgopsida pollen is moderately diverse (four taxa) and displays little change in abundance (Figure 5.3A) through the plant bed. *Chasmatosporites hians* exhibits the most pronounced abundance variation within the Cycadopsida/Ginkgopsida group; *C. hians* is relatively common in the claystone, but becomes increasingly rare within siltstone samples and is absent above sample HB19. Bennettitales are low in abundance and diversity throughout the plant bed (two taxa). The largest relative abundance variation within the Bennettitales is displayed by *Cycadopites carpentieri*, which occurs frequently in the basal and upper samples of the section, but is absent from samples HB26 to HB16.

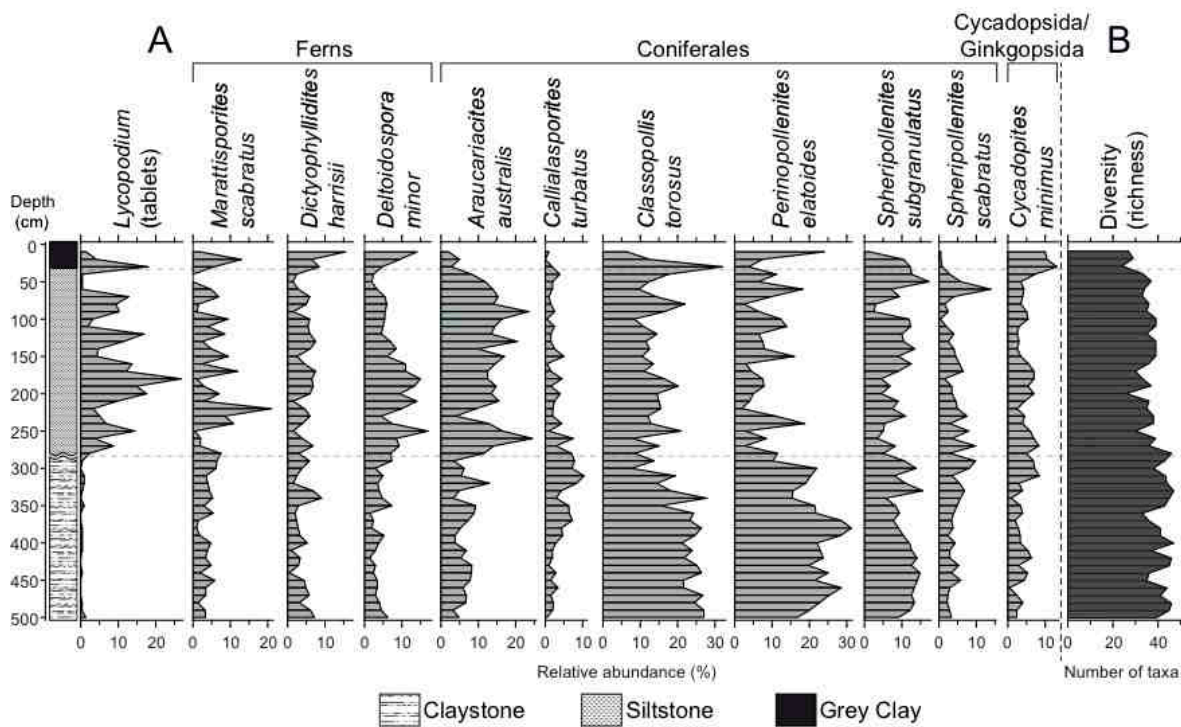


Figure 5.2: (A) Relative abundance chart of the ten most abundant sporomorph taxa in addition to spiked *Lycopodium*. Relative abundances of Jurassic taxa are calculated from counts of at least 200 grains. Spiked *Lycopodium* count data is shown as a percentage of the indigenous Jurassic taxa plus the spiked *Lycopodium* itself. (B) Sporomorph diversity (richness) for all samples.



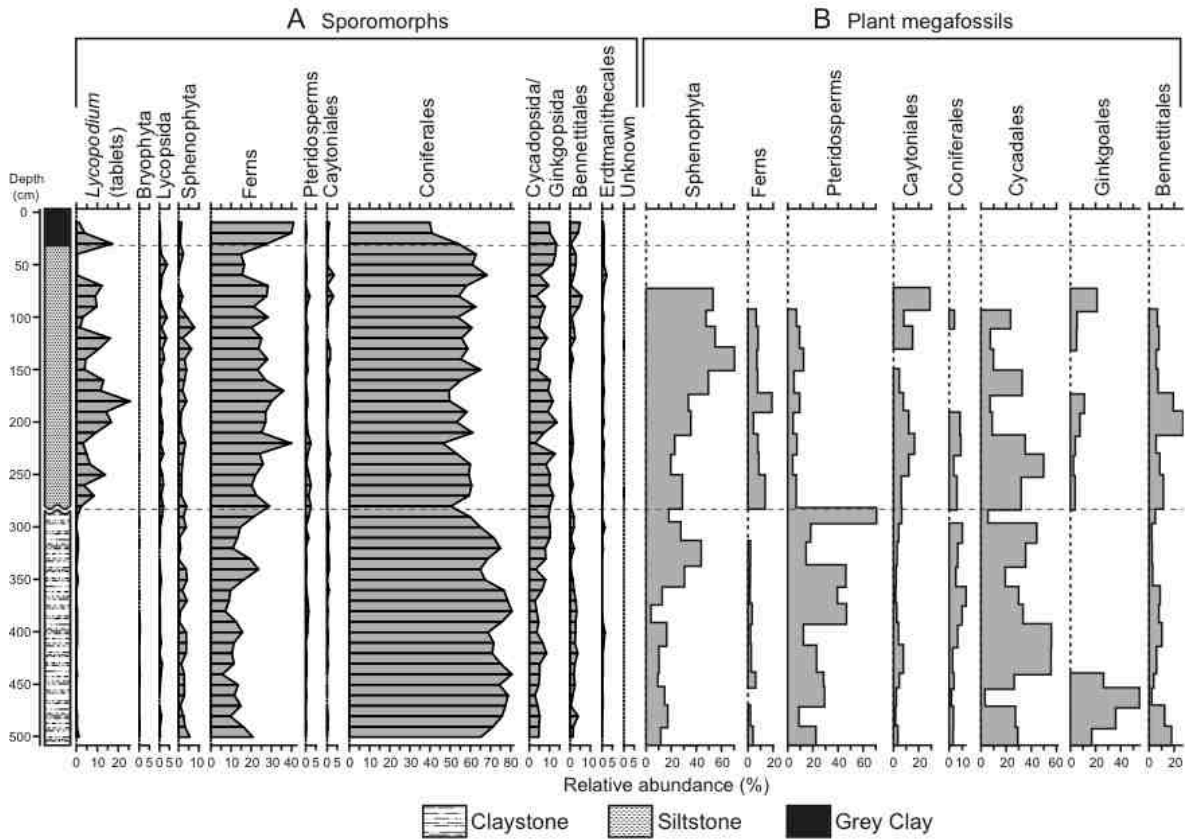


Figure 5.3: Relative abundance charts of (A) sporomorphs and (B) plant megafossils (Spicer and Hill 1979) grouped into their respective affinities. Relative abundances of Jurassic sporomorph taxa are calculated from counts of at least 200 grains. Spiked *Lycopodium* count data is shown as a percentage of the indigenous Jurassic taxa plus the spiked *Lycopodium* itself.

### ***5.3.2 Sporomorph Sample Ordination***

CA and NMDS (Figure 5.4) reveal samples from claystone, siltstone and grey clay units are well separated in ordination space, with only minimal overlap. This illustrates that lithology and apparent floristic composition are correlated and perhaps both are responding to the same principal factors of deposition and/or environment. Logarithmically transformed relative abundance (Figures 5.4A and C) and presence–absence sample multivariate plots (Figures 5.4B and D) demonstrate little clustering of stratigraphically adjacent samples within lithological point clouds, suggesting little temporal floral change and habitat partitioning within each of the three depositional settings. For logarithmically transformed relative abundance CA (Figure 5.4A) the variance is 14 % for axis 1 and 9 % for axis 2. For presence–absence CA (Figure 5.4B) the variance is 11 % for axis 1 and 8 % for axis 2. Grey clay samples display some volatility between relative abundance and presence–absence CA (Figures 5.4A and B), which potentially reflects the comparatively low diversity of the grey clay. However, in all ordinations (Figure 5.4) grey clay samples are consistently more similar to siltstone samples than claystone samples. In NMDS ordinations (Figures 5.4C and D) samples of different lithologies are separated predominantly on axis 1 suggesting this corresponds to depositional setting. Data for Figure 5.4 is provided in Appendices 9–12.

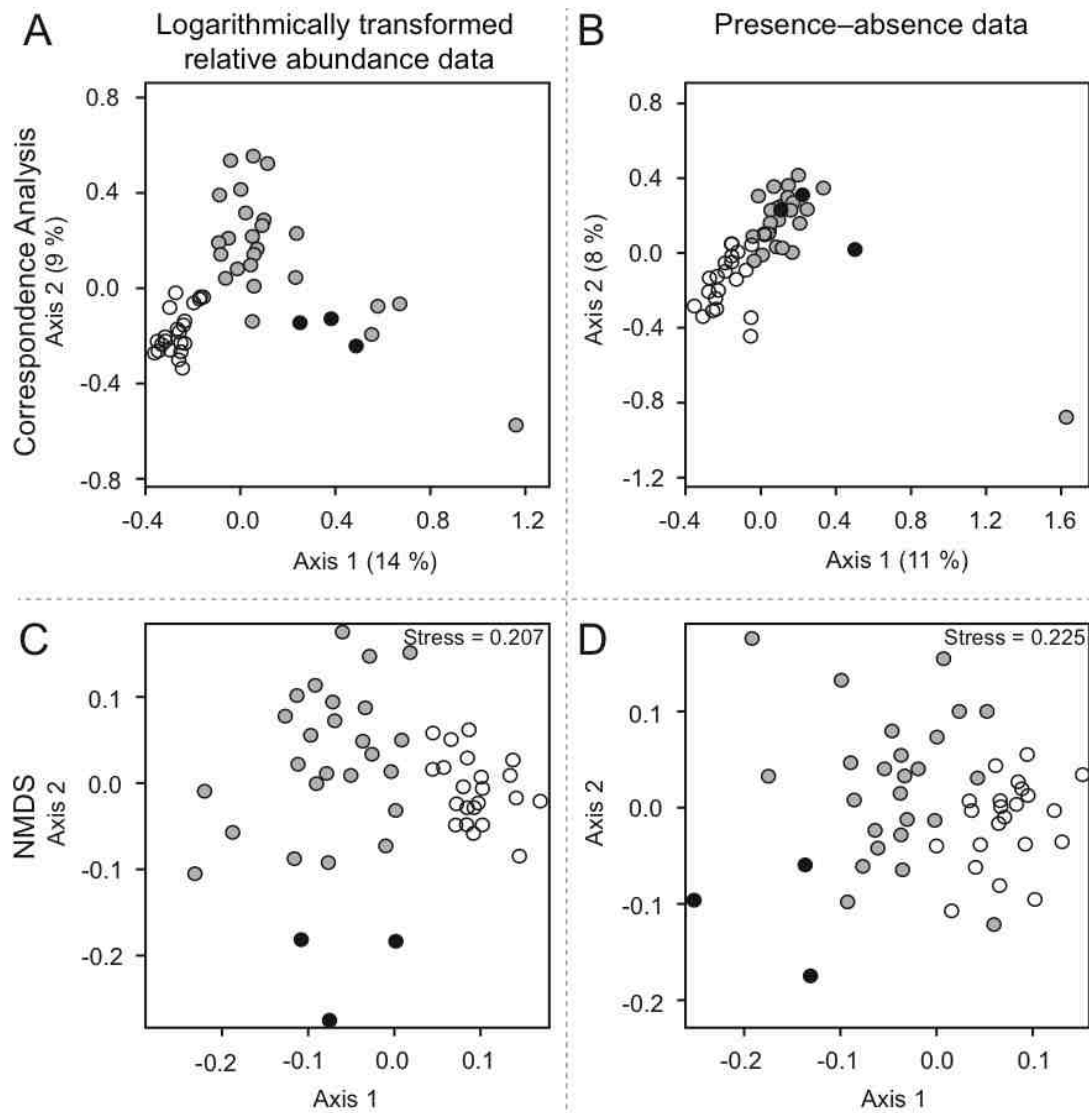


Figure 5.4: Combined ordination plots of samples (spiked *Lycopodium* excluded). (A) and (B) correspondence analysis; (C) and (D) nonmetric multidimensional scaling. (A) and (C) logarithmically transformed relative abundance data; (B) and (D) presence–absence data. White circles represent claystone samples; grey circles represent siltstone samples; black circles represent grey clay samples.

### 5.3.3 Taxon Correspondence Analysis

The scatter plot of the first two CA axes (43 % cumulative variation) of logarithmically transformed relative abundances of taxa reveals four groupings, labeled A-D (Figure 5.5A).

Eigenvalues and percentage variance data for Figure 5.5 is provided in Appendix 13.

Relative abundances of taxa from clusters A-D have been grouped and plotted in Figure 5.5B.

Cluster A (Figure 5.5A) is occupied by *P. elatoides* (Taxodiaceae [van Konijnenburg-van Cittert and van der Burgh 1989; Boulter and Windle 1993; Balme 1995; Couper 1958; Mander *et al.*, 2010; Mander 2011]), *Callialasporites turbatus* (Araucariaceae [Boulter and Windle 1993]), *C. torosus* (Cheirolepidiaceae [Harris 1979; Boulter and Windle 1993; Balme 1995; Couper 1958; Ziaja 2006; Mander *et al.*, 2010; Mander 2011]), *Spheripollenites subgranulatus* (Taxodiaceae [Couper 1958; Boulter and Windle 1993]), and

*Spheripollenites scabratus* (Taxodiaceae [Couper 1958; Boulter and Windle 1993]). Taxa from cluster A are considerably more abundant within claystone samples (Figure 5.5B).

Cluster B (Figure 5.5A) is occupied by *C. mesozoica* (Sphenophyta [Harris 1978; Boulter and Windle 1993; Balme 1995]), *Dictyophyllidites harrisii* (Dipteridaceae/Matoniaceae [Couper 1958; Boulter and Windle 1993; van Konijnenburg-van Cittert 1993; Guignard *et al.*, 2009]), and *Marattisporites scabratus* (Marattiaceae [Couper 1958; Filatoff 1975; Boulter and Windle 1993; Balme 1995]). Taxa from cluster B display little change in relative

abundances through the section (Figure 5.5B). Cluster C (Figure 5.5A) is occupied by *A. australis* (Araucariaceae [Couper 1958; Boulter and Windle 1993; Balme 1995; Mander *et al.*, 2010; Mander 2011; Bonis and Kürschner 2012]), *Pityosporites microalatus* (Pinaceae [Couper 1958; Boulter and Windle 1993]), *Cerebropollenites mesozoicus* (Coniferales [van Konijnenburg-van Cittert and van der Burgh 1989; Boulter and Windle 1993; Balme 1995]), *Cycadopites minimus* (Cycadales/Ginkgoales [Boulter and Windle 1993; Balme 1995; Mander *et al.*, 2010]), and *Deltoidospora minor*

(Cyatheaceae/Dicksoniaceae/Dipteridaceae/Matoniaceae [Couper 1958; Boulter and Windle 1993; van Konijnenburg-van Cittert 1993; Guignard *et al.*, 2009]). Taxa from cluster C are

considerably more abundant within siltstone and grey clay samples (Figure 5.5B). Cluster D is occupied by *Chasmatosporites apertus* (?Cycadales/?Ginkgoales/?Gnetales [Boulter and Windle 1993; Balme 1995]) and *Dictyophyllidites equiexinus* (Dipteridaceae/Matoniaceae [Boulter and Windle 1993; van Konijnenburg-van Cittert 1993]). Taxa from cluster D are more abundant within siltstone samples compared to claystone and grey clay samples (Figure 5.5B). *Cycadopites carpentieri* (Bennettitales [Boulter and Windle 1993]) plots separately in ordination space from clusters A–D. Figure 5.5B demonstrates that *C. carpentieri* is considerably more abundant within claystone samples. Relative abundances of clusters (Figure 5.5B) reveal each point cloud (Figure 5.5A) has a distinct abundance pattern between different lithological/depositional units that correlate with variation on axis 1 (29 % variation), signifying axis 1 corresponds to depositional setting.

The conifer-dominated clusters, A and C represent possible upland communities, as conifers are typical of upland and well-drained settings (e.g. Stukins *et al.*, 2013). Megafloral studies have hypothesized that Mesozoic ferns were typical of areas of high disturbance and water supply (Harris 1961b; van Konijnenburg-van Cittert and van der Burgh 1989; Stukins *et al.*, 2013). The co-occurrence of Sphenophyta and fern spores in cluster B is suggestive of such a community. Ascribing a specific control for axis 2 (14 % variation) with confidence is problematic as this could be one of a myriad of possible factors related to the principal driving mechanisms of vegetation dynamics; differential site availability, species availability and species performance (Picket and Cadenasso 2005; Stukins *et al.*, 2013).

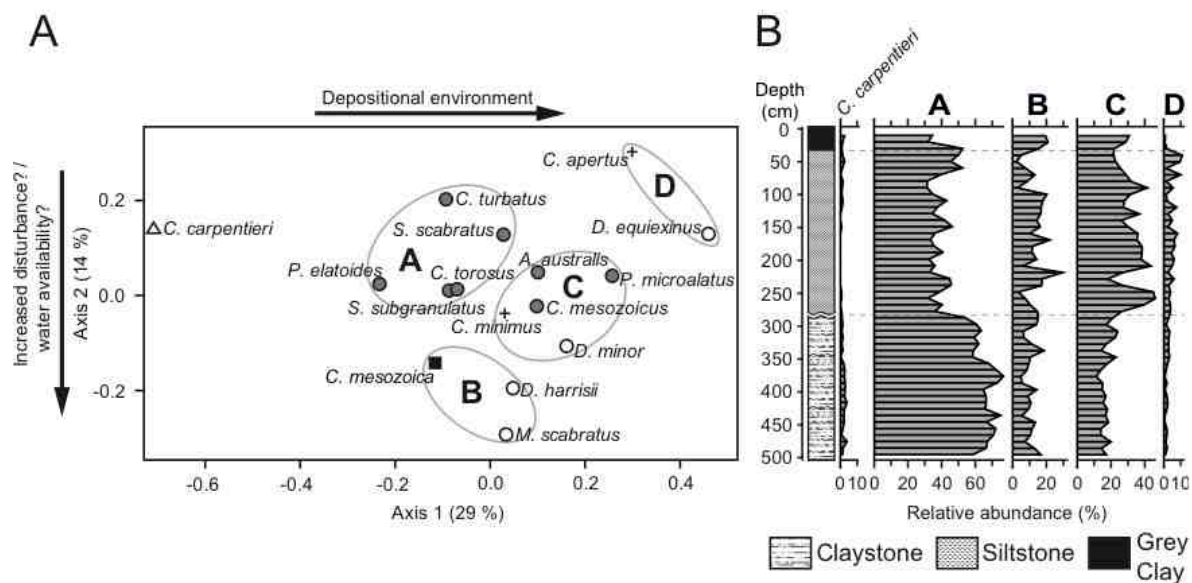


Figure 5.5: (A) Correspondence analysis of taxa using logarithmically transformed sporomorph relative abundance data (excluding spiked *Lycopodium*). Squares represent sphenophytes; white circles represent ferns; grey circles represent conifers; crosses represent Cycadopsida/Ginkgopsida; triangles represent Bennettitales. Ellipses A-D show clustering of plots. (B) Relative abundances of grouped taxa from clusters A-D from Figure 5.5A.

### 5.3.4 Palynofacies Analysis

Two palynofacies are recognized that correspond directly with lithological variation, herein referred to as palynofacies 1 and 2. Palynofacies 1 represents the grey clay and siltstone assemblage (samples HB1-HB28) and palynofacies 2 represents the claystone assemblage (samples HB29-HB50). Relative abundances of organic debris are provided in Figure 5.6. Palynofacies 1 is dominated by inertinite (~43 % (standard deviation = 13)) and unstructured vitrinite (~31 % (standard deviation = 10)). Palynofacies 2 comprises a more heterogeneous mixture of organic debris and is co-dominated by AOM (~23 % (standard deviation = 8)), pollen (~23 % (standard deviation = 7)), inertinite (~21 % (standard deviation = 6)) and unstructured vitrinite (~17 % (standard deviation = 5)).

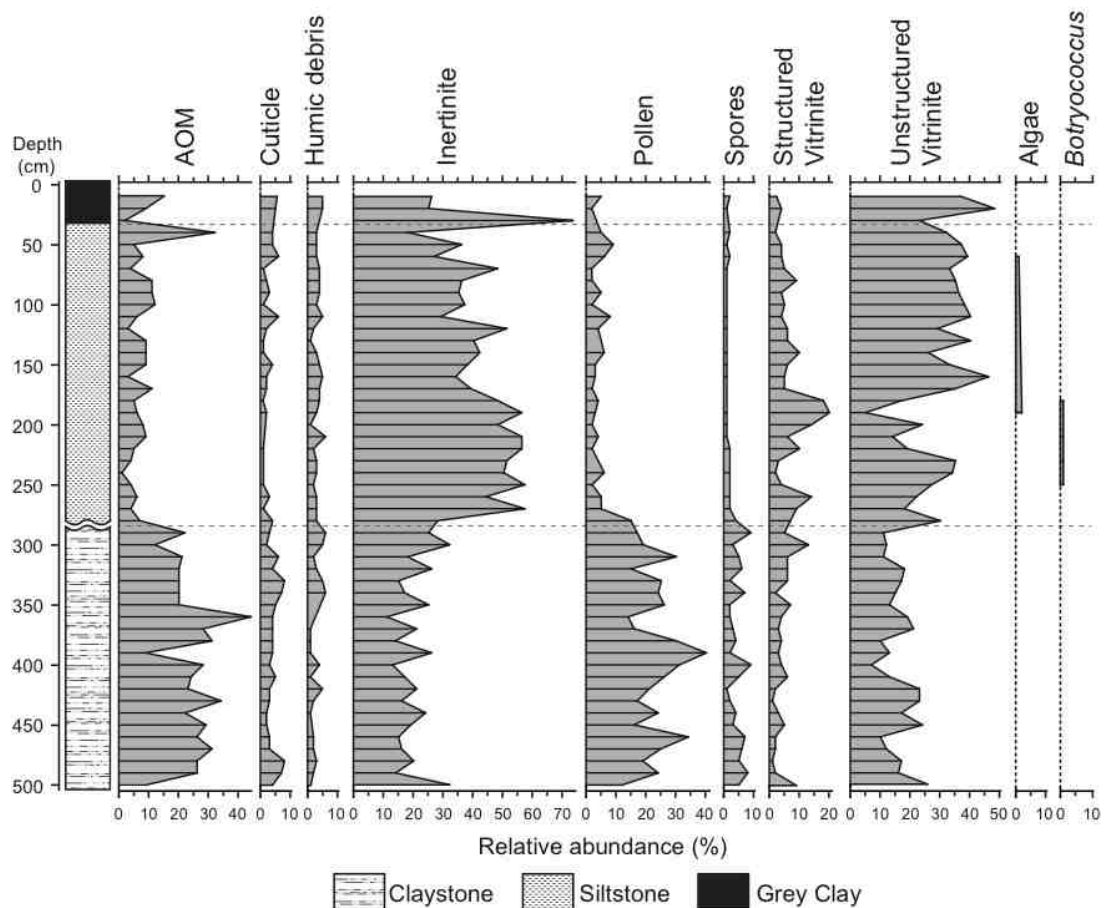


Figure 5.6: Relative abundance chart of palynofacies categories.

### 5.3.5 Comparison of Sporomorph and Plant Megafossil Assemblages

A direct comparison of sporomorph and plant megafossil abundance variation through the plant bed is provided in Figure 5.3. A comparison of the sporomorph and plant megafossil diversity (richness) data is provided in Figure 5.7. Sporomorph assemblages are more diverse (67 taxa) than megafossil assemblages (49 taxa in Spicer and Hill [1979]).

Bryophytes are represented by two species in sporomorph assemblages and are very low in abundance through the section (Figures 5.3 and 5.7). Bryophytes are absent from megafossil assemblages (Spicer and Hill 1979).

Lycopside are highly diverse (16 taxa) within the sporomorph assemblage, however they are absent from megafossil counts (Figure 5.7) (Spicer and Hill 1979). Abundances are low through the section within sporomorph assemblages (Figure 5.3).

Sphenophytes are markedly more abundant within the megafossil assemblage (Figure 5.3B) and diversity is the same (one species) in both sporomorph and megafossil assemblages (Figure 5.7). Abundances are relatively constant through the section within sporomorph assemblages, however, megafossil assemblages record an increase in abundance within the siltstone compared to the claystone (Figure 5.3).

Ferns are the most diverse plant group within sporomorph assemblages at Hasty Bank. Abundances (Figure 5.3) and diversities (Figure 5.7) are considerably higher within sporomorph assemblages (23 taxa) compared to megafossil assemblages (nine taxa). Abundances increase through the section in both sporomorph and plant megafossil assemblages (Figure 5.3).

Pteridosperms are considerably more abundant (Figure 5.3) and diverse (Figure 5.7) within megafossil assemblages (11 taxa) compared to sporomorph assemblages (two taxa). Interestingly, sporomorph and megafossil assemblages display conflicting records for pteridosperm temporal abundance variation. Specifically, megafossil assemblages record a large decrease in pteridosperm abundances across the claystone–siltstone boundary, however in sporomorph samples, pteridosperm abundances are slightly higher within the siltstone unit.

Caytoniales are more abundant (Figure 5.3) and diverse (Figure 5.7) in megafossil assemblages (two taxa) compared to sporomorph assemblages (one taxa). Both sporomorph and megafossil assemblages document a slight increase in Caytoniales abundance within the siltstone unit (Figure 5.3).

Coniferales are the most abundant plant group within sporomorph assemblages (Figure 5.3A) and diversity is high (14 taxa) (Figure 5.7). Abundance (Figure 5.3B) and diversity (eight taxa) (Figure 5.7) in megafossil assemblages is considerably lower. Abundances decrease through the section in both sporomorph and megafossil assemblages (Figure 5.3).

Cycadopsida/Ginkgopsida are considerably more abundant (Figure 5.3) and diverse (Figure 5.7) within megafossil assemblages (10 taxa), compared to sporomorph assemblages



(four taxa). Abundances of Cycadopsida/Ginkgopsida display little change through the section within sporomorph assemblages (Figure 5.3A). Conversely, abundances of Cycadales and Ginkgoales decrease through the section within megafossil assemblages (Figure 5.3B).

Bennettitales are notably more abundant (Figure 5.3) and diverse (Figure 5.7) in megafossil assemblages (eight taxa), compared to sporomorph assemblages (two taxa). Abundances are slightly higher in the siltstone unit within both sporomorph and plant megafossil assemblages (Figure 5.3).

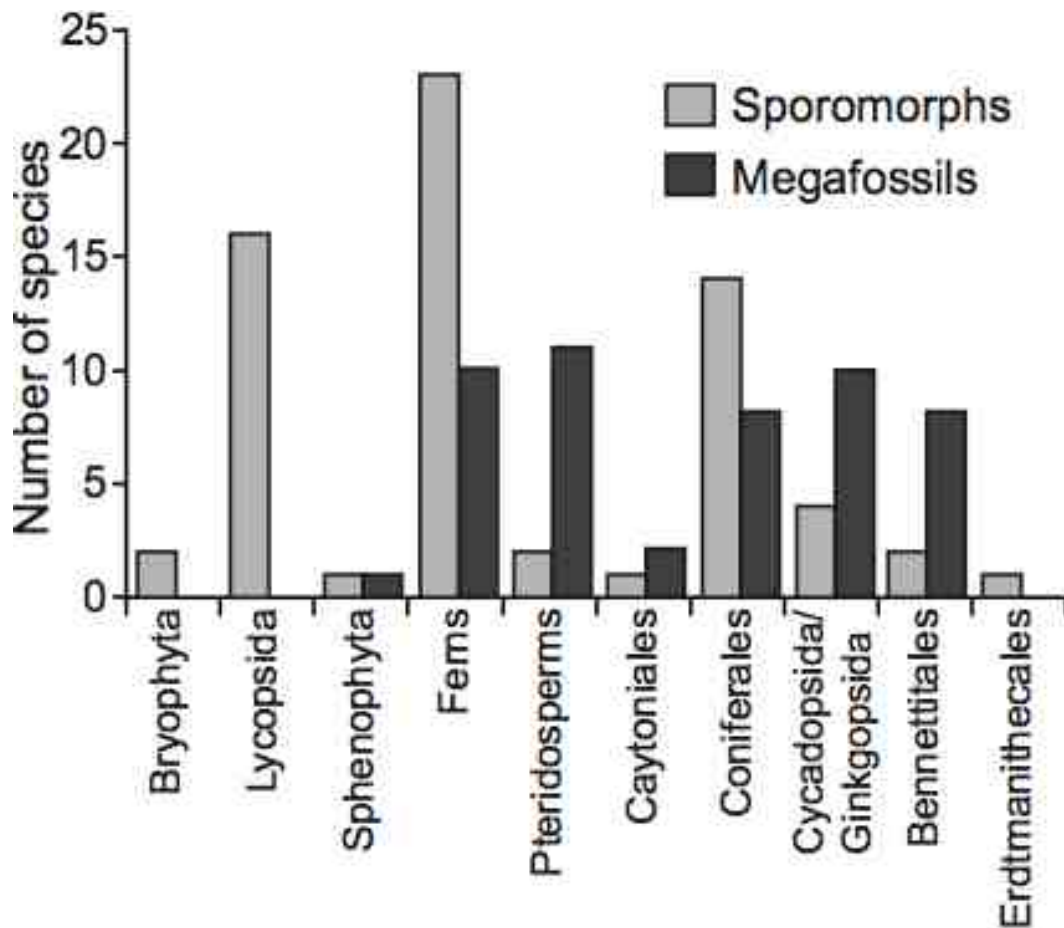


Figure 5.7: Comparative diversities (richness) of the dominant plant groups within sporomorph and plant megafossil assemblages.

## 5.4 Discussion

### 5.4.1 Depositional Environments

The sedimentology and palynofacies of the claystone indicates a low energy, low oxygen and high nutrient depositional environment. The occurrence of *Tasmanites* sp. and *Crassosphaera* sp. from samples HB50 to HB4 reveals a marine component through the plant bed and suggests periodic flooding by seawater, as described by Harris (1964). However, *Tasmanites* sp. and *Crassosphaera* sp. are very rare (typically less than one specimen per 1000 palynomorphs) and the presence of *Botryococcus* and absence of dinoflagellates in palynofacies counts demonstrates dominantly fresh water conditions (Gray 1960; Tyson 1995). The possibility that the rare marine palynomorphs could be reworked, potentially from the underlying marine Dogger Formation, cannot be discounted. Abundant AOM in claystone samples indicates relatively low oxygen and high nutrient levels within the original water during deposition (Tyson 1995; Roncaglia 2004; Traverse 2007; Paction *et al.*, 2011). It is difficult to state with certainty a definitive depositional setting for the claystone, however the results of this study agree with Harris' (1964) interpretations and are suggestive of a coastal plain periodically flooded by seawater, occupied by mangrove-like vegetation.

Interpretations of the depositional environment for the siltstone are consistent with previous studies that indicate this unit represents the slow moving part of a fluvial channel (Hill and van Konijnenburg-van Cittert 1973; van Konijnenburg-van Cittert and Morgans 1999). Decreased abundances of AOM signify lower nutrient levels than the claystone (Tyson 1995).

The absence of marine palynomorphs in the grey clay demonstrates marine influence is negligible to absent. Sample ordination (Figure 5.4) reveals that the grey clay is compositionally more similar to the siltstone than the claystone. Sporomorph assemblages of the grey clay contain higher abundances of ferns and lower abundances of wind blown taxa, suggesting a smaller catchment area and reduced sporomorph transportation distances

compared to the claystone and siltstone (Chaloner and Muir 1968). These combined factors are suggestive of a swamp or an abandoned channel environment for the grey clay.

Taphonomical models of time-averaging versus catchment area for multiple depositional environments demonstrate that the components of fossil assemblages can be used to indicate their temporal and spatial representations (Behrensmeyer and Kidwell 1985; Behrensmeyer *et al.*, 2000). Fossil assemblages that contain transported plant megafossils are typical of floodplain, pond and lake deposits. Such deposits generally represent time periods of ~100–10,000 years and source areas of ~100,000 m<sup>2</sup>. Sporomorphs are generally representative of larger source areas, frequently in excess of 1,000,000 m<sup>2</sup> (Behrensmeyer *et al.*, 2000). Estimates of source areas and time-averaging for floodplain and channel environments are highly variable (Behrensmeyer *et al.*, 2000). Channels generally represent increased time-averaging and source area sizes compared to floodplain deposits, although there is significant overlap in source area sizes and the degree of time-averaging between channels and floodplains. Interestingly, the claystone unit (coastal plain) at Hasty Bank is interpreted to represent a longer time interval and a larger source area than the siltstone (fluvial channel) due to slower sedimentation rates and the probability that numerous rivers potentially flowed into the coastal plain environment.

#### ***5.4.2 Explanations for Temporal Sporomorph Variation***

Variation in sporomorph and plant megafossil assemblages through the section can be correlated strongly with depositional change. The depositional environment is a primary control on parent vegetation, thus a change in depositional setting typically results in a change in sporomorph and megafossil assemblages. The erosional surface between the claystone and siltstone separates two distinct depositional environments by a period of unknown duration; therefore a change in floral composition between the claystone and the upper part of the section (siltstone and grey clay) is not particularly surprising. Although the claystone and grey clay are more similar to each other in terms of lithology than they are to

the siltstone, the reason for their differing sporomorph assemblages is attributed to their different depositional environments and associated variable catchment areas.

The higher number of sporomorphs within the claystone unit is a result of a combination of ecological and non-ecological variables. Non-ecological variables include lithological factors, sedimentation rates and the depositional environment. Although governed by the depositional environment, the lithology itself can impact on the preservation of sporomorphs and therefore result in apparent temporal floral variation. Spores and pollen can be considered as sedimentary particles during transportation and depositional processes; hence certain taxa are preferentially preserved based on factors such as particle size, particle shape and durability (Traverse 2007). Thus, changes in transportation and depositional processes between claystone, siltstone and grey clay units would have presumably resulted in the preferential preservation of particular taxa based on these physical factors. The preservation potential of sporomorphs is generally increased when sediment grain size is reduced and sedimentation rates are slower (Traverse 2007). Therefore, the high number of sporomorphs and high diversities within the claystone are probably a result of the relatively small grain size and slow sedimentation rates of this unit. Conversely, the siltstone is considered to have been deposited more rapidly than the claystone, thus the lower abundances and diversities of coniferous pollen within the siltstone are probably a result of faster sedimentation rates, as there would have been less time for such pollen “rain” to accumulate. The lower diversities within the siltstone compared to the claystone are also a consequence of the smaller catchment area supplying this deposit with sporomorphs. Specifically, the channel environment of the siltstone would have presumably had fewer tributaries feeding this deposit compared to the numerous rivers that would have potentially flowed into the coastal plain setting of the claystone.

Spicer and Hill (1979) postulated that differential rates of compaction could have affected floral compositions between lithologies. This could have had some influence on abundances; however, there is no conclusive sedimentological evidence that suggests compaction was vastly different between lithologies. The differential sedimentation rates and

sediment grain sizes between depositional environments are considered to be far larger contributors to such abundance differences. For example, diversity is likely to be lower within the fluvial siltstone (compared to the same unit of claystone), because it was deposited more rapidly.

#### ***5.4.3 Ecological Causes for Variation between Sporomorph and Plant Megafossil***

##### ***Assemblages***

Table 5.1 shows the generalized sporomorph dispersal methods of the dominant plant groups through the Hasty Bank plant bed. The majority of plant groups in Table 5.1 rely on wind to disperse sporomorphs. The life habits and reproductive methods of wind dispersed taxa result in abundance and diversity discrepancies between the sporomorph and megafossil assemblages. Pollen and spore production in wind-dispersed species is typically very high as the efficiency of wind pollination increases as the concentration of airborne pollen increases (Regal 1982; Whitehead 1983; Allison 1990; Friedman and Barrett 2009). The sporomorph and megafossil records at Hasty Bank reflect this bias; conifers and ferns that produce vast numbers of pollen and spores are considerably more abundant (Figure 5.3) and diverse (Figure 5.7) within sporomorph assemblages.

The nature of wind pollination means that sporomorph assemblages capture spores and pollen from a significantly larger geographic area compared to plant megafossil assemblages, which are more representative of the local palaeoflora (e.g. Prentice 1985). Many of the coniferous species within the sporomorph assemblage are therefore potentially not representative of the flora close to the site of deposition and are possibly more indicative of upland communities.

The physical size of parent plants also impacts on the composition of sporomorph assemblages. Pollen released at elevated heights increases dispersal distances as (i) wind speeds are greater, (ii) pollen remains within the airstream longer and (iii) there is usually less intervening vegetation to intercept pollen (Levin and Kerster 1974; Okubo and Levin 1989; Friedman and Barrett 2009). Many coniferous sporomorph taxa from the Hasty Bank

plant bed originate from large trees, this is a principal factor in contributing to their high abundances within sporomorph assemblages.

Harris (1964) described the pollen organ *Pteroma thomasi* from Hasty Bank and associated this with the pteridosperm *P. papillosa* based on their similar cuticles and co-occurrence. The pollen of *P. thomasi* is most similar to the wind dispersed pollen of *Alisporites thomasi* (Harris 1964; Ziaja 2006). Spicer and Hill (1979) demonstrated that the parent plant, *P. papillosa* is markedly more abundant within the claystone, however the dispersed pollen, *A. thomasi* does not record this abundance change and is low in abundance throughout the section. Temporal changes in local vegetation are generally less well recorded among wind-dispersed taxa in the sporomorph record as such taxa are captured from larger geographic areas than corresponding megafossils.

Animal-plant interactions could also be a cause of inconsistencies between sporomorph and plant megafossil assemblages. Potential insect assisted pollination in Caytoniales (Harris 1945; Labandeira 2010) could be a cause of the underrepresentation of such pollen in sporomorph assemblages (Figures 5.3 and 5.7) as pollen production in insect pollinated plants is typically very low compared to wind dispersed taxa (e.g. Norstog 1987).

Cycads and Bennettitales display markedly lower abundances (Figure 5.3) and diversities (Figure 5.7) within the sporomorph record. The reproductive methods of these plants differ considerably from the exclusively wind dispersed conifers and ferns. Some modern cycads rely on a combination of wind and insect pollination (Niklas and Norstog 1984; Clark and Clark 1987; Tang 1987; Norstog and Fawcett 1989; Ornduff 1990; Pellmyr *et al.*, 1991; Wilson 2002; Kono and Tobe 2007; Terry *et al.*, 2007) and both fossil cycads and Bennettitales display early evidence of possible insect pollination (Crepet *et al.*, 1991; Klavins *et al.*, 2005; Labandeira *et al.*, 2007). Pollen production varies greatly among modern cycads, depending on whether wind or insect pollination is dominant (Norstog 1987). Kono and Tobe (2007) demonstrated that the pollen of the modern cycad, *Cycas revoluta* occurs only in abundance within very close proximity (~2 m) to the cones from which it is released. If Jurassic cycads share such a characteristic, cycad pollen would almost

certainly be underrepresented in the sporomorph assemblage. *Nilssonia kendalliae* is the most common species within megafossil counts, constituting ~29 % of the total assemblage (Spicer and Hill 1979). Harris (1964) presumed *N. kendalliae* to be of cycad or pteridosperm affinity. In situ pollen studies have associated the pollen *Androstrobus* with *N. kendalliae* (van Konijnenburg-van Cittert 1968) and more generally Nilssoniaceae (Hill 1990). In situ *Androstrobus* pollen is considered to be equivalent to dispersed *Chasmatosporites* pollen (Balme 1995). As a genus *Chasmatosporites* constitutes only ~2.9 % of the total sporomorph assemblage. This abundance discrepancy is interpreted to be due to low pollen production and small dispersal ranges of cycads compared to many of the wholly wind-pollinated plants. Hence, the specialized reproductive nature of cycads, Bennettitales and potentially Caytoniales (Delevoryas 1963; Harris 1974; Labandeira 2010; Mander *et al.*, 2010) is probably the principal factor contributing to their underrepresentation in sporomorph assemblages.

The underrepresentation of cycads, Bennettitales and ginkgos in the sporomorph diversity record is potentially compounded by recognition biases. The leaves of these groups typically possess distinctive morphological features that enable easy differentiation to generic and species level (Lidgard and Crane 1990), thus diversity of such taxa in the megafossil assemblage is high. However, the pollen of these groups is often simple and monosulcate, with little morphological and sculptural variation visible under light microscopy (Frederiksen 1980). Sporomorph species therefore potentially represent numerous parent plant species, thus diversity in the dispersed sporomorph record is underrepresented.

The high diversities of lycopsids, ferns and bryophytes in sporomorph assemblages compared to megafossil assemblages (Figure 5.7) could be related to epiphytic communities. Epiphytes are generally poorly represented in the megafloral record as the burial and subsequent fossilization of such species is unlikely compared to most other plants (Schneider and Kenrick 2001; Frahm and Newton 2005; Tstutsumi and Kato 2006; Schuettpelez and Pryer 2007, 2009; Dubuisson *et al.*, 2009; Pšenička and Opluštil 2013). In contrast,

sporomorphs released from epiphytes do not experience this bias, thus diversities of epiphytic groups are comparatively unaffected in the sporomorph record.

The absence of lycopsids and low diversity of ferns in megafossil assemblages could also be linked to the relatively low preservation potential of many non-arborescent species. Scheihing (1980) demonstrated that non-arborescent taxa are frequently underrepresented in the megafloral record as a result of, (i) the increased biomass of arborescent species, (ii) difficulty in recognition of non-arborescent plant parts, and (iii) shielding of the non-arborescent understory by the arborescent canopy during high-energy transport and depositional processes.

Plant group	Typical sporomorph dispersal method	Typical sporomorph production level	Typical modern equivalent parent plant heights	References
Bryophyta	Mostly wind	Relatively high	Very low (Some epiphytic)	Pohjamo <i>et al.</i> , 2006
Lycopsida	Mostly wind	High	Low (Some epiphytic)	Brack-Hanes 1981; Traverse 2007
Sphenophyta	Wind	High	Relatively small	van Konijnenburg-van Cittert and Morgans 1999
Ferns	Mostly wind	Very High	Variable, mostly low (Some epiphytic)	Durand and Goldstein 2001
Pteridosperms	Mostly wind, some potentially insect	–	–	Labandeira <i>et al.</i> , 2007
Caytoniales	Wind and ?insect	–	–	Harris 1933, 1945; Schwendemann <i>et al.</i> , 2007; Ren <i>et al.</i> , 2009; Labandeira 2010
Coniferales	Wind	Very high	Variable, mostly very tall	Critchfield 1985; van Konijnenburg-van Cittert and Morgans 1999
Cycadales	Wind and insect	Variable (Relatively high in wind pollinated taxa, low in wind and insect pollinated taxa)	Variable, low to moderately tall	Norstog 1987
Ginkgoales	Wind and ?insect	High	Very tall	Del Tredici 1989; van Konijnenburg-van Cittert 2010; Crane 2013; Bhowmik and Parveen 2014
Bennettitales	Wind and ?insect	–	–	Crepet <i>et al.</i> , 1991

Table 5.1: Sporomorph dispersal methods, sporomorph production levels, and relative parent plant heights of modern equivalents of the major plant groups in the Hasty Bank plant bed.



#### ***5.4.4 Variation in Plant and Sporomorph Durability Causing Megafossil–Sporomorph Inconsistencies***

Many of the inconsistencies between the plant megafossil and sporomorph assemblages are interpreted to be a result of differences in durability between parent plants and associated sporomorphs.

*Equisetum columnare* is the second most abundant plant species in megafossil assemblages, constituting ~19 % of the megaf flora (Spicer and Hill 1979). However, its corresponding microspore, *C. mesozoica* represents only ~2.5 % of the sporomorph assemblage. This discrepancy is probably due to the highly durable nature of *Equisetum*, which means that this genus is overrepresented compared to other megaf floral taxa.

Conversely, *C. mesozoica* has a low preservation potential due to its thin wall and low sporopollenin content (Traverse 2007; Grauvogel-Stamm and Lugardon 2009), thus this species is underrepresented in the sporomorph assemblage. These combined factors give rise to a notable differential preservation potential between the parent plant and sporomorph.

The high diversity of lycopsids (16 taxa) in sporomorph assemblages and their absence from megafossil assemblages suggests an extremely low preservation potential for lycopsid remains within this deposit. The same pattern is also present within Triassic–Jurassic plant beds from East Greenland (Mander *et al.*, 2010, 2013) and Lower Jurassic deposits of Odrowąż, central Poland (Ziaja 2006). Lycopsids are notable both for their diversity in the megaspore record of the Middle Jurassic deposits of Yorkshire (reviewed in Slater *et al.*, 2015) and for their lack of megafossils within these deposits. Harris (1961b) summarizes studies on the lycopsid megafossil *Selaginellites falcatus*. With the exception of this species there are no other convincing reports of lycopsid megafossils from the Middle Jurassic of Yorkshire (Lindley and Hutton 1833; Hill *et al.*, 1985; Schweitzer *et al.*, 1997). The absence of lycopsid megafossils may also be exacerbated by the lack of recognition of delicate lycopsid remains (Skog and Hill 1992).

#### ***5.4.5 Are Sporomorphs or Plant Megafossils More Informative regarding Palaeofloristic Reconstructions?***

Comparison of palynological and plant megafossil records demonstrates that respective data sets reflect different aspects of the palaeoflora as they preferentially preserve certain taxa based on a multitude of ecological and non-ecological variables. Such variables include spore/pollen and plant durability, absolute abundances of plant species in life, proximity of parent plants to depositional location, spore/pollen dispersal methods, spore/pollen dispersal distances, absolute numbers of spores/pollen released from parent plants, transportation distances, transportation processes, climatic variations, and the depositional environment. This study illustrates that sporomorphs preserve some aspects of the palaeoflora more completely (mostly wind dispersed taxa) than megafossil assemblages. However, megafossil assemblages equally preserve other aspects of the palaeoflora (mostly reproductively specialized taxa) more completely than sporomorph assemblages.

Direct quantitative comparative studies of dispersed sporomorph and plant megafossil assemblages from pre-angiosperm Mesozoic floras are relatively uncommon in the literature due to the rarity of such fossil sites (e.g. Pedersen and Lund 1980; Ziaja 2006; Mander *et al.*, 2010). Most previous studies that incorporate dispersed sporomorphs and plant megafossils are confined to Palaeozoic (e.g. Dimitrova *et al.*, 2005; Looy and Hotton 2014), Cretaceous (e.g. Lidgard and Crane 1990; Bercovici *et al.*, 2008, 2009) and Cenozoic (e.g. Tinner *et al.*, 1996; Wing and Harrington 2001) floras. These floras are fundamentally different to pre-angiosperm Mesozoic communities, thus comparison of such floras with those at Hasty Bank is highly problematic. Rare examples where combined sporomorph and megafossil data have been used in vegetation reconstructions from pre-angiosperm Mesozoic floras demonstrate consistency with findings from Hasty Bank. Specifically, conifers and ferns are typically well represented in sporomorph assemblages (Jana and Hilton 2007), cycads, Bennettitales and pteridosperms are generally well represented in megafossil assemblages (Pedersen and Lund 1980; Götz *et al.*, 2011) and bryophytes and lycopsids are often confined to sporomorph assemblages (Ziaja 2006; Mander *et al.*, 2010, 2013). Such large discrepancies

between parent plant and dispersed sporomorph assemblages questions the reliability of local vegetation reconstructions based on megafossil or sporomorph evidence in isolation and suggests a combined approach is considerably more informative.

## **5.5 Conclusions**

Variation in sporomorph assemblages through the Hasty Bank plant bed is the result of a change in depositional setting between the three lithological units. Changes in the depositional environments consequently influence the vegetation, catchment areas and preservation potential of sporomorphs and plant megafossils; hence the fossil assemblages vary notably between lithologies. Discrepancies between sporomorph and plant megafossil assemblages are primarily a result of the different life habits and reproductive strategies employed by parent plants. Such differences often cause large variation in sporomorph production and dispersal distances. Differential preservation potentials between parent plants and associated spores/pollen also has a substantial impact on generating inconsistencies between sporomorph and plant megafossil data sets. This is particularly apparent regarding the absence of lycopsids and the elevated abundances of *E. columnare* in plant megafossil assemblages (Spicer and Hill 1979). Based on the results at Hasty Bank and similar studies (e.g. Ziaja 2006; Mander *et al.*, 2010; 2013), explaining discrepancies between sporomorph and plant megafossil assemblages requires considerable analysis and there is no “best” method of reconstructing palaeofloras. Assemblage compositions are the product of a complex array of biological, geographical and depositional factors that act inconsistently between and within sporomorph and megafossil assemblages, resulting in notable disparities between respective data sets. Refining parent plant affinities with spore and pollen in situ studies will aid in future reconstructions of palaeofloras using dispersed sporomorphs.

**CHAPTER 6: MORPHOLOGY AND WALL ULTRASTRUCTURE OF A NEW AND  
HIGHLY DISTINCTIVE MEGASPORE FROM THE MIDDLE JURASSIC OF  
YORKSHIRE, UK**

This chapter reviews the occurrence of megaspores in the Middle Jurassic of Yorkshire and describes a new megaspore genus. Analyses of megaspore wall ultrastructure are utilized to determine possible parent plant affinities. This chapter is published in the journal *Review of Palaeobotany and Palynology* (Slater *et al.*, 2015). John Poulter initially discovered the megaspore during an M.Biol.Sci. Level 4 research project at the University of Sheffield. Subsequently, Alexandra Beck, Emily Berry, Sophie Brookes and Rhiannon Doughty undertook preliminary investigations of the megaspore during B.Sc. Level 3 research projects. SMS collated the previous research and undertook further LM, SEM and TEM analyses. The paper was written by SMS, with contributions from Wilson A. Taylor, David J. Batten and Christopher R. Hill, under the guidance of CHW. Permission to include this paper within this thesis was gained by all co-authors and the publishers. See Appendix 15 for the published paper.

## CHAPTER 7: CONCLUSIONS

- Diverse and well-preserved terrestrial sporomorph assemblages have been documented following the analysis of 114 palynological samples from multiple sections through the Middle Jurassic Ravenscar Group, North Yorkshire, UK.
- Quantitative analytical methods have been used to assess variation in sporomorph assemblages through time. Such analyses have demonstrated that assemblage composition varies significantly through the Middle Jurassic of Yorkshire. Aalenian, Bajocian and Bathonian palynofloras possess relatively distinct sporomorph and palynofacies assemblages respectively, which suggests significant changes in vegetation and/or depositional environments. Specifically, Aalenian assemblages are composed of abundant conifers, ferns, simple monosulcate pollen producers, sphenophytes and Caytoniales; Bajocian floras are more homogeneous in composition and are co-dominated by conifers and ferns; and Bathonian assemblages are composed of abundant fern, conifer, lycophyte, pteridosperm/conifer and Caytoniales assemblages with high richness levels.
- Short-term temporal variations between samples are highly influenced by taphonomic biases between different depositional environments. Long-term temporal variations between the Aalenian, Bajocian and Bathonian palynofloras are visible regardless of local depositional environments, suggesting that long-term changes are more significant than short-term changes. These reflect changes in depositional environments through time, which give rise to both (i) variable depositional taphonomic processes and (ii) different parent vegetation occupying these different environments.
- Quantitative comparisons of sporomorph and plant megafossil records from the Hasty Bank plant bed, North Yorkshire reveals that the two fossil records are markedly different regarding their respective parent vegetation reconstructions. Specifically, conifers and ferns are underrepresented in plant megafossil

assemblages, bryophytes and lycopsids are confined to sporomorph assemblages, and sphenophytes, pteridosperms, Caytoniales, Cycadales, Ginkgoales and Bennettitales are underrepresented in sporomorph assemblages. Such differences are due to a multitude of biases that act inconsistently between and within the megafloral and sporomorph record, e.g. differential parent plant reproductive strategies that give rise to variable sporomorph production levels between plant groups, differential physical durability between spormorphs and parent plants, and variable catchment areas between different depositional environments.

- A new and highly unusual megaspore, *Reticuspinosporites whytei* Slater *et al.*, 2015 has been formally described using light microscope, SEM and TEM analysis. Parent plant affinities are tentatively suggested as lycopsid, possibly selaginellalean based on wall ultrastructural analysis. The discovery of *Reticuspinosporites whytei* Slater *et al.*, 2015 in association with previous megaspore studies from these deposits demonstrates that heterosporous lycopsids were reasonably diverse in the Middle Jurassic of Yorkshire, but are underrepresented in the megafloral record.

### **7.1 Possible Future Work:**

- Vegetation reconstructions using sporomorphs would be improved with additional in situ sporomorph records to improve sporomorph–parent plant connections.
- Wall ultrastructural studies of species that have not been found in situ could shed light on possible parent plant affinities and also improve vegetation reconstructions.
- High-resolution sampling for other microfossils (possibly foraminifera and ostracods) could provide useful biostratigraphic information relevant to the disputed time-gap between the Scarborough and Scalby formations.
- Detailed quantitative comparison of the sporomorph assemblages from the Middle Jurassic of Yorkshire with assemblages from other Middle Jurassic regional localities (e.g. Cotswolds, North Sea, Bornholm) and global localities (e.g. Argentina) could provide insight into phytogeographic realms.



# APPENDICES



# Appendix 1

Appendix 1: Botanical affinities of sporomorphs. The ages (period) of deposits from which sporomorphs were recovered from are provided in the ‘Reference’ column. ‘–’ indicates an unknown affinity or a lack of published information available. Adapted from Slater and Wellman (In press).

Taxon	Family	Order	Class	Division	Reference
<i>Foveosporites moretonensis</i>	Sphagnaceae-type	Sphagnales	Sphagnopsida	Bryophyta	Filatoff (1975) (Jurassic)
<i>Rogalskisporites cicatricosus</i>	Sphagnaceae-type	Sphagnales	Sphagnopsida	Bryophyta	Filatoff (1975) (Jurassic)
<i>Stereisporites</i> sp.	Sphagnaceae-type	Sphagnales	Sphagnopsida	Bryophyta	Filatoff (1975) (Jurassic); Boulter and Windle (1993) (Jurassic)
<i>Neveisporites bigranulatus</i>	–	–	–	Bryophyta	Bonis and Kürschner (2012) (Triassic–Jurassic boundary)
<i>Anapiculatisporites</i> sp.	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Boulter and Windle (1993) (Jurassic); Balme (1995) (Carboniferous and Permian)
<i>Densoisporites circumundulatus</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Filatoff (1975) (Jurassic); Boulter and Windle (1993) (Jurassic)
<i>Densoisporites velatus</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Boulter and Windle (1993) (Jurassic); Balme (1995) (Cretaceous)
<i>Densoisporites</i> cf. <i>velatus</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Boulter and Windle (1993) (Jurassic); Balme (1995) (Cretaceous)
<i>Kraeuselisporites whitfordensis</i>	–	Lycopodiales	Lycopsida	Lycophyta	McLoughlin <i>et al.</i> , (1997) (Permian–Triassic boundary); Raine (2008) (Cretaceous–Paleogene); Kustatscher <i>et al.</i> , (2010) (Triassic)
<i>Kraeuselisporites</i> sp. 1	–	Lycopodiales	Lycopsida	Lycophyta	McLoughlin <i>et al.</i> , (1997) (Permian–Triassic boundary); Raine (2008) (Cretaceous–Paleogene); Kustatscher <i>et al.</i> , (2010) (Triassic)
<i>Lycopodiacidites cerniidites</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Couper (1958) (Jurassic–Cretaceous); Filatoff (1975) (Jurassic); Boulter and Windle (1993) (Jurassic)
<i>Lycopodiacidites rugulatus</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Filatoff (1975) (Jurassic); Ziaja (2006) (Jurassic)
<i>Neoraistrickia truncatus</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Couper (1958) (Jurassic); Filatoff (1975) (Jurassic); Boulter and Windle (1993) (Jurassic)
<i>Retitriletes austroclavitudites</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Boulter and Windle (1993) (Jurassic); Mander <i>et al.</i> , (2010) (Triassic–Jurassic boundary); Srivastava (2011) (Jurassic)
<i>Retitriletes clavatooides</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Couper (1958) (Jurassic–Cretaceous); Boulter and Windle (1993) (Jurassic); Srivastava (2011) (Jurassic)
<i>Retitriletes semimuris</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Boulter and Windle (1993) (Jurassic)
<i>Retitriletes singhii</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Srivastava (2011) (Jurassic)
<i>Leptolepidites bossus</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Filatoff (1975) (Jurassic); Boulter and Windle (1993) (Jurassic)
<i>Leptolepidites crassibalteus</i>	–	Lycopodiales	Lycopsida	Lycophyta	Filatoff (1975) (Jurassic)
<i>Leptolepidites equatibossus</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Boulter and Windle (1993) (Jurassic)
<i>Leptolepidites major</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Boulter and Windle (1993) (Jurassic)
<i>Sestrosporites pseudoalveolatus</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Dettmann (1963) (Cretaceous); Boulter and Windle (1993) (Jurassic)
<i>Staplinisporites</i> sp.	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Boulter and Windle (1993) (Jurassic)
<i>Staplinisporites mathurii</i>	Lycopodiaceae/ Selaginellaceae-type	Lycopodiales/ Selaginellales	Lycopsida/ Isoetopsida	Lycophyta	Srivastava (1966) (Jurassic); Filatoff (1975) (Jurassic)
<i>Uvaesporites argenteaformis</i>	Lycopodiaceae	Lycopodiales	Lycopsida	Lycophyta	Boulter and Windle (1993) (Jurassic); Balme (1995) (Triassic and Cretaceous)
<i>Reticuspinosporites whytei</i>	–	?Selaginellales	?Isoetopsida	Lycophyta	Slater <i>et al.</i> , (2015) (Jurassic)
<i>Paxillitriletes phyllicus</i>	–	Isoteales	Isoetopsida	Lycophyta	Kovach and Dilcher (1985) (Cretaceous); Baldoni and Taylor (1987) (Cretaceous)
<i>Calamospora mesozoica</i>	Equisetaceae	Equisetales	Sphenopsida	Sphenophyta	Couper (1958) (Jurassic); Harris (1978) (Jurassic); Boulter and Windle (1993) (Jurassic); Balme (1995) (Triassic and Jurassic)
<i>Laevigatosporites</i> sp.	–	–	–	Pteridophyta/ Sphenophyta	Balme (1995) (Carboniferous); Srivastava (2011) (Jurassic)
<i>Marattisporites scabratus</i>	Marattiaceae	Marattiales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic–Cretaceous); Filatoff (1975) (Jurassic); Boulter and Windle (1993) (Jurassic); Balme (1995) (Triassic and Jurassic)
<i>Baculatisporites comaumensis</i>	Osmundaceae	Filicales	Filicopsida	Pteridophyta	Boulter and Windle (1993) (Jurassic); van Konijnenburg–van Cittert (2000) (Jurassic); Mander <i>et al.</i> , (2010) (Triassic–Jurassic boundary); Mander (2011) (Triassic–Jurassic boundary)
<i>Osmundacidites wellmanii</i>	Osmundaceae	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic–Cretaceous); Filatoff (1975) (Jurassic); Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic)
<i>Todisporites major</i>	Osmundaceae	Filicales	Filicopsida	Pteridophyta	Balme (1995) (Triassic and Jurassic); Boulter and Windle (1993) (Jurassic); Couper (1958) (Jurassic)
<i>Todisporites minor</i>	Osmundaceae	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic); Boulter and Windle (1993) (Jurassic); Balme (1995) (Triassic)
<i>Gleicheniidites senonicus</i>	Gleicheniaceae	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic–Cretaceous); Filatoff (1975) (Jurassic); Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic and Cretaceous)
<i>Conbaculatisporites mesozoicus</i>	Dipteridaceae	Filicales	Filicopsida	Pteridophyta	Pedersen and Lund (1980) (Triassic–Jurassic boundary); Mander <i>et al.</i> , (2010) (Triassic–Jurassic boundary); Mander (2011) (Triassic–Jurassic boundary); Gedl and Ziaja (2012) (Jurassic)
<i>Concavisporites</i> sp.	Dipteridaceae/Matoniaceae	Filicales	Filicopsida	Pteridophyta	van Konijnenburg–van Cittert (1993) (Triassic–Recent); Boulter and Windle (1993) (Jurassic); Mander (2011) (Triassic–Jurassic boundary)
<i>Concavisporites</i> sp. 1	Dipteridaceae/Matoniaceae	Filicales	Filicopsida	Pteridophyta	van Konijnenburg–van Cittert (1993) (Triassic–Recent); Boulter and Windle (1993) (Jurassic); Mander (2011) (Triassic–Jurassic boundary)
<i>Dictyophyllidites equixinus</i>	Dipteridaceae/Matoniaceae	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic–Cretaceous); Boulter and Windle (1993) (Jurassic); van Konijnenburg–van Cittert (1993) (Triassic–Recent); Guignard <i>et al.</i> , (2009) (Jurassic)
<i>Dictyophyllidites harrisii</i>	Dipteridaceae/Matoniaceae	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic); Boulter and Windle (1993) (Jurassic); van Konijnenburg–van Cittert (1993) (Triassic–Recent); Guignard <i>et al.</i> , (2009) (Jurassic)
<i>Matonisporites phlebopteroides</i>	Matoniaceae	Filicales	Filicopsida	Pteridophyta	van Konijnenburg–van Cittert (1993) (Triassic–Recent); Balme (1995) (Jurassic)
<i>Matonisporites</i> cf. <i>phlebopteroides</i>	Matoniaceae	Filicales	Filicopsida	Pteridophyta	van Konijnenburg–van Cittert (1993) (Triassic–Recent); Balme (1995) (Jurassic)
<i>Contignisporites</i> sp.	Schizaeaceae	Filicales	Filicopsida	Pteridophyta	Filatoff (1975) (Jurassic); Balme (1995) (Cretaceous)
<i>Duplexisporites problematicus</i>	Schizaeaceae	Filicales	Filicopsida	Pteridophyta	Filatoff (1975) (Jurassic)
<i>Ischyosporites</i> sp.	Schizaeaceae	Filicales	Filicopsida	Pteridophyta	Filatoff (1975) (Jurassic); Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic and Cretaceous)

Taxon	Family	Order	Class	Division	Reference
<i>Trilobosporites</i> sp.	Schizaeaceae/Cyatheaceae/ Dicksoniaceae/Matoniaceae	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic–Cretaceous); Filatoff (1975) (Jurassic); Juhasz (1979) (Cretaceous); Boulter and Windle (1993) (Jurassic); Schrank (2010) (Jurassic–Cretaceous); Limarino <i>et al.</i> , (2012) (Cretaceous); Pestchevitskaya <i>et al.</i> , (2012) (Cretaceous); Krupnik <i>et al.</i> , (2014) (Triassic–Jurassic)
<i>Cibotiumspora jurienensis</i>	Dicksoniaceae/Cyatheaceae/ ?Gleicheniaceae	Filicales	Filicopsida	Pteridophyta	Boulter and Windle (1993) (Jurassic); Filatoff (1975) (Jurassic)
<i>Obtusisporis canadensis</i>	Dicksoniaceae	Filicales	Filicopsida	Pteridophyta	Boulter and Windle (1993) (Jurassic)
<i>Concavissimiporites punctatus</i>	Cyatheaceae/Dicksoniaceae	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Cretaceous); Boulter and Windle (1993) (Jurassic)
<i>Concavissimiporites subgranulosus</i>	Cyatheaceae/Dicksoniaceae	Filicales	Filicopsida	Pteridophyta	Boulter and Windle (1993) (Jurassic)
<i>Concavissimiporites variverrucatus</i>	Cyatheaceae/Dicksoniaceae	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic–Cretaceous); Boulter and Windle (1993) (Jurassic)
<i>Deltoidospora australis</i>	Cyatheaceae/Dicksoniaceae/ Dipteridaceae/Matoniaceae	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic–Cretaceous); Boulter and Windle (1993) (Jurassic); van Konijnenburg–van Cittert (1993) (Triassic–Recent); Guignard <i>et al.</i> , (2009) (Jurassic); Mander (2011) (Triassic–Jurassic boundary)
<i>Deltoidospora concavus</i>	Cyatheaceae/Dicksoniaceae/ Dipteridaceae/Matoniaceae	Filicales	Filicopsida	Pteridophyta	Boulter and Windle (1993) (Jurassic); van Konijnenburg–van Cittert (1993) (Triassic–Recent); Guignard <i>et al.</i> , (2009) (Jurassic); Mander (2011) (Triassic–Jurassic boundary)
<i>Deltoidospora minor</i>	Cyatheaceae/Dicksoniaceae/ Dipteridaceae/Matoniaceae	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic–Cretaceous); Boulter and Windle (1993) (Jurassic); van Konijnenburg–van Cittert (1993) (Triassic–Recent); Guignard <i>et al.</i> , (2009) (Jurassic); Mander (2011) (Triassic–Jurassic boundary)
<i>Pilosiporites brevipapillosus</i>	–	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic)
<i>Pilosiporites trichopapillosus</i>	–	Filicales	Filicopsida	Pteridophyta	Couper (1958) (Jurassic–Cretaceous)
<i>Alisporites dunrobinensis</i>	Corystospermaceae	Coniferales/ Corystospermales	Coniferopsida/ Pteridospermopsida	Coniferophyta/ Pteridospermophyta	Couper (1958) (Triassic); Boulter and Windle (1993) (Jurassic); Osborn and Taylor (1993) (Triassic); Balme (1995) (Permian–Cretaceous); Traverse (2007) (Triassic); Mander (2011) (Triassic–Jurassic boundary)
<i>Alisporites microsaccus</i>	Corystospermaceae	Coniferales/ Corystospermales	Coniferopsida/ Pteridospermopsida	Coniferophyta/ Pteridospermophyta	Couper (1958) (Jurassic); Boulter and Windle (1993) (Jurassic)
<i>Alisporites thomasi</i>	Corystospermaceae	Coniferales/ Corystospermales	Coniferopsida/ Pteridospermopsida	Coniferophyta/ Pteridospermophyta	Couper (1958) (Jurassic); Boulter and Windle (1993) (Jurassic); Osborn and Taylor (1993) (Triassic); Balme (1995) (Permian–Cretaceous); Traverse (2007) (Triassic); Mander (2011) (Triassic–Jurassic boundary)
<i>Vitreisporites pallidus</i>	–	Caytoniales	Pteridospermopsida	Pteridospermophyta	Couper (1958) (Jurassic–Cretaceous); Boulter and Windle (1993) (Jurassic); Balme (1995) (Permian–Jurassic); Traverse (2007) (Triassic and Jurassic); Mander <i>et al.</i> , (2010) (Triassic–Jurassic boundary); Mander (2011) (Triassic–Jurassic boundary); Gedl and Ziája (2012) (Jurassic)
<i>Pityosporites microalatus</i>	Pinaceae	Coniferales	Coniferopsida	Coniferophyta	Couper (1958) (Jurassic–Cretaceous); Boulter and Windle (1993) (Jurassic)
<i>Pityosporites minimus</i>	Pinaceae	Coniferales	Coniferopsida	Coniferophyta	Boulter and Windle (1993) (Jurassic)
<i>Podocarpidites ellipticus</i>	Podocarpaceae	Coniferales	Coniferopsida	Coniferophyta	Boulter and Windle (1993) (Jurassic)
<i>Quadraeculina anellaeformis</i>	Podocarpaceae	Coniferales	Coniferopsida	Coniferophyta	Couper (1958) (Jurassic); Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic)
<i>Araucariacites australis</i>	Araucariaceae	Coniferales	Coniferopsida	Coniferophyta	Couper (1958) (Jurassic–Cretaceous); Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic–Paleogene); Mander (2011) (Triassic–Jurassic boundary); Mander <i>et al.</i> , (2010) (Triassic–Jurassic boundary); Bonis and Kürschner (2012) (Triassic–Jurassic boundary)
<i>Callialasporites dampieri</i>	Araucariaceae	Coniferales	Coniferopsida	Coniferophyta	Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic–Cretaceous)
<i>Callialasporites minus</i>	Araucariaceae	Coniferales	Coniferopsida	Coniferophyta	Filatoff (1975) (Jurassic)
<i>Callialasporites segmentatus</i>	Araucariaceae/Pinaceae	Coniferales	Coniferopsida	Coniferophyta	Boulter and Windle (1993) (Jurassic); Gedl and Ziája (2012) (Jurassic)
<i>Callialasporites trilobatus</i>	Araucariaceae	Coniferales	Coniferopsida	Coniferophyta	Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic–Cretaceous)
<i>Callialasporites turbatus</i>	Araucariaceae	Coniferales	Coniferopsida	Coniferophyta	Boulter and Windle (1993) (Jurassic)
<i>Classopollis torosus</i>	Cheirolepidiaceae	Coniferales	Coniferopsida	Coniferophyta	Couper (1958) (Jurassic–Cretaceous); Harris (1979) (Jurassic); Boulter and Windle (1993) (Jurassic); Balme (1995) (Triassic–Cretaceous); Ziája (2006) (Jurassic); Mander <i>et al.</i> , (2010) (Triassic–Jurassic boundary); Mander (2011) (Triassic–Jurassic boundary)
<i>Cerebropollenites mesozoicus</i>	?Taxodiaceae	Coniferales	Coniferopsida	Coniferophyta	van Konijnenburg–van Cittert and van der Burgh (1989) (Jurassic); Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic)
<i>Spheripollenites psilatus</i>	Taxodiaceae	Coniferales	Coniferopsida	Coniferophyta	Boulter and Windle (1993) (Jurassic)
<i>Spheripollenites scabratus</i>	Taxodiaceae	Coniferales	Coniferopsida	Coniferophyta	Couper (1958) (Jurassic–Cretaceous); Boulter and Windle (1993) (Jurassic)
<i>Spheripollenites subgranulatus</i>	Taxodiaceae	Coniferales	Coniferopsida	Coniferophyta	Couper (1958) (Jurassic–Cretaceous); Boulter and Windle (1993) (Jurassic)
<i>Perinopollenites elatoides</i>	Taxodiaceae	Coniferales	Coniferopsida	Coniferophyta	Couper (1958) (Jurassic–Cretaceous); van Konijnenburg–van Cittert and van der Burgh (1989) (Jurassic); Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic–Cretaceous); Mander <i>et al.</i> , (2010) (Triassic–Jurassic boundary); Mander (2011) (Triassic–Jurassic boundary)
<i>Chasmatosporites apertus</i>	–	?Cycadales/ ?Ginkgoales/ ?Gnetales	?Cycadopsida/ ?Ginkgopsida	Cycadophyta/ Ginkgophyta	Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic); Batten and Dutta (1997) (Jurassic–Cretaceous); Bonis and Kürschner (2012) (Triassic–Jurassic boundary)

Taxon	Family	Order	Class	Division	Reference
<i>Chasmatosporites hians</i>	–	?Cycadales/ ?Ginkgoales/ ?Gnetales	?Cycadopsida/ ?Ginkgopsida	Cycadophyta/ Ginkgophyta	Boulter and Windle (1993) (Jurassic); Batten and Dutta (1997) (Jurassic–Cretaceous); Mander <i>et al.</i> , (2010) (Triassic–Jurassic boundary); Mander (2011) (Triassic–Jurassic boundary)
<i>Chasmatosporites major</i>	–	?Cycadales/ ?Ginkgoales/ ?Gnetales	?Cycadopsida/ ?Ginkgopsida	Cycadophyta/ Ginkgophyta	Boulter and Windle (1993) (Jurassic); Balme (1995) (Jurassic)
<i>Cycadopites minimus</i>	–	Cycadales/ ?Bennettitales/ Ginkgoales/ ?Peltaspermales	Cycadopsida/ Ginkgopsida/ ?Pteridospermopsida	Cycadophyta/ Ginkgophyta/ ?Pteridospermophyta	Boulter and Windle (1993) (Jurassic); Balme (1995) (Triassic–Jurassic); Mander <i>et al.</i> , (2010) (Triassic–Jurassic boundary); Mander (2011) (Triassic–Jurassic boundary)
<i>Cycadopites carpentieri</i>	–	?Cycadales/ Bennettitales/ ?Ginkgoales/ ?Peltaspermales	Cycadopsida/ ?Ginkgopsida/ ?Pteridospermopsida	Cycadophyta/ ?Ginkgophyta/ ?Pteridospermophyta	Boulter and Windle (1993) (Jurassic); Mander (2011) (Triassic–Jurassic boundary)
<i>Cycadopites subgranulosus</i>	–	?Cycadales/ Bennettitales/ ?Ginkgoales/ ?Peltaspermales	Cycadopsida/ ?Ginkgopsida/ ?Pteridospermopsida	Cycadophyta/ ?Ginkgophyta/ ?Pteridospermophyta	van Konijnenburg–van Cittert (1971) (Jurassic); Mander (2011) (Triassic–Jurassic boundary)
<i>Eucommiidites troedssonii</i>	Erdtmanitheceae	Erdtmanithecales	–	–	Pedersen <i>et al.</i> , (1989) (Cretaceous); Friis and Pedersen (1996) (Cretaceous); Mander <i>et al.</i> , (2010) (Triassic–Jurassic boundary); Mander (2011) (Triassic–Jurassic boundary)
Striate bisaccate sp.	–	–	–	–	–
Trisaccate sp. 1	–	–	–	–	–

# Appendix 2

Appendix 2: Sample processing details.

Sample	Sample Height (m)	Locality	Lithology	Collector	Processor	Processing method	Number of <i>Lycopodium</i> tablets (for other studies)	Analysed	Seive size (µm)
SS03/10.1	159.52	Burniston Bay	Coal	SMS	SMS	HNO3 + Schulze	0	SMS	20
JP2/11	156.17	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/12	156.15	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP2/12	156.09	Burniston Bay	Fine sandstone	CHW/JP	SMS	HCl + HF	0	SMS	10
JP2/10	156.02	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/11	156.00	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/10	155.40	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/9	155.12	Burniston Bay	Fine sandstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP2/9	155.10	Burniston Bay	Fine sandstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/8	154.87	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP2/8	154.77	Burniston Bay	Fine sandstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/7	154.64	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP2/7	154.61	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/5A	154.22	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP2/6A	154.02	Burniston Bay	Fine sandstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/5	153.73	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP2/5	153.70	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/4	153.40	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/3	153.19	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP2/4	153.09	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP2/3	152.79	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP1/1	152.64	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP2/2	152.37	Burniston Bay	Fine sandstone	CHW/JP	SMS	HCl + HF	1	SMS	10
JP2/1	152.09	Burniston Bay	Siltstone	CHW/JP	SMS	HCl + HF	1	SMS	10
SS05/03	151.59	Burniston Bay	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
10311	126.72	Cloughton Wyke	Siltstone	NMC	NMC	HCl + HF	0	SMS	20
10312	115.72	Cloughton Wyke	Claystone	NMC	NMC	HCl + HF	0	SMS	20
10313	98.42	Cloughton Wyke	Fine sandstone	NMC	NMC	HCl + HF	0	SMS	20
10314A	96.82	Cloughton Wyke	Siltstone	NMC	NMC	HCl + HF	0	SMS	20
SB-22	96.62	Cloughton Wyke	Siltstone	NMC	NMC	HCl + HF	0	SMS	20
10315	95.82	Cloughton Wyke	Claystone	NMC	NMC	HCl + HF	0	SMS	20
P1	89.82	Cloughton Wyke	Coal	CHW	CHW	HCl + HF	0	SMS	10
P2	89.52	Cloughton Wyke	Coal	CHW	CHW	HCl + HF	0	SMS	10
P3	89.37	Cloughton Wyke	Coal	CHW	CHW	HCl + HF	0	SMS	10
P5	89.34	Cloughton Wyke	Coal	CHW	CHW	HCl + HF	0	SMS	10
P10	89.32	Cloughton Wyke	Coal	CHW	CHW	HCl + HF	0	SMS	10
P6	89.02	Cloughton Wyke	Claystone	CHW	CHW	HCl + HF	0	SMS	10
10317	88.97	Cloughton Wyke	Claystone	NMC	NMC	HCl + HF	0	SMS	20
P4	88.37	Cloughton Wyke	Claystone	CHW	CHW	HCl + HF	0	SMS	10
P7	87.06	Cloughton Wyke	Claystone	CHW	CHW	HCl + HF	0	SMS	10
P8	84.76	Cloughton Wyke	Claystone	CHW	CHW	HCl + HF	0	SMS	10
P9	84.42	Cloughton Wyke	Siltstone	CHW	CHW	HCl + HF	0	SMS	10
MPB above	81.32	Cloughton Wyke	Fine sandstone	NMC	NMC	HCl + HF	0	SMS	20
MPB14	80.37	Cloughton Wyke	Limestone	NMC	NMC	HCl + HF	0	SMS	20
MPB13	80.12	Cloughton Wyke	Fine sandstone	NMC	NMC	HCl + HF	0	SMS	20
MPB12	79.92	Cloughton Wyke	Fine sandstone	NMC	NMC	HCl + HF	0	SMS	20
MPB10	79.72	Cloughton Wyke	Fine sandstone	NMC	NMC	HCl + HF	0	SMS	20
MPB9	79.57	Cloughton Wyke	Fine sandstone	NMC	NMC	HCl + HF	0	SMS	20
MPB5	79.27	Cloughton Wyke	Fine sandstone	NMC	NMC	HCl + HF	0	SMS	20
MPB4	79.12	Cloughton Wyke	Fine sandstone	NMC	NMC	HCl + HF	0	SMS	20
MPB3	78.77	Cloughton Wyke	Fine sandstone	NMC	NMC	HCl + HF	0	SMS	20
MPB2	78.57	Cloughton Wyke	Fine sandstone	NMC	NMC	HCl + HF	0	SMS	20
MPB1	78.37	Cloughton Wyke	Limestone	NMC	NMC	HCl + HF	0	SMS	20
10319	75.37	Cloughton Wyke	Claystone	NMC	NMC	HCl + HF	0	SMS	20
10320	70.17	Cloughton Wyke	Claystone	NMC	NMC	HCl + HF	0	SMS	20
HW3	35.42	Hayburn Wyke	Coal	SMS	SMS	HNO3 + Schulze	0	SMS	20
HW2	35.07	Hayburn Wyke	Coal	SMS	SMS	HNO3 + Schulze	0	SMS	20
HB1	10.42	Hasty Bank	Grey Clay	SMS	SMS	HCl + HF	2	SMS	10
HB2	10.32	Hasty Bank	Grey Clay	SMS	SMS	HCl + HF	2	SMS	10
HB3	10.22	Hasty Bank	Grey Clay	SMS	SMS	HCl + HF	2	SMS	10
HB4	10.12	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB5	10.02	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB6	9.92	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB7	9.82	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB8	9.72	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB9	9.62	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB10	9.52	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB11	9.42	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB12	9.32	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB13	9.22	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB14	9.12	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB15	9.02	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10

Sample	Sample Height (m)	Locality	Lithology	Collector	Processor	Processing method	Number of <i>Lycopodium</i> tablets (for other studies)	Analysed	Seive size (µm)
HB16	8.92	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB17	8.82	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB18	8.72	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB19	8.62	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB20	8.52	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB21	8.42	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB22	8.32	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB23	8.22	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB24	8.12	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB25	8.02	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB26	7.92	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB27	7.82	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB28	7.72	Hasty Bank	Siltstone	SMS	SMS	HCl + HF	2	SMS	10
HB29	7.62	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB30	7.52	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB31	7.42	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB32	7.32	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB33	7.22	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB34	7.12	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB35	7.02	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB36	6.92	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB37	6.82	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB38	6.72	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB39	6.62	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB40	6.52	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB41	6.42	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB42	6.32	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB43	6.22	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB44	6.12	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB45	6.02	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB46	5.92	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB47	5.82	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB48	5.72	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB49	5.62	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
HB50	5.52	Hasty Bank	Claystone	SMS	SMS	HCl + HF	2	SMS	10
SS06/08	85.5	Yons Nab	Coal	SMS	SMS	HCl + HF	2	SMS	10
SS06/07	85.75	Yons Nab	Fine sandstone	SMS	SMS	HCl + HF	2	SMS	10
SS06/05	86.45	Yons Nab	Fine sandstone	SMS	SMS	HCl + HF	2	SMS	10
SS06/04	87.2	Yons Nab	Coal	SMS	SMS	HCl + HF	2	SMS	10
SS06/02	87.74	Yons Nab	Coal	SMS	SMS	HNO <sub>3</sub> + Schulze	0	SMS	20
SS06/01	88	Yons Nab	Claystone	SMS	SMS	HCl + HF	2	SMS	10
CB1/3	89.3	Cayton Bay	Coal	SMS	SMS	HNO <sub>3</sub> + Schulze	0	SMS	20

SMS S. M. SLATER  
 CHW C. H. WELLMAN  
 JP J. POULTER  
 NMC N. M. CADMAN

NB: Samples from section 4 (Yons Nab and Cayton Bay) have not been incorporated into the main section as the exact sample points are too closely spaced to be correlated with other samples with certainty.

# Appendix 3











Sample	Sample Height (m)	HB36	HB37	HB38	HB39	HB40	HB41	HB42	HB43	HB44	HB45	HB46	HB47	HB48	HB49	HB50	SS06/08	SS06/07	SS06/05	SS06/04	SS06/02	SS06/01	GB1/3	
<i>Foveosporites morstonensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nevesisporites bigramulatus</i>	0	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rogalskisporites cicatricosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Strepisporites</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Anopicalatisporites</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Densosporites circumundulatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Densosporites velatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Densosporites</i> cf. <i>velatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Kraeuselisporites whiffordensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Kraeuselisporites</i> sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lycopodiacidites cerniidites</i>	1	P	1	P	1	P	1	P	1	P	1	P	1	P	1	P	1	P	1	P	1	P	1	P
<i>Lycopodiacidites rugulatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Neosariricka truncatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Retitriletes anstroclavatioides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Retitriletes clavatioides</i>	P	P	1	P	1	P	1	P	1	P	1	P	1	P	1	P	1	P	1	P	1	P	1	P
<i>Retitriletes semimuris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Retitriletes singhii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptolepidites boszus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptolepidites crasibalteus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptolepidites equatibossus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptolepidites major</i>	0	P	P	0	P	0	P	0	P	0	P	0	P	1	0	P	1	0	P	1	0	0	0	0
<i>Sectrosporites pseudothelovatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Staphisporites</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Staphisporites mathurii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Uvaeosporites argenteiformis</i>	0	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Reticspinosporites whytei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pastillitriletes phyllicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calamospora mesozoa</i>	4	9	2	1	8	8	3	6	6	2	6	8	12	0	0	0	0	0	0	0	0	0	0	0
<i>Laevigatosporites</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Marattisporites scabratus</i>	11	3	2	4	10	8	7	10	4	12	7	3	8	7	0	0	0	0	0	0	0	0	0	0
<i>Baculatisporites comamensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Omundacioidites wellmanii</i>	0	P	0	P	1	P	0	P	0	P	1	P	0	P	1	P	0	P	1	P	0	0	0	0
<i>Tobisporites major</i>	P	P	0	0	P	0	P	0	P	0	P	0	P	0	0	0	0	0	0	0	0	0	0	0
<i>Tobisporites minor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gleichenioidites senonicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dicynophylloides harrisi</i>	4	5	6	7	11	2	7	6	1	9	10	12	7	15	15	5	0	1	3	3	2	1	0	0
<i>Combaculatisporites mesozocus</i>	1	3	2	1	2	1	P	P	0	P	P	2	1	1	6	0	0	0	0	0	0	0	0	0
<i>Dicynophylloides equitimus</i>	P	2	P	1	P	3	2	0	0	1	P	P	2	1	2	0	9	1	1	P	0	0	11	0
<i>Matonisporites phleboterooides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Matonisporites</i> cf. <i>phleboterooides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Concisporites</i> sp.	P	P	P	1	2	1	P	0	P	1	P	1	P	1	P	1	P	0	0	0	0	0	0	0
<i>Concisporites</i> sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Contignisporites</i> sp.	1	0	0	P	0	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Duplexisporites problematicus</i>	P	P	P	1	P	P	1	P	P	0	P	0	P	1	P	0	0	0	0	0	0	0	0	0

Sample	Sample Height (m)	HB36	HB37	HB38	HB39	HB40	HB41	HB42	HB43	HB44	HB45	HB46	HB47	HB48	HB49	HB50	SS060805	SS060707	SS060505	SS060404	SS060207	SS060101	CR1/3	
<i>Ischyosporites</i> sp.	6.92	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	2
<i>Trilobosporites</i> sp.		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Clavospora jurtensis</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Obusisporis canadensis</i>		P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Concavissimiporites punctatus</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Concavissimiporites subgranulosus</i>		P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Concavissimiporites variverrucatus</i>		P	P	1	P	P	P	1	P	P	P	P	P	P	P	P	0	1	P	P	4	0	0	0
<i>Deloidospora australis</i>		0	P	1	0	P	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Deloidospora concavus</i>		0	1	P	1	P	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Deloidospora minor</i>	3.5	4	11	8	6	3	6	5	7	6	9	11	13	116	151	56	43	93	99	63				
<i>Phiosporites brevipapillosum</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phiosporites trichopapillosum</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alisporites durabensis</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alisporites microsacculus</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alisporites thomasi</i>		1	2	3	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Vireosporites pallidus</i>		2	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Piposporites microalatus</i>		4	1	2	1	1	1	1	3	1	3	6	3	6	3	0	2	1	2	6	4	1		
<i>Piposporites minimus</i>		0	0	P	P	P	P	P	1	P	2	P	P	P	P	0	0	0	0	0	0	0	0	0
<i>Podocarpulites ellipticus</i>		0	0	1	0	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Quadraaculina anellaeformis</i>		0	P	P	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Araucariacites australis</i>	18	15	11	8	8	14	11	17	17	16	12	14	15	8	10	3	2	3	8	9	5	6		
<i>Callialasporites dampieri</i>		P	P	P	P	P	P	1	P	1	P	1	P	1	P	1	2	1	P	P	0	P	1	
<i>Callialasporites minus</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Callialasporites segmentatus</i>		P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Callialasporites trilobatus</i>		0	0	1	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Callialasporites barbatus</i>		13	15	9	10	6	4	2	6	3	7	3	5	5	1	2	P	1	P	1	0	0	0	0
<i>Classopollis torosus</i>		49	48	55	52	44	49	45	52	55	44	44	55	55	66	56	49	15	112	125	21	19	54	
<i>Cerebropollanites mesozoicus</i>		2	3	2	3	2	3	4	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>Spheropollanites psilans</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spheropollanites scabratus</i>		8	7	8	5	9	6	6	11	7	12	6	5	5	7	7	P	1	1	4	0	P	0	0
<i>Spheropollanites subgranulatus</i>		19	16	19	22	25	26	29	26	31	29	27	26	30	30	19	6	0	5	7	1	1	0	0
<i>Perinopollanites elatoides</i>		44	59	65	60	46	47	49	41	52	44	58	52	51	49	35	7	23	14	6	28	37	59	
<i>Chasmatosporites aperte</i>		4	1	3	1	1	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
<i>Chasmatosporites hians</i>		1	1	1	P	2	1	2	1	P	1	2	1	3	3	0	0	0	0	0	0	0	0	0
<i>Chasmatosporites major</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cycadophites minimus</i>		8	4	6	7	11	13	6	11	9	1	5	9	6	5	2	1	3	2	8	3	2		
<i>Cycadophites carpentieri</i>		4	6	5	6	5	8	5	4	5	3	1	9	4	3	2	0	0	P	1	4	0		
<i>Cycadophites subgranulosus</i>		0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Encommidiites moodsonii</i>		P	P	1	3	2	1	1	1	P	1	P	P	0	0	0	0	0	0	0	0	0	0	0
<i>Striatie bisaccate</i> sp.		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trisaccate</i> sp. 1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>Total</b>		<b>202</b>	<b>206</b>	<b>208</b>	<b>211</b>	<b>208</b>	<b>205</b>	<b>206</b>	<b>206</b>	<b>208</b>	<b>204</b>	<b>203</b>	<b>205</b>	<b>224</b>	<b>244</b>	<b>207</b>	<b>210</b>	<b>209</b>	<b>212</b>	<b>210</b>	<b>204</b>	<b>211</b>	<b>203</b>	

# Appendix 4





Sample	Sample Height (m)	HR40	HR41	HR42	HR43	HR44	HR45	HR46	HR47	HR48	HR49	HB50	SS06/08	SS06/07	SS06/05	SS06/04	SS06/02	SS06/01	CB1/3
Spores	19	10	2	5	9	7	14	25	10	16	10	23	18	18	14	0	5	2	89.3
Pollen	63	53	43	35	49	32	69	100	38	48	25	21	4	48	28	1	7	0	88
Algae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dinoflagellates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acritarchs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Humic debris	8	3	11	5	3	1	4	10	6	5	3	1	2	0	4	3	0	0	0
AOM	56	49	46	68	45	59	52	127	53	52	18	83	59	28	38	111	83	183	0
<i>Boryococcus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Structured Vitrinite	8	13	4	2	7	10	5	10	3	4	18	0	0	0	0	0	0	0	0
Unstructured Vitrinite	14	27	46	46	34	48	20	51	34	33	52	27	72	64	80	68	50	15	0
Cuticle	6	11	6	7	4	4	6	12	16	14	9	1	1	0	7	0	1	0	0
Inertinite	26	34	42	32	49	39	30	65	40	28	65	44	44	42	29	17	54	0	0
<b>TOTAL</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>400</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>

# Appendix 5

Appendix 5: Nonmetric multidimensional scaling data of samples using relative abundance data.  
Refers to Fig. 4.9A.

Analysing 85 taxa, 114 samples

Bray-Curtis dissimilarity metric

Stress = 0.144

	Axis 1	Axis 2
SS03/10.1	-0.196229991	0.050720743
JP2/11	-0.197877191	-0.301033577
JP1/12	-0.326031474	-0.101437486
JP2/12	-0.165433256	-0.343117923
JP2/10	-0.152697088	-0.37856315
JP1/11	-0.387828783	-0.168007767
JP1/10	-0.51304178	0.015731518
JP1/9	-0.444797219	-0.034580003
JP2/9	-0.380519702	-0.078001823
JP1/8	-0.476923381	-0.013227084
JP2/8	-0.380110496	-0.182813001
JP1/7	-0.542388352	0.007061061
JP2/7	-0.189291128	0.003451407
JP1/5A	-0.299263074	-0.223195496
JP2/6A	-0.347601917	-0.042639984
JP1/5	-0.526803298	-0.048375932
JP2/5	-0.369684821	-0.079589961
JP1/4	-0.380299645	-0.023114326
JP1/3	-0.338565375	-0.19040237
JP2/4	-0.309685646	-0.126115377
JP2/3	-0.233808393	-0.209444179
JP1/1	-0.312494577	-0.018072985
JP2/2	-0.144242362	-0.198784969
JP2/1	-0.18793464	-0.202369838
SS05/03	-0.214667044	0.119396941
10311	0.191515589	0.166213053
10312	0.137417124	0.196163617
10313	-0.014496574	0.110831488
10314A	0.093063626	0.122239172
SB-22	0.085595764	0.149220792
10315	-0.289768005	0.099382743
P1	-0.065812591	0.02571886
P2	-0.143990149	0.139006686
P3	-0.010109983	0.144913185
P5	-0.204239602	0.223952639
P10	-0.275363011	0.187255006
P6	-0.558732952	0.08675277
10317	-0.296875549	0.013121631
P4	-0.442409007	0.187339679
P7	-0.121647348	0.09116734
P8	-0.043281347	0.161432159
P9	-0.165566446	0.124714847
MPB above	0.015318155	0.139003727
MPB14	0.079858888	0.283107267
MPB13	0.070594675	0.155484921
MPB12	0.107652744	0.180207047
MPB10	0.071239184	0.242319529
MPB9	0.113556146	0.270451334
MPB5	0.07044085	0.112409434
MPB4	0.086378446	0.073823485
MPB3	0.094652849	0.137220368
MPB2	0.10509069	0.132740574
MPB1	0.086316489	0.135202162
10319	0.104891554	0.230768787
10320	-0.112095392	0.112069567
HW3	-0.194043075	0.026826216
HW2	-0.441009725	0.120755311
HB1	0.038687673	-0.231805441
HB2	0.215803539	-0.228422094
HB3	0.360032469	0.070953769
HB4	0.292218016	-0.064467191
HB5	0.316316846	-0.19053809
HB6	0.289789483	-0.087785999
HB7	0.203152124	-0.119003594
HB8	0.127191442	-0.18876156
HB9	0.152551052	-0.216594095
HB10	0.242744666	-0.165624825
HB11	0.242487697	-0.084137974

HB12	0.235951707	-0.142132211
HB13	0.20387834	-0.178027152
HB14	0.191085779	-0.116855505
HB15	0.215626672	-0.082179579
HB16	0.151827484	-0.147324184
HB17	0.174186354	-0.168147266
HB18	0.08746462	-0.079291134
HB19	0.118623586	-0.045530638
HB20	0.166247289	-0.151029748
HB21	0.103655797	-0.105176888
HB22	0.187931039	-0.186464141
HB23	0.284169655	-0.135651462
HB24	0.204152566	-0.051282932
HB25	0.069846226	-0.057211004
HB26	0.135642252	-0.224038763
HB27	0.16585651	-0.140546151
HB28	0.208972846	-0.15864707
HB29	0.262770602	-0.108641713
HB30	0.363805729	-0.045790107
HB31	0.238139254	0.013055185
HB32	0.266931578	-0.029751044
HB33	0.277280191	-0.028780983
HB34	0.226064593	0.04788862
HB35	0.219459793	-0.005043997
HB36	0.268321276	0.045671281
HB37	0.257762589	0.102436367
HB38	0.268452012	0.12298603
HB39	0.23577463	0.089950738
HB40	0.28014884	0.031044848
HB41	0.273127111	0.059826915
HB42	0.293092779	0.05047468
HB43	0.251011735	0.043077304
HB44	0.272369308	0.095170237
HB45	0.262844274	0.028804887
HB46	0.260240787	0.068859918
HB47	0.246844226	0.078109047
HB48	0.240002689	0.059858147
HB49	0.238911084	0.053381596
HB50	0.221469929	0.051086831
SS06/08	-0.256610128	0.115508243
SS06/07	-0.364368397	0.105255392
SS06/05	-0.091075541	0.272154149
SS06/04	-0.033209002	0.323360293
SS06/02	-0.195888887	0.013789192
SS06/01	-0.231580792	0.031343468
CB1/3	-0.054107372	0.175347564

# Appendix 6

Appendix 6: Nonmetric multidimensional scaling data of samples using presence-absence data.  
Refers to Fig. 4.9B.

Analysing 85 taxa, 114 samples

Bray-Curtis dissimilarity metric

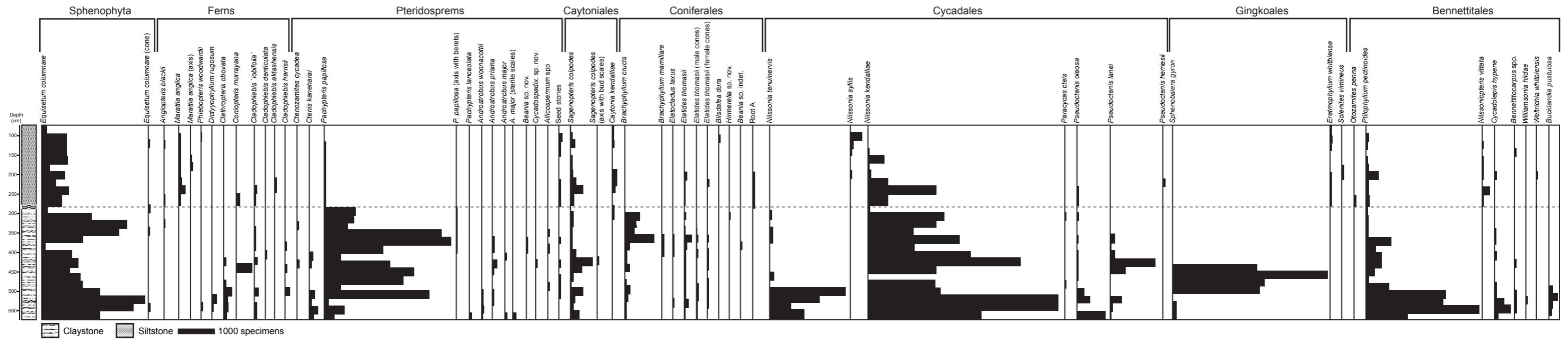
Stress = 0.233

	Axis 1	Axis 2
SS03/10.1	-0.122205315	-0.258791953
JP2/11	0.152630885	-0.042017706
JP1/12	0.040059948	0.135218647
JP2/12	0.082746422	0.126797605
JP2/10	0.124357015	0.060409506
JP1/11	0.168768525	-0.03412285
JP1/10	0.104200375	-0.058258798
JP1/9	0.15901858	0.20078418
JP2/9	0.133002752	0.072779645
JP1/8	0.234555131	0.109813234
JP2/8	0.115438474	-0.010866333
JP1/7	0.175478076	0.078206891
JP2/7	0.075057291	-0.205970852
JP1/5A	0.082503407	0.096626139
JP2/6A	0.142191823	0.042700686
JP1/5	0.137230046	-0.000220132
JP2/5	0.131586538	0.009009876
JP1/4	0.145927791	0.005995642
JP1/3	0.138576657	-0.007744371
JP2/4	0.08723754	-0.009341037
JP2/3	0.100082384	0.026164627
JP1/1	-0.198628563	-0.004997935
JP2/2	0.140164688	0.051071122
JP2/1	0.166608965	0.033055421
SS05/03	-0.099504319	0.002911679
10311	0.101438559	-0.096614774
10312	-0.056072509	0.141492799
10313	-0.031809641	0.078544871
10314A	-0.041054063	0.105529064
SB-22	0.018508951	0.105774568
10315	0.004181661	0.064983272
P1	-0.143306407	0.208703004
P2	-0.176698427	0.166371781
P3	0.144188395	-0.10945251
P5	-0.393500666	0.074544135
P10	-0.41235829	-0.1786987
P6	-0.101596551	0.290328734
10317	-0.100851342	0.043748241
P4	-0.000183235	0.279615162
P7	-0.088082837	0.146644503
P8	-0.087240313	0.173583292
P9	-0.153254627	0.223557117
MPB above	0.022727856	0.049573324
MPB14	-0.13864217	0.068240471
MPB13	-0.163438184	-0.055352738
MPB12	0.007011373	0.040972156
MPB10	0.041901056	0.02428534
MPB9	0.077507599	0.048308413
MPB5	0.052356488	0.032830002
MPB4	-0.00060564	0.040101202
MPB3	-0.006790442	0.148334123
MPB2	0.039159448	0.059471607
MPB1	-0.082082864	0.102613732
10319	0.010630066	0.079264594
10320	-0.015317318	0.054288237
HW3	-0.320324569	0.169751395
HW2	-0.342903753	-0.030164913
HB1	-0.101608487	-0.107261067
HB2	-0.049050585	-0.098949226
HB3	-0.068943292	-0.139419803
HB4	-0.045579154	-0.024236743
HB5	5.25E-05	-0.012060176
HB6	-0.026921141	-0.040587
HB7	-0.031408035	-0.012976912
HB8	0.05195065	-0.114854814
HB9	-0.004909763	-0.07365709
HB10	-0.001814815	-0.029693347
HB11	-0.004613285	-0.032347272

HB12	-0.022189095	-0.070006948
HB13	0.001390268	-0.057384254
HB14	0.008870191	-0.025534631
HB15	0.013175642	-0.018737275
HB16	-0.005739799	-0.02009165
HB17	-0.030422168	-0.025116759
HB18	-0.022299663	-0.021218909
HB19	0.007245729	-0.037186814
HB20	-0.051446029	-0.151555138
HB21	-0.008200141	-0.042286456
HB22	-0.01111495	-0.045830382
HB23	0.017024303	-0.044959926
HB24	0.025270007	-0.069652115
HB25	-0.023687723	-0.104743778
HB26	0.023493638	-0.077799355
HB27	-0.001093951	-0.089831228
HB28	0.04404019	-0.052949932
HB29	0.0223366	-0.057734193
HB30	0.025450051	-0.125374011
HB31	0.029850256	-0.025705079
HB32	0.057315298	-0.061462665
HB33	0.04279904	-0.018557179
HB34	0.0411654	-0.030684179
HB35	0.040077559	-0.046506286
HB36	0.00434889	-0.101723775
HB37	0.00270978	-0.044592489
HB38	0.028402191	-0.048417709
HB39	0.05186801	-0.064039045
HB40	0.054657773	-0.022421524
HB41	0.009971345	-0.057014078
HB42	0.040295673	-0.026099937
HB43	0.055278053	-0.032566155
HB44	0.017948195	-0.081407814
HB45	-0.003571395	-0.058291909
HB46	0.043742813	-0.034838319
HB47	0.047654117	-0.073516495
HB48	0.052129373	-0.030335628
HB49	0.04380845	-0.022939728
HB50	0.059035363	-0.08582492
SS06/08	-0.091243313	0.07451511
SS06/07	-0.141981046	0.041521213
SS06/05	0.057199933	0.055670777
SS06/04	0.097404798	0.072180822
SS06/02	-0.112739473	-0.1649922
SS06/01	-0.099739603	-0.06252448
CB1/3	-0.238227895	-0.195773561

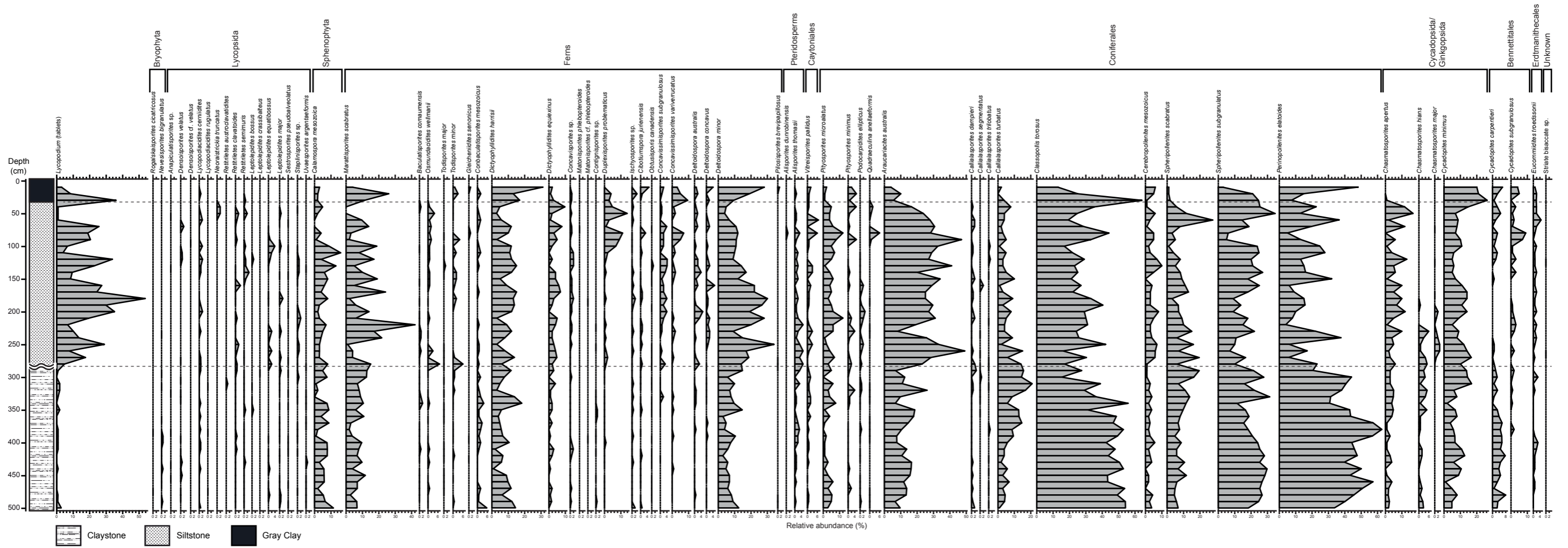
# Appendix 7





Appendix 7: Histogram of abundances and distributions of plant megafossils through the Hasty Bank plant bed. Modified from Spicer and Hill (1979).

# Appendix 8



Appendix 8: Relative abundance chart of all sporomorph taxa from the Hasty Bank plant bed. Relative abundances of Jurassic taxa are calculated from counts of at least 200 grains. Spiked *Lycopodium* count data is shown as a percentage of the indigenous Jurassic taxa plus the spiked *Lycopodium* itself.

# Appendix 9

Appendix 9. Correspondence analysis data of samples and taxa using logarithmically transformed sporomorph relative abundances (refers to Fig. 5.4A).

Analyzing 67 taxa, 50 samples

Eigenvalues	Sample scores																					
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	Axis 11	Axis 12	Axis 13	Axis 14	Axis 15	Axis 16	Axis 17	Axis 18	Axis 19	Axis 20	Axis 21	
	0.0967382	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321	0.0637321
HB1	0.48756	-0.24235	-0.98158	-0.023358	-0.3853	-0.20916	0.08448	-0.18946	-0.33638	-0.19616	0.12395	0.3788	-0.08353	-0.12984	0.08947	0.06824	-0.063241	0.11737	-0.050412	0.03127	-0.036925	0.067063
HB2	0.38281	-0.12776	-0.14063	0.080986	-0.3596	-0.09927	-0.25129	0.050646	0.04761	0.23442	-0.060947	-0.005291	0.25269	0.577	0.14189	-0.19673	0.18757	-0.12134	0.14819	-0.104212	0.01827	0.067063
HB3	0.25127	-0.14449	-0.12334	0.19636	-0.073123	-0.22989	-0.16479	-0.073354	0.038636	0.33161	0.31425	-0.31095	-0.020055	0.17654	-0.03278	0.038178	0.02653	0.2291	-0.063635	0.2291	-0.11788	0.097439
HB4	0.55313	-0.19386	0.506	-0.17814	0.15602	-0.32739	-0.060861	0.15367	-0.31433	0.018071	0.20476	0.10485	-0.016251	-0.02223	-0.058508	-0.026478	0.036562	0.13667	0.14568	-0.026415	0.17665	-0.026415
HB5	0.57874	-0.075946	0.69537	0.14905	0.24807	-0.29397	-0.075331	-0.13981	-0.067285	-0.2004	0.16644	0.15068	-0.056448	-0.0352	0.17619	-0.10888	0.17065	0.0060896	-0.057787	0.027056	0.17065	-0.057787
HB6	0.057281	0.0087975	0.086166	0.031035	0.07874	-0.052346	0.013154	-0.12618	-0.014514	0.2275	-0.23737	0.026733	0.16638	0.052496	0.29283	0.029538	-0.026122	0.089024	-0.23469	-0.147354	-0.11906	-0.23469
HB7	0.099343	0.28685	0.12441	0.20334	-0.21216	-0.083123	0.41221	0.073947	-0.18922	0.16652	-0.10333	-0.040032	-0.14228	-0.21454	-0.15901	-0.043176	0.10135	-0.099907	-0.10744	-0.15834	0.026185	-0.099907
HB8	1.1605	-0.5743	-0.31898	-0.16354	0.47141	0.32055	0.27163	0.12159	0.17692	-0.043688	-0.20557	-0.17238	-0.044205	0.001942	-0.05644	0.038117	-0.081896	-0.027842	-0.046388	0.039988	0.096211	-0.027842
HB9	0.0711	-0.065512	0.2243	-0.16249	-0.2231	0.010818	-0.090097	0.010568	0.1888	0.0016124	0.039987	0.076631	0.036717	0.18182	-0.1849	0.10142	0.061672	-0.2084	0.024793	-0.16722	-0.1021	-0.2084
HB10	0.23276	0.045081	0.19863	0.38829	-0.22612	0.33186	-0.17593	-0.34612	0.044245	0.043183	0.019734	-0.20996	-0.015216	-0.18637	0.16919	0.22267	-0.11691	0.10424	-0.062563	-0.039027	0.12959	-0.062563
HB11	0.050619	-0.13933	0.048719	0.16266	-0.21733	0.19293	0.092665	-0.092535	0.21697	0.016611	-0.05248	0.0055849	-0.24458	0.0017497	-0.070581	-0.080392	0.20132	0.012999	0.14638	-0.045139	0.043221	-0.080392
HB12	0.09198	0.26348	0.1031	0.50708	-0.055777	0.29293	0.18765	-0.1712	-0.25679	-0.25986	-0.013201	-0.14744	0.20539	-0.053406	-0.1077	0.047261	0.095618	-0.10252	0.1274	0.04703	-0.17169	-0.10252
HB13	0.0018516	0.41505	-0.34085	0.73915	0.51451	-0.07839	-0.40698	0.35083	0.17277	-0.0046724	-0.035456	0.25253	-0.21006	-0.0041243	-0.073676	0.1517	0.029223	-0.070709	0.021484	-0.081505	-0.01196	-0.073676
HB14	0.23686	0.23	0.065031	0.23589	-0.12009	-0.010048	-0.033479	0.19067	-0.014906	0.026448	0.033201	0.046481	0.222091	0.21525	0.03807	-0.027399	-0.10126	0.13849	-0.13428	0.18101	-0.049946	-0.027399
HB15	-0.062139	0.041854	0.087685	0.10061	-0.16925	0.019549	0.1491	0.16398	0.22142	0.0547	0.10045	0.05054	-0.011851	0.0016564	-0.14625	-0.024106	-0.042051	0.25076	-0.10133	0.13955	-0.035774	-0.024106
HB16	0.054382	0.55461	-0.12421	-0.12863	0.029528	-0.66342	0.18313	-0.27954	0.22912	-0.18511	-0.22011	-0.2462	0.039519	0.013946	0.0008636	0.21637	-0.0007912	-0.10903	-0.040285	0.023438	0.1046	-0.040285
HB17	-0.082379	0.1422	-0.13151	-0.019759	0.029904	-0.0003089	0.18228	0.11055	0.040813	0.10827	0.010085	-0.1273	-0.0033705	-0.17905	0.0080102	-0.15262	0.052527	0.13556	-0.022289	0.027346	-0.014828	-0.022289
HB18	0.057697	0.14239	-0.091935	0.031481	-0.12884	-0.075137	0.043349	0.2045	0.22765	-0.099781	0.20989	-0.19217	-0.13702	-0.22209	0.35033	-0.12695	0.0042099	-0.12665	0.095982	0.073759	-0.099166	-0.12665
HB19	-0.050373	0.20981	-0.0441	0.010108	-0.02451	-0.047904	0.053569	0.1076	0.021366	0.021463	0.011413	-0.084483	0.10757	-0.068729	0.083727	-0.057428	-0.039208	-0.10968	0.042295	0.063141	0.052656	-0.039208
HB20	-0.041239	0.53638	-0.061478	-0.026746	0.16024	0.20844	0.086321	-0.012749	-0.11139	0.05434	0.075527	0.11404	0.21425	-0.026161	0.0055421	-0.24094	-0.17378	-0.027833	0.09454	0.11573	0.28875	-0.027833
HB21	0.11464	0.52357	-0.033837	-0.19832	0.05468	0.04132	0.13722	-0.023732	-0.075638	0.039227	0.12519	0.18488	0.091165	0.037743	-0.16843	-0.046247	-0.01082	-0.05096	-0.10924	-0.096252	0.0065842	-0.05096
HB22	0.070476	0.16501	-0.20759	-0.046438	0.055661	0.10547	0.073682	0.017441	0.042002	-0.034313	-0.070028	0.10103	-0.060034	-0.076924	-0.14716	0.08024	0.086317	0.043675	-0.0038634	-0.25311	0.043675	-0.0038634
HB23	0.043337	0.09746	-0.10438	-0.19412	-0.14822	0.087445	-0.33951	0.048986	-0.19911	0.012869	-0.026704	-0.26704	-0.21049	-0.024631	0.049618	0.070703	-0.099914	-0.14312	0.049558	0.048306	-0.11945	-0.099914
HB24	-0.091171	0.19138	-0.067197	-0.23771	0.033748	0.098113	-0.2361	-0.1147	-0.2099	0.11079	0.089723	-0.15249	-0.17795	0.053331	-0.15487	0.063337	-0.066711	0.063001	0.039241	0.059884	0.15264	-0.066711
HB25	-0.087647	0.3913	-0.1938	-0.37533	0.32987	0.053354	0.020225	-0.26313	0.0063824	-0.060584	0.11237	0.019981	-0.12506	0.1746	0.094293	-0.18323	0.08955	0.082872	0.053538	-0.15192	-0.073857	-0.18323
HB26	0.02846	0.31637	0.11909	-0.36737	0.12077	0.35992	-0.08173	-0.17298	-0.031014	-0.012437	-0.012225	0.1082	-0.20087	0.12752	0.059365	0.074464	0.20628	0.017886	-0.04664	0.10094	-0.04945	-0.04664
HB27	-0.012264	0.081549	0.073381	-0.18179	-0.028965	0.083583	-0.14813	0.098089	0.039917	0.00408	0.19404	-0.13296	-0.046436	0.0093636	0.048444	-0.098898	-0.20212	0.024144	0.057567	0.15399	-0.0091489	-0.098898
HB28	0.050949	0.21761	0.21471	-0.15956	-0.4123	0.16693	-0.040913	0.070925	0.31745	-0.25599	-0.14924	0.28342	-0.097722	0.025434	-0.07963	0.063133	0.011249	0.054906	-0.054793	0.10057	0.10755	-0.054793
HB29	-0.15561	-0.03686	0.07832	-0.19123	-0.12123	0.039383	0.010575	0.13731	0.12112	-0.023353	0.022017	0.031347	0.026089	-0.065448	0.085012	0.023526	-0.22153	0.032408	-0.070692	-0.14099	-0.25164	-0.070692
HB30	-0.29741	-0.080746	-0.081538	-0.023368	0.062808	-0.23065	-0.046991	-0.082209	0.15767	-0.095919	-0.33226	-0.12945	0.11527	0.11048	-0.1158	0.01177	-0.12627	0.17503	0.25129	0.075311	-0.079622	-0.12627
HB31	-0.27207	-0.018747	0.007165	-0.2968	0.10183	0.041932	0.24195	0.31152	0.039544	0.19011	0.33325	0.020495	0.22565	-0.075265	0.18599	0.55484	0.21386	0.12244	0.15314	0.028246	0.052044	-0.075265
HB32	-0.19571	-0.06145	0.073522	-0.21143	-0.15688	-0.079083	-0.067317	0.15303	-0.063143	-0.023323	-0.10675	0.12927	0.12501	0.054973	-0.16866	-0.0004984	-0.17682	-0.032106	0.10116	-0.12453	0.039435	-0.17682
HB33	-0.17161	-0.045128	-0.0031588	-0.12711	-0.0017695	-0.043278	-0.17002	0.21769	-0.21861	0.053122	-0.15378	-0.059605	0.024564	0.08773	0.02599	0.062322	0.025459	-0.1012	-0.046477	0.02665	0.079368	-0.1012
HB34	-0.16748	-0.03616	0.06882	-0.11313	0.025558	0.069419	-0.19219	0.13036	-0.21732	0.095678	-0.35557	-0.0027063	-0.029774	-0.1501	-0.028059	0.032906	0.088089	0.018237	-0.19586	0.11558	-0.048675	-0.028059
HB35	-0.29752	-0.2592	-0.031118	0.075666	0.012382	0.026647	-0.038154	0.1735	-0.20434	-0.58029	0.177	-0.25186	0.11804	0.23556	-0.09192	-0.039852	0.22818	0.057065	-0.11996	0.013876	0.023198	-0.039852
HB36	-0.361	-0.27195	0.018223	0.004845	0.14097	0.053193	-0.024967	0.061846	-0.020416	-0.17615	0.0047202	-0.034216	0.13153	0.035549	-0.049754	0.1954	-0.07565	-0.042946	-0.21209	-0.092755	0.031774	-0.042946
HB37	-0.34541	-0.2632	-0.031427	-0.026462	0.11028	-0.023622	-0.014478	-0.075413	0.032588	-0.037695	-0.013365	0.13058	-0.030794	-0.071572	-0.066952	0.049719	0.11256	0.044333	0.038298	-0.1009	-0.04522	-0.066952
HB38	-0.25694	-0.18302	0.012236	0.063771	0.11546	0.21481	-0.056428	-0.23498	-0.073543	-0.044497	-0.1413	0.20549	0.36171	-0.048267	0.070355	0.15746	-0.090886	-0.060617	0.18092	-0.12839	-0.020406	-0.090886
HB39	-0.24424	-0.23131	-0.03593	-0.02141	0.11816	-0.1812	0.015095	-0.23167	0.085364	0.12949	0.21688	0.10625	0.046	-0.042836	0.021818	0.012443	0.14977	-0.24969	-0.15338	0.084448	-0.028327	-0.042836
HB40	-0.25917	-0.29867	-0.031528	0.15412	0.17112	-0.011494	-0.058554	-0.22308	0.1443	0.18752	0.023409	0.061351	0.085968	-0.04979	0.036999	-0.1622	0.031531	-0.066147	-0.039632	0.11679	-0.048789	-0.039632
HB41	-0.23905	-0.1543	0.082178	-0.029506	0.10638	-0.10042	-0.085321	-0.1734	0.0041722	0.015181	-0.17624	-0.029788	-0.11206	-0.051598	-0.048942	-0.						

	AXIS 1	AXIS 2	AXIS 3	AXIS 4	AXIS 5	AXIS 6	AXIS 7	AXIS 8	AXIS 9	AXIS 10	AXIS 11	AXIS 12	AXIS 13	AXIS 14	AXIS 15	AXIS 16	AXIS 17	AXIS 18	AXIS 19	AXIS 20	AXIS 21
<i>Rogalskioporia cicutaricus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nevadomyces bigraminus</i>	-0.24369	-0.3353	0.057345	0.050062	-0.010459	0.0077264	-0.11067	-0.28261	0.14984	0.19675	0.22502	0.059762	0.02339	-0.02181	-0.22354	0.051602	-0.05509	-0.18003	-0.073669	0.23882	-0.021646
<i>Amphicladia sp.</i>	-0.31688	-0.22121	0.032697	0.15316	0.028306	0.001573	0.30865	-0.058588	0.05888	0.12272	0.0052785	0.050182	-0.11789	-0.037833	-0.12383	-0.023999	-0.06213	-0.038663	0.063329	-0.12885	0.054787
<i>Densomyces velans</i>	-0.23429	-0.13707	0.098624	-0.045769	-0.11603	0.001333	0.094829	-0.039141	0.1025	-0.13693	0.0086537	-0.057956	-0.10781	-0.14613	-0.06503	0.04211	0.091381	-0.023112	-0.10752	0.051335	0.01006
<i>Densomyces cf. velans</i>	-0.25067	-0.22865	0.040751	0.026576	0.020978	0.037168	-0.094135	-0.098477	0.01598	0.06863	0.028086	-0.028086	-0.09464	-0.12007	0.07012	0.056717	0.13614	-0.072879	0.057617	-0.094138	0.01006
<i>Lycopodiaceae serritoides</i>	-0.34939	-0.22205	-0.0089529	-0.063678	0.028407	-0.0007347	0.001791	0.050273	0.16665	-0.17515	0.17528	-0.076938	0.022942	-0.090556	-0.011373	-0.12947	-0.098137	-0.18051	-0.23101	0.0093617	0.034361
<i>Lycopodiaceae rugulatus</i>	-0.3311	-0.23599	-0.070889	0.019857	-0.058939	0.020795	-0.036966	0.095022	-0.0298	-0.033426	-0.22917	0.028504	-0.011069	-0.020142	0.30929	-0.17221	0.021923	0.023802	-0.018574	-0.098235	0.2295
<i>Neorisiclia trunctus</i>	1.8197	-0.53353	2.6789	-0.066935	1.0675	-1.7268	-0.40134	0.039913	-1.2206	-0.60121	0.6278	0.87842	-0.2571	-0.39307	0.44401	-0.52602	0.09016	0.46203	0.64066	0.42227	0.0041328
<i>Retrirelles austroclavarioides</i>	-0.87473	-0.07426	0.031936	-1.4227	0.53756	0.23311	1.4255	1.9405	0.25355	1.4884	2.2324	1.4082	1.5929	-0.55053	1.9316	4.303	1.8344	0.0792	1.379	0.27368	0.5174
<i>Retrirelles clavarioides</i>	0.29859	0.69699	0.42715	-0.62751	0.34225	-0.66098	0.086989	-0.1678	0.47147	-0.36506	-0.093113	0.26137	-0.14063	0.33422	0.25935	0.13102	0.22865	0.0215	-0.41433	-0.30447	-0.27037
<i>Retrirelles semimaris</i>	0.43508	0.21797	0.56294	1.3391	0.072447	-0.090741	-0.095307	0.20874	-0.25259	-0.36324	0.52077	-0.11467	0.07195	0.75739	0.11057	0.16862	-0.18987	0.77758	-0.36736	0.30895	-0.067357
<i>Leptodiales bosae</i>	-0.32405	0.019013	0.16345	1.4072	-0.11637	0.89583	0.44715	-0.0037699	-1.48	-2.7479	0.5217	-1.3881	1.1447	0.65545	-0.74685	0.032167	1.3829	-0.20768	0.04796	0.15403	-0.74794
<i>Leptodiales scabotossus</i>	0.25056	0.22524	0.42217	0.090455	-0.72146	1.0485	-0.56736	-0.78674	0.23211	-0.14623	0.0045491	-0.21191	-0.65013	-0.11786	-0.073943	0.61132	0.084685	-0.18763	0.10284	0.22095	0.18397
<i>Leptodiales major</i>	0.098359	-0.01977	0.42565	-0.0023276	-0.28301	0.099567	-0.48001	0.074846	0.36656	-0.4301	0.74867	-0.64787	-0.50527	-0.75183	1.0471	-0.1501	-0.86386	-0.27166	0.0015758	-0.33333	-0.31776
<i>Leptodiales crassihelens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sarcosporites pseudobovellatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stapiosporites sp.</i>	0.067899	1.2836	-0.30362	0.15997	0.66861	0.44818	0.021622	-0.11652	-0.11283	-0.08389	0.013513	0.36576	0.34486	0.41186	-0.35677	-0.31769	0.0759	0.18785	0.2004	0.11479	-0.41803
<i>Uvaeosporites argenteiformis</i>	-0.85238	-0.67712	0.69068	1.2474	-0.049901	-0.1472	2.8194	0.44581	-1.4723	0.79676	-0.39646	0.37595	-2.5956	0.4916	1.7425	0.17315	-1.7651	-0.90227	0.39548	0.96068	-0.32113
<i>Calamospora mesozetia</i>	-0.1495	-0.097372	-0.050442	0.1204	0.024693	0.034533	-0.065141	-0.0083272	0.15437	-0.13211	-0.0348	-0.02177	-0.12412	-0.069804	-0.046371	-0.058152	0.019869	0.078587	0.05845	0.1501	-0.005062
<i>Marasmiopsis scabratus</i>	-0.14791	0.031767	-0.084612	0.081928	-0.14508	0.091955	0.029675	0.0325589	-0.0069091	0.14455	-0.078849	-0.11681	0.048311	0.026308	-0.080605	-0.02798	-0.085389	-0.037081	0.041525	-0.0007622	0.0000000
<i>Bacillatoporia comanensis</i>	-0.68282	0.081946	0.37362	-0.82894	0.21148	0.14405	-0.99597	0.17175	-1.1201	0.36062	-0.77013	-0.27052	-0.68629	-0.32948	-0.16876	0.28526	0.35582	-0.038489	-0.23467	0.87161	-0.18784
<i>Osmundicladia velutina</i>	0.58409	0.30086	0.77973	-0.023613	0.2696	0.11151	0.22301	-0.14689	0.16522	-0.24748	-0.35451	0.38113	-0.34714	0.095506	-0.065519	0.17716	0.22885	0.19911	-0.31902	0.13876	0.032553
<i>Tediosporites sp.</i>	0.0059531	1.6441	-1.546	3.543	2.7161	-0.4358	-2.3977	2.1854	1.1078	-0.030683	-0.23738	1.7351	-1.4829	-0.030167	-0.62324	1.1765	0.25066	-0.052324	0.19346	-0.7897	-0.1189
<i>Tediosporites minor</i>	0.35496	0.11984	0.010921	-0.13915	-0.99507	-0.13251	-0.1106	0.30083	0.86008	-0.29675	-0.039619	0.26724	0.080808	0.30137	-0.020046	-0.13857	-0.066682	-0.059625	0.20355	0.1123	-0.07359
<i>Glaucialladites semonius</i>	2.694	-1.6174	-2.8984	-0.44794	0.22728	0.30963	0.91341	-0.21137	-0.78754	-0.27338	0.70913	-0.31051	-0.46774	0.12477	0.39685	-0.62247	0.39456	-0.43583	0.34522	0.2947	0.0000000
<i>Combacillatoporia mesozetia</i>	-0.3851	-0.2768	0.054248	0.064526	0.060152	0.048258	-0.28128	-0.08058	0.0906149	0.059988	-0.58799	0.1504	0.091436	-0.087322	0.21939	-0.20663	0.47427	0.099065	-0.13011	-0.24052	0.1383
<i>Dicycopilioides harrisii</i>	-0.027525	-0.021615	-0.14862	0.07028	-0.058858	-0.0017545	-0.010422	0.049427	0.039986	-0.022938	0.055622	-0.019777	-0.01877	0.048814	-0.034634	-0.0036508	0.0081057	-0.012159	-0.011974	0.045665	0.0000000
<i>Dicycopilioides equisetinus</i>	0.24695	0.18454	0.083408	-0.23929	-0.067519	-0.13535	0.11669	0.083663	-0.030957	0.026773	0.15343	-0.13921	-0.025497	-0.16784	-0.11151	0.1075	-0.099894	0.0064161	-0.16057	0.0000000	0.0000000
<i>Concavosporites sp.</i>	0.11509	0.22147	-0.17973	0.40501	0.17795	-0.12695	0.061527	0.0043496	0.31412	-0.00114	-0.055653	-0.32896	-0.16684	-0.19221	-0.083596	-0.37217	0.2008	0.076295	0.32282	0.11935	-0.15823
<i>Matosporites phleboporioides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Matosporites cf. phleboporioides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coniopsis sp.</i>	-1.0785	-1.0003	-0.031626	0.042522	0.32964	0.15432	-0.12673	0.60534	-0.1804	-0.20773	0.77618	-0.84314	0.66501	0.49139	-0.39508	-0.35588	0.19907	-0.43647	-1.6726	-0.34244	0.29397
<i>Duplexisporites problematicus</i>	1.2625	-0.29252	0.58646	0.14506	0.028495	0.093949	-0.17333	-0.20713	0.15159	0.14064	0.075363	-0.1896	0.021002	0.04925	0.14673	-0.033826	0.075767	0.097576	0.028245	-0.22133	0.087895
<i>Ichthyosporia</i>	0.019282	0.08022	-0.11868	-0.11868	-0.24933	-0.36223	0.10136	0.38772	-0.14292	-0.19210	-0.029012	-0.28944	0.19251	0.26949	0.0034118	0.57794	-0.4516	0.066398	0.31516	-0.10671	0.03147
<i>Chromospora jurensis</i>	0.7423	-0.46255	-1.2433	-0.25659	-0.32127	0.16837	0.17451	0.033642	-0.02916	-0.15199	-0.020012	0.1018	-0.30263	-0.10179	0.34661	-0.034248	0.29797	0.24249	0.16257	0.087473	-0.126148
<i>Othiosporia canadensis</i>	0.0059531	1.6441	-1.546	3.543	2.7161	-0.4358	-2.3977	2.1854	1.1078	-0.030683	-0.23738	1.7351	-1.4829	-0.030167	-0.62324	1.1765	0.25066	-0.052324	0.19346	-0.7897	-0.1189
<i>Concavosporites subgraminis</i>	0.55175	0.64997	0.34774	0.07058	0.12542	0.02297	0.04535	-0.14895	-0.028135	0.058245	0.049212	-0.24291	-0.05204	-0.021209	0.0232941	-0.02746	0.023941	-0.02746	-0.08792	0.20169	0.057679
<i>Concavosporites variverrucatus</i>	1.0461	-0.39982	-0.27213	0.13326	-0.18529	-0.097241	-0.39871	0.18929	0.0085794	0.24662	0.38037	-0.02123	0.04166	-0.30044	0.005186	0.099512	0.059026	-0.083081	-0.098043	-0.19554	0.0000000
<i>Delatodospira anstralis</i>	0.29431	0.69207	0.11909	0.28039	-0.14381	-0.067336	-0.070461	0.058617	-0.19874	-0.07753	0.36153	0.36241	-0.02752	-0.02199	-0.094519	-0.03459	-0.2382	-0.010788	-0.067971	0.10636	0.38066
<i>Delatodospira concava</i>	0.2583	0.66134	-0.76357	0.17194	-0.071905	-0.55283	-0.029409	-0.44892	-0.24132	0.018169	0.12827	-0.19512	-0.26519	-0.19619	-0.064949	-0.04192	0.045393	-0.1182	-0.21191	-0.121872	-0.040375
<i>Delatodospira minor</i>	0.0083095	0.10915	-0.13466	-0.044327	-0.02123	0.0031174	0.022634	0.01532	0.024702	0.0079148	0.063095	-0.018566	-0.0040189	0.0097975	0.039471	-0.04889	0.033682	-0.026489	-0.0075744	0.013607	0.0000000
<i>Plotosporites brevipapillosus</i>	1.5676	-0.96	-4.3751	-0.11196	-2.034	-1.628	2.2663	-1.1801	-2.1568	-1.2882	0.83035	2.6027	-0.59892	-0.94969	0.67395	0.3144	-0.54246	1.0345	-0.45395	0.30298	-0.36708
<i>Asporites dumbrivillus</i>	3.7311	-2.2749	-1.4218	-0.78391	2.4886																

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	Axis 11	Axis 12	Axis 13	Axis 14	Axis 15	Axis 16	Axis 17	Axis 18	Axis 19	Axis 20	Axis 21
<i>Alisporites thomasi</i>	-0.0007683	0.12485	-0.03397	-0.21327	0.17607	0.37185	-0.0091996	0.055886	0.28204	0.067821	0.12273	0.17456	-0.0051258	0.060663	0.10036	0.040311	0.070986	-0.038368	0.030768	0.057152	-0.25641
<i>Finesporites pallidus</i>	0.26209	-0.015403	-0.33073	-0.086284	0.31639	-0.057133	-0.17534	0.059113	-0.013372	0.11961	-0.33049	-0.14237	0.060528	0.13138	0.25677	0.22634	-0.18053	0.03186	-0.19343	-0.0055323	-0.18985
<i>Ptyosporites microdatus</i>	0.11006	0.056563	0.071489	-0.093863	-0.010241	0.11171	0.16236	0.11763	-0.007898	0.042264	0.017072	-0.03913	-0.026206	-0.11383	-0.005163	0.0096556	-0.047152	-0.065026	-0.11348	-0.049697	0.015428
<i>Ptyosporites minimus</i>	0.55144	0.045425	0.15371	-0.40546	-0.59195	-0.38738	-0.44701	0.20683	-0.29537	0.18002	-0.057686	0.1973	0.071934	0.088465	-0.34432	-0.020778	-0.062652	-0.2858	0.10343	-0.12664	-0.10023
<i>Podocarpidites ellipticus</i>	-0.19535	1.0415	-0.21547	-0.71963	0.33173	0.11352	0.29226	-0.25391	0.093265	-0.048148	0.12562	0.17202	0.38707	0.036245	-0.066286	-0.073058	-0.034733	0.14852	0.014567	0.44289	0.002394
<i>Quadracutina anellaformis</i>	2.7842	-1.3571	0.42468	-0.59039	1.4117	0.20644	0.54907	0.47981	0.17822	-0.29249	-0.43735	-0.18068	-0.061451	-0.22777	-0.31932	0.070419	-0.20789	-0.30639	0.13013	0.2153	0.29304
<i>Araucariacites australis</i>	0.0040645	0.071394	0.048563	0.020196	0.052184	0.040942	0.044724	-0.011714	0.048739	-0.0032514	0.0018994	0.003862	-0.026384	0.01658	-0.008991	0.0021027	0.0079567	-0.0014848	0.013336	-0.037694	0.022537
<i>Callialasporites dampieri</i>	-0.12309	0.25154	0.31658	-0.075943	-0.38253	0.17496	0.47649	0.33599	0.12974	0.19772	-0.07212	0.26975	-0.081005	-0.14893	0.2277	-0.058173	-0.063057	0.19698	-0.29923	-0.15046	0.068939
<i>Callialasporites segmentatus</i>	-0.23308	1.2892	-0.48503	-0.4346	0.21924	-2.8205	0.58994	-1.298	1.3038	-1.0043	-1.7455	-1.4023	0.47183	0.35666	-0.31117	1.1224	-0.39496	-0.058034	0.58418	0.46412	0.37934
<i>Callialasporites triobovatus</i>	0.080456	0.17531	0.46988	1.5448	-0.3001	1.5589	-0.082559	-1.5615	-0.6154	-0.57706	-0.29519	-0.36299	1.289	-0.70432	0.32454	1.1019	-0.31393	-0.17218	0.73164	-0.37964	-0.21128
<i>Callialasporites turbatus</i>	-0.19514	-0.085859	0.07887	-0.15285	0.05442	0.054502	-0.027971	0.087538	0.035077	-0.058206	0.08552	0.07978	0.073859	-0.020214	-0.096165	0.11223	-0.02861	0.045816	0.016566	0.05008	-0.050678
<i>Classopolis torosus</i>	-0.10497	-0.10903	0.0024232	-0.0005131	0.053856	-0.021056	0.023982	-0.0098805	-0.0097828	0.045194	0.028349	-0.0059045	0.00906	-0.0040471	-0.028206	-0.0063298	0.0051942	-0.036511	-0.0062756	-0.021376	0.025626
<i>Cerebropollenites mesozoicus</i>	0.053792	0.089774	-0.13291	0.047422	0.16527	0.051521	-0.033887	-0.03761	-0.065487	-0.075812	0.059822	0.053477	0.0041241	0.10489	0.13264	-0.044576	0.046548	-0.081964	0.058428	-0.048291	0.041596
<i>Spheripollenites scabratus</i>	-0.17138	0.022138	0.076278	-0.076597	0.096268	-0.033112	0.048635	0.020464	-0.030372	0.0075314	-0.064524	-0.011783	0.022903	0.03194	-0.0010655	-0.021695	-0.065203	0.022816	-0.028105	-0.051001	-0.10295
<i>Spheripollenites subgramulatus</i>	-0.13737	-0.083393	0.069306	0.069884	0.02443	-0.070388	0.001013	-0.017424	0.0019318	0.047778	0.0095064	-0.025396	0.0082411	-0.0031925	-0.035132	-0.0015409	-0.023271	0.0018024	0.020583	-0.0071243	0.013869
<i>Perrinipollenites elatoides</i>	-0.21057	-0.19732	0.0047168	0.02471	-0.025559	-0.021348	-0.0049533	-0.037216	-0.037968	0.0082715	-0.0081197	0.084516	-0.0031184	-0.024039	-0.016542	0.062492	-0.0042229	-0.010484	-0.0011805	0.022748	0.025319
<i>Chamaetopories aperius</i>	-0.0116	0.26552	0.21701	0.01261	0.044625	-0.12196	0.060023	0.12188	-0.1204	-0.16474	0.025406	-0.056451	-0.041103	-0.054774	0.01172	-0.039992	-0.015448	-0.12049	0.062208	0.0018201	0.014946
<i>Chamaetopories hians</i>	-0.56765	-0.1806	0.052367	-0.47179	-0.15804	0.09866	-0.36137	0.29857	-0.12466	-0.41319	-0.22819	-0.17534	-0.12697	0.16396	-0.039252	0.050424	-0.20622	0.076535	0.11865	-0.11594	0.069006
<i>Chamaetopories major</i>	-0.066533	1.2861	-0.18548	-1.1857	0.66613	0.84982	-0.39902	-0.61676	-0.49238	0.10354	0.45849	0.008078	-0.54177	0.50566	-0.015589	-0.45378	-0.040386	0.094291	0.19871	-0.01528	0.28975
<i>Cycadophytes minimus</i>	0.009146	-0.013567	-0.0581	-0.049789	-0.034426	-0.061845	-0.0094761	-0.039559	0.015661	0.052476	0.10092	-0.019592	0.012006	0.010331	0.022137	0.017734	-0.0074567	0.039132	0.06047	-0.012209	0.020322
<i>Cycadophytes carpentieri</i>	-0.18321	-0.65619	0.030461	0.078776	0.053786	-0.084832	0.087951	-0.28691	-0.0051074	-0.1265	0.04028	0.2687	0.0083203	0.078494	0.013146	-0.0053906	-0.0089072	-0.055728	0.11967	-0.034831	-0.0087838
<i>Cycadophytes subgramulatus</i>	0.9196	-0.668122	-0.14364	-0.098041	-0.13629	0.25399	0.0099178	-0.031187	-0.18605	0.04673	-0.26531	0.13817	0.38623	0.085803	-0.0284	0.0001382	-0.024171	-0.17506	0.10554	-0.059105	-0.35036
<i>Eucommidites troedssonii</i>	0.15785	0.052209	-0.0068435	0.21835	0.061278	-0.21368	-0.019601	-0.20187	-0.024898	0.33053	0.065491	-0.15383	0.050352	-0.0069646	0.041362	-0.22226	-0.11418	0.23613	0.083887	0.16494	-0.073929
<i>Strate bisaccate sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Axis 22	Axis 23	Axis 24	Axis 25	Axis 26	Axis 27	Axis 28	Axis 29	Axis 30	Axis 31	Axis 32	Axis 33	Axis 34	Axis 35	Axis 36	Axis 37	Axis 38	Axis 39	Axis 40	Axis 41	Axis 42
HB1	-0.047633	0.019229	-0.061034	0.015566	0.021074	-0.013982	0.002952	-0.025115	-0.043607	-0.002776	-0.034883	0.012914	-0.015545	0.009778	-0.000938	-0.0010085	0.0048735	-0.011804	-0.006279	0.0076799	-0.0013175
HB2	-0.012114	0.040707	0.0097728	0.041217	-0.018693	0.085188	0.056573	0.044363	-0.063349	0.071128	0.097544	-0.022695	0.044735	-0.027246	-0.071819	-0.012945	-0.011388	0.019418	-0.004219	-0.010929	-0.034164
HB3	0.040129	-0.1082	0.032479	0.016131	-0.032208	-0.044083	0.11953	0.089685	-0.04341	0.039251	-0.09194	0.023452	-0.028405	-0.057267	0.068984	0.055121	-0.039078	0.02228	0.065088	0.019646	0.033596
HB4	0.084328	0.21634	0.056679	-0.028988	-0.12733	-0.0083738	-0.017895	0.060792	-0.038312	-0.049044	0.038481	-0.0078972	0.0285984	-0.0065419	0.038481	0.066718	-0.023286	0.031744	-0.011131	0.0093921	-0.022256
HB5	-0.07705	-0.087302	-0.011577	0.09039	0.14954	-0.035833	0.016664	0.016694	0.056875	0.041007	-0.0040581	-0.019168	0.0089274	0.017394	-0.043475	-0.052713	0.02499	-0.044257	0.013479	0.0014987	0.01194
HB6	-0.21295	0.089406	-0.039687	-0.14286	-0.072189	0.010367	-0.12752	0.019034	0.04503	-0.013984	0.022757	0.041494	-0.010865	-0.016171	-0.027677	0.088019	-0.018291	0.0058309	0.0005878	0.0082209	0.0551
HB7	-0.18039	-0.036019	0.0059206	-0.10235	-0.0655899	-0.10413	0.076922	-0.031242	-0.03406	-0.0091975	0.099698	-0.064902	-0.026029	0.027363	0.028782	-0.031252	0.032799	0.002122	0.010382	-0.055325	-0.010559
HB8	-0.0017444	-0.056971	0.077951	-0.055427	0.028826	0.0060245	0.01494	0.011445	0.0147	0.0078906	0.03428	-0.0002076	-0.0001	0.0012268	-0.011371	-0.0041934	-0.0033828	0.0012142	0.0043042	-0.001169	-0.0053519
HB9	0.0001383	-0.029169	-0.15327	0.048755	-0.079574	0.044071	-0.062653	-0.13547	-0.019238	-0.018932	-0.10234	0.062373	-0.020834	-0.017417	0.057859	-0.05927	0.023526	0.00283	-0.022715	0.0001875	0.026162
HB10	0.10839	0.14784	0.057843	0.036929	-0.066461	-0.013847	-0.019199	-0.087192	-0.018684	0.01378	-0.010514	-0.0002146	0.028328	0.0076012	0.027106	-0.026628	-0.0090415	-0.018547	-0.04488	-0.017638	-0.030634
HB11	-0.034512	0.085361	-0.16775	0.053986	0.109	-0.024136	0.017461	0.10676	0.07237	-0.12321	-0.02867	0.022382	-0.017608	-0.048392	-0.045477	0.079075	0.047065	-0.018899	-0.016109	-0.022885	-0.0013914
HB12	-0.051513	-0.092631	0.043349	-0.032359	0.071948	0.060587	0.0003833	-0.0082242	-0.012898	0.0048889	-0.018871	0.041465	0.0025481	-0.0029223	0.007696	0.0283789	-0.025414	0.034214	-0.016992	0.060988	-0.020966
HB13	-0.035397	0.059122	0.042423	-0.010437	-0.013909	0.018716	-0.0039028	0.0023149	-0.039125	0.0025382	-0.011506	0.0061968	0.017724	0.0067286	-0.0093122	0.0016076	0.0023185	0.0008803	0.0004699	-0.0071251	-0.0001952
HB14	0.13888	-0.031251	-0.097408	-0.084044	0.044402	-0.0006927	0.018855	-0.066008	0.069178	-0.13873	0.078054	-0.063516	0.0015135	0.050504	0.062843	-0.033339	0.0033707	0.018004	0.031666	-0.021029	0.0006203
HB15	0.098592	-0.052397	-0.010605	-0.061603	-0.090849	0.014341	0.0063076	0.081922	-0.0091585	-0.043124	0.0089256	0.024101	0.0075628	0.028756	-0.11562	0.0032098	0.061259	0.01087	-0.082696	0.063789	-0.013187
HB16	-0.091419	-0.0085021	0.0065327	0.063565	0.021786	0.055909	-0.043575	0.05556	-0.045513	-0.013819	0.0076527	-0.0087916	0.014012	0.014126	-0.037089	-0.015285	0.017819	0.033123	0.0088308	0.011475	0.015311
HB17	-0.011775	0.035389	0.062269	0.10593	-0.10604	-0.0017594	-0.076482	-0.093165	-0.011166	-0.015514	-0.15257	-0.11267	0.084514	-0.05944	-0.018535	-0.013505	0.051264	0.043236	0.0002872	-0.030095	0.0093597
HB18	0.056207	-0.061709	-0.06726	-0.10077	-0.14794	-0.10321	0.051308	-0.0031682	0.056628	0.030056	0.028846	0.060075	-0.060566	-0.065379	-0.030685	-0.047135	-0.083998	-0.012966	-0.010505	-0.0037268	0.027515
HB19	-0.033009	-0.09349	-0.026221	0.034739	-0.11803	0.041859	-0.082555	0.011514	-0.025561	-0.034511	-0.039382	0.037405	-0.051336	0.073297	0.058664	0.070592	0.053099	-0.12287	0.085121	0.034682	-0.039908
HB20	-0.10031	0.020171	-0.086434	-0.015116	0.023263	0.042704	0.02004	0.032226	0.0037024	0.071496	-0.0728	0.059526	-0.03821	-0.057639	-0.0077438	-0.030585	0.038316	0.039006	0.014061	-0.024296	0.0090647
HB21	0.21552	0.073152	0.073734	-0.010975	0.077491	0.041389	0.047381	-0.000278	0.069556	0.087644	0.054154	0.028841	-0.03005	-0.043382	0.019283	0.05994	-0.029038	-0.029781	-0.069375	-0.010374	0.041047
HB22	0.092927	0.11429	0.056638	0.24253	0.051563	-0.10063	-0.1032	-0.0022698	0.02823	0.10525	0.05976	-0.036504	0.03715	0.019655	-0.0042444	-0.01144	-0.011462	0.062958	0.029398	5.93E-05	-0.0020118
HB23	-0.068892	0.049336	0.078	0.008659	0.12324	0.041256	0.015815	0.073771	0.1625	-0.01504	0.0082574	-0.043717	-0.036897	0.03705	-0.0074375	-0.020583	0.053912	0.034893	0.001759	0.010514	0.031434
HB24	-0.091748	0.0038033	-0.0065567	-0.017331	-0.071134	-0.095865	-0.089694	0.066714	-0.037576	-0.040149	0.10597	0.097263	0.089336	-0.0051621	0.01326	-0.044548	-0.014023	-0.016769	-0.017679	0.0022682	-0.008537
HB25	-0.042286	-0.019778	0.046885	0.025379	-0.05794	0.058809	0.040376	-0.046789	0.052313	-0.17641	-0.0027412	-0.06044	-0.027098	-0.0031989	0.0094317	-0.015641	-0.068264	0.013389	-0.024273	0.01292	-0.06263
HB26	0.080783	0.069965	-0.10594	-0.13328	-0.054167	-0.056219	0.076967	-0.025463	-0.083618	0.082411	-0.0446	-0.010149	0.028729	0.081352	-0.029814	-0.0002618	0.036743	0.0070789	0.065576	0.01731	0.020914
HB27	-0.031652	-0.16121	0.0008632	-0.010116	0.098804	-0.0081091	-0.1011	-0.025569	-0.2659	-0.082436	0.036049	-0.058065	-0.080944	0.04178	-0.016023	0.061979	0.0082973	-0.0045641	-0.041605	-0.0074722	0.0072146
HB28	-0.14604	-0.069447	0.14465	0.058058	-0.0033925	-0.042137	-0.037921	0.054935	0.020058	0.042391	0.0073643	-0.049948	0.011112	-0.022443	0.049288	0.032617	-0.078001	0.0097708	0.029203	0.0050729	-0.010516
HB29	0.047601	0.017755	0.078267	-0.10553	0.082513	0.081872	0.0439	0.15126	-0.059156	0.035142	-0.078083	0.046274	0.06459	-0.042484	0.028166	-0.033177	0.030647	0.026444	0.038459	-0.022669	-0.053072
HB30	-0.034102	0.15309	-0.11104	-0.14614	0.11458	-0.17459	0.099273	-0.070033	-0.039573	0.044412	-0.047347	-0.011788	-0.049788	-0.011742	0.034007	0.014361	-0.020116	-0.037501	-0.022158	-0.025788	-0.019673
HB31	-0.13646	0.048705	-0.012111	0.061567	0.11941	0.048824	0.031801	-0.033326	-0.0048762	-0.016092	0.028232	0.013717	-0.017459	-0.009854	0.0060071	-0.011418	-0.0051666	0.0014314	-0.0066357	-0.0011504	-0.0095942
HB32	-0.066381	0.064748	0.10011	-0.028258	-0.019381	-0.037734	-0.031835	-0.1	0.090709	-0.074604	0.036701	0.059953	0.051976	-0.0075137	-0.051839	-0.036722	0.024569	-0.029637	0.012507	0.0050722	-0.012077
HB33	-0.054283	-0.20447	-0.056316	-0.02233	-0.082773	0.04558	-0.05848	0.052857	0.056299	-0.098381	-0.14109	0.090641	-0.024117	-0.017627	0.02289	-0.013028	-0.047956	-0.069063	0.053815	0.0046746	-0.0048017
HB34	0.11755	-0.15472	-0.1448	0.1826	0.084013	0.047335	0.0075287	0.022281	-0.081929	-0.074501	-0.0018308	0.055729	-0.049194	-0.076213	-0.018439	-0.0099403	-0.055482	0.015971	0.014303	-0.045804	-0.002728
HB35	-0.018932	0.073063	0.069833	-0.071223	-0.039438	-0.0076211	-0.09215	-0.0028334	-0.0006438	0.015074	0.013989	-0.048725	-0.051639	-0.003985	0.0015721	-0.021066	0.030909	-0.051584	0.002958	-0.004917	0.022958
HB36	-0.13038	0.15489	-0.2296	0.13409	-0.13455	0.0055243	0.10893	0.068391	0.01042	0.04933	-0.091436	-0.019409	-0.030293	-0.013318	0.043441	-0.041274	0.020352	0.043441	-0.041274	0.020352	-0.048017
HB37	0.17049	-0.11575	-0.014959	-0.055965	-0.15014	-0.092012	0.018654	0.014957	0.058399	0.14198	0.0055593	-0.081393	-0.065406	0.051556	-0.032539	0.088981	0.043517	0.021157	0.053657	-0.010912	0.010912
HB38	0.099628	-0.15995	0.099885	0.085248	-0.18744	-0.12316	0.14371	0.13184	-0.010677	-0.096118	-0.021675	0.038395	-0.0036773	0.027286	-0.043665	-0.002947	0.013704	-0.011313	0.012049	-0.046741	0.051422
HB39	0.0037611	-0.14087	0.061372	-0.11898	0.059652	-0.11183	-0.027688	0.021762	0.046763	0.028592	-0.064632	0.035484	0.076298	0.027577	-0.010303	0.018061	0.013154	0.0078356	-0.04033	-0.064928	-0.020223
HB40	-0.13671	-0.013423	0.0081892	0.03792	0.10481	-0.073655	-0.045961	-0.056377	-0.024434	0.013545	0.042507	0.024388	-0.043086	0.035049	-0.029782	-0.015727	0.0606769	0.014777	0.066807	-0.024634	0.024634
HB41	-0.11305	-0.12574	0.025963	-0.0039626	-0.12038	0.28577	0.12357	-0.060261	0.0041502	0.086388	0.062941	0.06461	-0.0058967	-0.033288	0.05152	-0.014007	0.038104	-0.074425	-0.034541	-0.025783	-0.0048099
HB42	-0.041867	-0.07225	0.015493	0.0028094	-0.080563	0.10613	-0.017893	-0.013178	0.050748	-0.050497	0.068244	-0.050497	0.068244	-0.050497	0.068244	-0.050497	0.068244	0.068244	0.068244	-0.050497	0.068244
HB43	0.040976	0.021702	0.084945	-0.15521	-0.049238	-0.037525	0.0028011	-0.027961	-0.015298	0.034851	-0.015598	0.0									





	Axis 22	Axis 23	Axis 24	Axis 25	Axis 26	Axis 27	Axis 28	Axis 29	Axis 30	Axis 31	Axis 32	Axis 33	Axis 34	Axis 35	Axis 36	Axis 37	Axis 38	Axis 39	Axis 40	Axis 41	Axis 42
H844	-0.01793	0.094071	0.15484	-0.089107	0.015284	0.090883	-0.069481	-0.013217	-0.016629	-0.037603	-0.023315	-0.13115	-0.15265	-0.037108	-0.057081	-0.026635	-0.010746	-0.058538	0.017844	-0.022642	0.022651
H845	0.063543	0.057216	-0.12774	-0.11224	0.036869	0.14374	-0.01338	0.12729	-0.066465	-0.023234	-0.012009	-0.081312	0.093281	0.026448	0.0052534	-0.092378	-0.059525	-0.064236	0.0328152	0.051417	0.03147
H846	0.082196	-0.068939	-0.11177	0.018435	0.051773	0.0039264	-0.18862	0.011647	0.10644	0.022277	-0.05007	0.1049	0.038566	0.15326	0.0009176	-0.061469	0.0042317	-0.019789	-0.052739	0.0049046	
H847	0.008093	0.020082	0.17078	-0.0016267	-0.0052385	-0.0037161	0.082453	-0.15108	0.031527	0.024875	-0.094625	0.094004	-0.10169	0.13646	-0.10344	-0.0097911	-0.052029	0.059347	0.044601	0.02095	0.082226
H848	0.16342	-0.016136	-0.14407	-0.041702	0.034811	0.11876	0.008637	-0.16348	0.068129	0.044407	0.094625	0.094004	0.05494	-0.072898	0.089772	-0.0006675	0.043306	0.07724	0.043731	-0.032875	
H849	-0.038618	0.13829	-0.048316	0.16093	0.038814	-0.041036	0.23139	-0.055949	-0.066815	-0.072352	0.043338	0.062624	0.000866	0.049499	0.034981	0.040143	0.018659	-0.023281	-0.003606	0.025312	0.029105
H850	0.18292	0.077527	0.14641	-0.082454	0.10776	0.052591	-0.0847591	0.016213	-0.0048731	-0.032699	-0.053686	0.024448	-0.057273	0.020919	-0.10274	-0.052653	0.031829	-0.013736	-0.0057165	0.023858	0.010655
Taxon scores																					
<i>Rogalskiasporites eactricus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nesactinopteria bigemulata</i>	-0.49357	0.17247	0.64101	-0.084633	0.67534	-0.42869	0.21246	-0.36505	-0.32167	-0.41652	-0.079611	0.0056027	0.13032	-0.051161	0.10781	-0.022377	0.01931	-0.072668	-0.073157	0.017941	0.031297
<i>Amphicladia sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Densosporites velatus</i>	-0.52869	0.016454	-0.31226	-0.23421	0.34505	-0.079957	0.33518	0.36764	-0.2627	-0.35847	0.28835	-0.31285	0.01707	-0.082987	0.05615	-0.11771	-0.043341	-0.18497	0.07557	-0.05381	-0.08309
<i>Lycopodioides ceratoides</i>	-0.29675	-0.055285	0.11557	0.013764	0.076753	0.36119	-0.10162	0.21418	-0.13366	0.039467	-0.045433	0.0009702	-0.30428	-0.020962	0.11567	-0.035031	0.059259	0.0072494	-0.0009375	-0.024247	
<i>Lycopodioides rugulatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Neosarsotia truncata</i>	0.034587	0.68271	0.14066	0.36154	0.14211	-0.28388	-0.0076234	0.56189	-0.046094	-0.06589	-0.13719	-0.24125	0.13453	0.11221	-0.086091	0.17032	0.024525	-0.17228	0.044725	0.17522	-0.18372
<i>Retrioides uncinulatus</i>	-1.4084	0.51973	-0.13666	0.72005	1.4628	0.62346	0.43757	-0.48431	-0.072548	-0.2677	0.48418	0.24418	-0.3299	0.020218	0.1334	-0.28643	-0.13513	0.038851	-0.18116	-0.037113	-0.034394
<i>Retrioides clavatus</i>	-0.085728	-0.24455	0.13084	-0.049038	0.083635	0.39261	0.37488	0.10361	0.13313	0.07752	-0.14856	0.076627	0.18225	-0.014531	0.0052563	-0.11398	-0.03554	-0.042238	-0.063092	-0.092742	-0.12062
<i>Retrioides seminis</i>	0.34407	-0.16552	0.077989	-0.0097003	0.15574	-0.080549	0.10263	-0.10158	0.18426	-0.30012	0.056393	-0.066153	0.058546	0.09346	-0.001816	-0.22903	0.11909	-0.0021341	0.094235	0.056596	-0.037615
<i>Leptolepidites bosus</i>	-0.36526	-0.1134	0.63707	-0.6034	0.20606	0.3426	-0.62487	-0.080745	-0.42935	0.029612	-0.158	0.50562	0.15514	-0.52507	-0.4812	0.3153	-0.31538	0.18476	0.19146	0.17015	0.027847
<i>Leptolepidites equatibosus</i>	-0.005162	0.43524	-0.022024	-0.038508	0.074257	0.025878	-0.14772	-0.11668	0.25992	-0.041796	-0.09439	-0.15549	0.031345	-0.036576	-0.02271	0.11218	0.092015	0.017695	0.094106	0.0062336	-0.061664
<i>Leptolepidites major</i>	0.23298	-0.044094	-0.064985	-0.073271	0.28475	-0.05847	0.38065	-0.12789	-0.030389	0.18935	0.253386	0.044638	0.016639	-0.18291	-0.23603	-0.10667	-0.063235	-0.026693	0.060018	-0.092192	0.040858
<i>Leptolepidites crassifolius</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sectosporites pseudovolutus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stipulinsporites sp.</i>	0.44667	0.43305	-0.09592	-0.20191	0.39017	-0.098121	0.3218	-0.27374	0.15153	0.24712	0.053945	-0.046898	-0.15045	0.018092	0.21719	0.14455	-0.25261	-0.10436	-0.11807	-0.012586	-0.014926
<i>Uvacopites argentiiformis</i>	0.42293	0.23158	0.98584	1.7918	-0.60315	-0.47918	0.038542	-0.40634	-0.45672	0.57977	-0.26235	0.49338	-0.53245	-0.65023	-0.048817	0.25352	0.15843	0.14937	-0.20856	-0.14243	-0.13735
<i>Calamospores mesozoa</i>	0.16712	0.09972	-0.0036912	0.052682	0.023038	0.068271	-0.051077	0.062892	-0.023026	0.045923	0.060587	0.03601	-0.037935	-0.036344	0.050383	-0.027653	-0.0097328	-0.0025681	0.0018941	0.0008702	0.021995
<i>Moratisporites scabratus</i>	-0.050886	0.056273	0.018577	0.068918	0.031924	0.0090508	-0.030446	0.042835	0.001577	0.092006	0.0051163	-0.0045109	0.088321	0.0072468	-0.001209	-0.047459	-0.0026725	0.0064292	-0.016767	0.011907	-0.02715
<i>Baculatisporites cananensis</i>	0.11278	-0.3447	-0.39923	0.13046	-0.13399	0.26704	0.29845	0.18111	-0.1972	-0.0086164	0.042474	0.12163	0.21704	-0.20552	-0.0097266	-0.023476	-0.047606	-0.1312	-0.14696	-0.049424	0.082217
<i>Comandaculites weilmanni</i>	-0.15163	-0.13714	0.057601	0.059042	0.01584	-0.026655	0.1142	-0.074991	-0.0666133	0.13317	0.017666	0.033955	-0.079027	0.11527	-0.022216	0.041925	-0.083445	0.015488	0.0231	-0.0953835	0.090738
<i>Idosporites major</i>	-0.36534	0.6309	0.47872	-0.12206	-0.17038	0.239	-0.053701	0.03364	-0.38211	0.042225	-0.19732	0.11031	0.33491	0.13806	-0.20679	0.040329	0.060641	0.023725	0.013397	-0.22986	-0.0707372
<i>Idosporites minor</i>	-0.09865	-0.12972	-0.22721	0.031286	-0.13602	-0.0041564	0.30377	0.037808	-0.094042	-0.2109	0.062476	0.075925	0.03456	0.0035091	0.066691	0.051393	-0.042489	-0.011118	-0.067379	0.050797	-0.05163
<i>Glacanthoides senonicus</i>	-0.25482	-0.20138	0.095445	-0.23254	0.30563	-0.050806	0.12312	-0.099524	-0.21504	0.045537	-0.005171	0.1131	-0.14781	0.11249	-0.23048	-0.065249	0.019495	-0.14271	-0.028153	0.10502	-0.1202
<i>Combacanthoides mesozoa</i>	0.09428	-0.019923	0.03474	0.097476	0.092011	-0.25097	0.091913	-0.13228	-0.074446	-0.037084	0.016844	-0.026005	-0.097659	-0.12817	-0.032653	0.016859	0.070496	-0.025292	-0.023484	0.007272	-0.062656
<i>Dicropylidites burialii</i>	0.036305	-0.047033	-0.03528	0.019093	0.047211	-0.051808	0.021446	0.015292	-0.062108	-0.0065475	-0.07159	0.02893	0.036213	0.05153	0.02162	0.021847	-0.022875	0.041309	0.05277	0.0036163	-0.0042722
<i>Dicropylidites equatus</i>	0.08762	-0.045755	0.10906	0.0071056	-0.13038	0.038557	0.10706	-0.11984	-0.12667	-0.020399	0.080661	-0.070928	0.0047353	0.007161	0.04799	0.03249	0.079133	0.054938	-0.0003519	-0.03332	0.02133
<i>Concavosporites sp.</i>	-0.29026	-0.09819	0.047076	0.11899	-0.017995	0.13943	-0.36491	-0.014325	0.14768	0.023259	-0.0018502	0.15711	-0.070986	-0.013259	-0.12159	0.040451	0.10013	0.0064419	-0.005678	0.10167	0.0087107
<i>Mitansporites phlebotomoides</i>	-0.66121	1.2961	-0.65408	0.82788	-0.60501	-0.13479	0.54278	0.29834	-0.17433	0.22627	0.25348	-0.14443	-0.14016	0.28201	-0.013513	0.000489	0.038382	0.026045	-0.13396	-0.10205	-0.0060754
<i>Concavosporites cf. phlebotomoides</i>	-0.12897	0.054523	-0.087631	0.068268	-0.0035797	-0.14507	-0.10085	-0.051719	-0.13239	0.06118	0.035136	0.077378	0.048122	-0.01384	0.057117	-0.03061	-0.072343	-0.046052	-0.025642	0.010072	0.048376
<i>Duflexosporites problematicus</i>	0.20318	0.1268	0.094806	-0.3424	-0.2671	0.0026303	-0.043851	0.12426	0.067417	0.07316	0.072018	-0.014237	0.005874	0.16467	-0.055034	0.030485	0.014239	-0.07109	0.003849	0.025054	0.0071753
<i>Ichtyosporites sp.</i>	-0.12626	0.11863	0.26166	0.15143	0.050494	0.024571	-0.12452	0.073572	0.1837	-0.078021	-0.019196	-0.2351	0.01537	-0.045214	-0.038006	-0.049956	-0.084952	0.053736	-0.060894	-0.1602	0.080155
<i>Chloanthospora jurensis</i>	-0.36534	0.6309	0.47872	-0.12206	-0.17038	0.239	-0.053701	0.03364	-0.38211	0.042225	-0.19732	0.11031	0.33491	0.13806	-0.20679	0.040329	0.060641	0.023725	0.013397	-0.22986	-0.0707372
<i>Obusosporites canadensis</i>	-0.030624	-0.099124	-0.011009	-0.079387	-0.1232	-0.080145	0.035276	-0.12406	0.073533	0.15715	-0.089638	-0.13171	0.0045793	-0.024408	0.057008	-0.11599	0.011844	-0.015338	-0.036171	0.048833	0.016043
<i>Concavosporites subgraciliosus</i>	0.078947	-0.14331	-0.025152	-0.04182	0.10843	0.00033716	0.14534	0.15309	0.083896	-0.01951	-0.13243	-0.0									

	Axis 22	Axis 23	Axis 24	Axis 25	Axis 26	Axis 27	Axis 28	Axis 29	Axis 30	Axis 31	Axis 32	Axis 33	Axis 34	Axis 35	Axis 36	Axis 37	Axis 38	Axis 39	Axis 40	Axis 41	Axis 42
<i>Allopsorites thomasi</i>	-0.0073565	-0.15745	0.07178	0.14124	0.048361	-0.18175	-0.0488078	0.20624	-0.012412	0.041925	0.0484049	-0.082973	-0.004957	0.063156	-0.043079	0.035894	0.00812	0.03697	-0.0069146	0.014205	0.0027915
<i>Viresporites pallidus</i>	-0.1464	0.11513	-0.14429	0.010405	-0.13391	0.0099335	0.072566	-0.059677	0.12791	-0.16991	0.024491	-0.090288	0.04244	-0.062938	0.0074256	0.049935	-0.085055	0.056237	0.044684	0.062055	-0.015067
<i>Pytoporites microadans</i>	0.081478	0.016122	-0.097602	0.082384	0.11211	0.08438	-0.064506	-0.035664	0.041003	0.0013773	-0.036809	0.028877	-0.011857	0.035042	-0.044066	0.068628	0.022181	0.0001699	-0.049694	0.016687	-0.015556
<i>Pytoporites minimus</i>	0.0083074	0.16037	0.24544	0.13416	0.073065	0.059496	-0.015931	-0.074523	0.035007	-0.010944	0.050757	-0.0036157	-0.070353	-0.014563	-0.10391	-0.11592	-0.083235	0.088547	0.012903	0.058229	-0.0060495
<i>Podocarpidites ellipticus</i>	-0.012315	0.16116	0.21539	0.43667	-0.16044	-0.025437	0.11586	0.038896	0.085995	-0.11441	-0.050544	0.081973	0.16203	-0.12792	-0.029147	-0.0046787	0.055175	-0.13023	0.15443	-0.0008317	0.086088
<i>Quadraculitha anelaciformis</i>	0.087071	0.081254	0.26012	-0.16473	-0.081599	0.027022	-0.048868	0.046425	-0.040386	-0.075594	-0.022547	0.073608	-0.0090328	-0.020225	0.1274	-0.047575	-0.0092021	0.062977	-0.053792	0.061397	-0.090416
<i>Araucariacites australis</i>	0.0017532	0.018534	-0.017628	-0.027328	-0.079773	0.0038009	-0.06007	-0.037941	-0.0077081	-0.011691	0.0091276	-0.0079159	-0.033746	0.010796	-0.043584	-0.011006	0.01297	-0.037465	-0.013711	0.01031	0.0036859
<i>Callialasporites dampieri</i>	0.092293	0.39188	0.24096	-0.3433	-0.0009107	0.022701	0.15878	0.15006	-0.0003329	-0.071559	-0.091132	0.1507	0.08021	-0.095769	0.031889	0.016239	0.026853	0.076872	-0.065842	0.040237	0.065666
<i>Callialasporites segmentatus</i>	0.47632	0.53119	-0.40478	-0.14111	0.67681	-0.3476	0.10931	0.14916	-0.64527	0.11949	-0.20894	-0.17574	-0.17003	0.09842	-0.25422	-0.11522	0.10822	0.20625	-0.066876	-0.063363	0.097087
<i>Callialasporites trilobatus</i>	0.53159	-0.36358	0.75263	0.34297	-0.72608	-0.31227	0.56005	0.1617	-0.20993	-0.42097	-0.29134	0.024533	0.1729	0.21512	-0.057726	-0.040259	-0.18656	0.044301	-0.48008	-0.019189	-0.019054
<i>Callialasporites turbatus</i>	-0.025682	-0.025157	-0.071351	-0.084303	-0.026256	-0.14158	-0.010409	0.054011	0.028122	0.048574	-0.01557	0.034932	-0.020146	-0.074936	-0.020438	-0.014892	0.010099	0.0059934	0.014085	-0.0082017	-0.016407
<i>Classopolis torosus</i>	0.040378	-0.049754	0.015414	0.030251	-0.02639	0.029249	0.016397	-0.0053947	0.012817	-0.0046621	-0.001295	0.0085967	-0.038232	0.010792	0.015644	-0.0061029	-0.030357	0.0008389	0.01948	-0.0023549	0.0034381
<i>Cerebropollenites mesozoicus</i>	-0.0036754	-0.059211	-0.094313	0.043183	0.070142	0.030359	-0.059566	-0.078995	-0.039926	0.012211	0.035248	0.010452	0.074524	-0.031055	0.042916	-0.010348	0.037398	0.028645	-0.015079	0.028857	0.037345
<i>Sphaeripollenites scabratus</i>	-0.034718	-0.020488	0.0036675	-0.025162	0.050161	0.000149	-0.062202	0.021858	-0.022834	-0.042802	-0.034627	-0.066169	-0.0090476	-0.016129	-0.019469	-0.0041088	0.011976	-0.019505	-0.011919	0.02238	0.045491
<i>Sphaeripollenites subgranulatus</i>	0.032953	0.0022124	0.026394	0.0009762	0.024474	0.02561	0.020548	-0.0006143	0.028727	0.0033519	0.0033464	-0.042092	0.014934	0.028427	-0.013279	0.016808	-0.0091731	-0.0084793	-0.0047403	-0.0050433	0.0031407
<i>Perinipollenites elatoides</i>	-0.0073412	-0.0015145	-0.020855	-0.041119	-0.039768	-0.0012772	0.029409	-0.0099301	0.015063	0.036056	-0.0045947	0.033644	-0.018271	-0.016554	-0.0057729	-0.0006643	-0.010202	-0.018314	-0.014349	-0.010242	
<i>Chaumatospores apertus</i>	-0.092233	-0.037458	-0.064587	0.018617	0.024835	-0.046948	-0.032285	-8.64E-05	0.11544	-0.054055	-0.073503	0.029967	-0.019578	-0.0091138	0.058264	-0.010703	0.0037974	0.048123	-0.014349	-0.047719	-0.010242
<i>Chaumatospores hians</i>	-0.17624	-0.083634	0.27084	-0.07169	0.13245	-0.061776	0.053315	-0.081574	-0.012728	0.013612	0.026909	0.010845	0.037411	0.075344	0.10954	0.043673	0.050255	-0.096282	-0.015866	0.010953	-0.0058997
<i>Chaumatospores major</i>	-0.11798	0.11565	-0.14455	-0.33376	-0.040838	-0.010752	0.1399	0.0711	-0.2151	-0.14381	0.072768	0.057624	-0.098004	0.19575	-0.082862	-0.146	0.0084056	0.21022	-0.055343	0.046489	-0.045216
<i>Cycadapites minimus</i>	-0.047708	0.027452	0.0088845	-0.050111	-0.06261	0.041788	0.061127	0.0077327	-0.063178	0.052138	-0.044184	-0.06549	-0.021574	-0.040641	0.022722	0.022822	-0.0058798	-0.0010199	0.018252	0.0024851	-0.0064925
<i>Cycadapites carpenteri</i>	0.0053535	0.0015348	-0.041566	-0.05166	-0.0238495	0.094812	0.039984	-0.018708	0.049003	0.073669	0.06472	-0.019684	0.085635	-0.019556	0.027512	0.017226	0.034815	0.05483	0.001494	0.028552	-0.0080394
<i>Cycadapites subgranulatus</i>	0.099459	0.16165	-0.095387	-0.017381	0.042108	0.014164	0.074113	0.023699	0.0034267	-0.000401	0.016029	0.095284	0.018021	0.060121	0.015644	-0.023356	0.13165	-0.042126	0.08681	-0.077266	0.014558
<i>Eucommidites troedssonii</i>	-0.29196	0.1106	0.054272	-0.079539	-0.049095	-0.094389	-0.11527	-0.097075	0.029031	-0.017965	0.052821	0.084947	0.012423	0.022451	-0.027288	0.054563	0.0007069	0.011631	-0.026516	-0.080732	-0.0043588
<i>Sriate bisaccata</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Axis-43	Axis-44	Axis-45	Axis-46	Axis-47	Axis-48	Axis-49
HB1	-0.0042954	-0.0012302	0.0007296	0.0010329	0.0009738	-0.0008555	3.75E-06
HB2	0.012011	-0.011164	0.0004552	-0.0060638	-0.016716	-0.0041107	0.0030606
HB3	-0.019548	0.010269	-0.0098931	0.021404	-0.0031599	-0.0031342	0.0045869
HB4	-0.013988	-0.014292	-0.0033923	0.0089278	0.0042568	0.0032038	-0.0047379
HB5	0.020557	0.013424	0.0028811	-0.0098016	-0.0047052	-0.0041137	0.0049089
HB6	0.022209	0.0021911	0.0081357	0.0079219	-0.0021968	-0.0049313	-0.0072785
HB7	0.0057034	-0.011013	-0.0045404	0.015762	-0.0011158	0.0062843	0.013449
HB8	-0.0041842	0.0038359	0.0008558	-0.003209	-0.0020464	-0.0003399	0.001026
HB9	0.037805	-0.0072434	-0.0046387	0.0060022	0.010492	0.0011527	-0.000412
HB10	-0.012316	-0.0013088	0.011165	0.0001782	-0.010703	0.01737	-0.0046141
HB11	-0.04545	-0.0089924	0.020479	-0.014759	0.0079676	-0.0008772	-0.00419
HB12	0.0024574	0.017023	0.0013335	0.0023267	-0.0022816	-0.017367	0.0009643
HB13	0.0007924	0.0019778	-0.0003438	0.0013341	-0.0002279	-0.0001123	-4.64E-05
HB14	-0.033111	-0.0092005	-0.004281	-0.0098258	0.0096591	-0.0064743	-0.0072103
HB15	0.051333	0.0086083	-0.016703	0.019024	0.0022806	0.011406	0.0073175
HB16	-0.02664	-0.0004751	0.0088283	0.0044697	0.0046162	0.0001324	0.0003697
HB17	0.0044612	-0.0022142	-0.024087	-0.029272	-0.012447	-0.019652	-0.0028742
HB18	-0.015352	0.010685	0.0016387	-0.0016462	0.0018978	-0.0042675	0.0014431
HB19	0.025194	0.0058354	-0.0001362	-0.025207	-0.0090468	0.011497	0.005945
HB20	0.010937	-0.0065719	0.012923	0.024142	0.0052875	0.0070074	-0.012335
HB21	-0.001181	-0.0064298	-0.0086154	-0.03744	-0.0077115	0.0044341	0.006478
HB22	-0.0026259	0.010492	0.0094541	0.028449	0.023139	0.0036663	-0.0038596
HB23	0.021	-0.008617	-0.027489	0.0007622	-0.0040134	0.0080556	-0.0075056
HB24	0.037481	0.0026581	0.010895	-0.026015	0.01852	-0.019087	0.0074841
HB25	0.018236	-0.015932	0.0070802	0.015133	-0.0077574	0.0067506	0.0017055
HB26	-0.036759	0.019895	-0.0037421	0.0053119	-0.0080997	-0.0022913	0.0068466
HB27	-0.040412	0.0096974	-0.012726	0.0003692	0.0042673	-0.0019161	-0.0087793
HB28	0.0072792	-0.010452	-0.014734	0.0058463	1.77E-05	-0.0021365	-0.0045325
HB29	-0.0034786	-0.019722	0.025885	-0.0091199	0.0023979	-0.0004583	0.009927
HB30	0.04592	0.001166	-0.014796	-0.0054037	-0.0072493	-0.0005966	0.0002365
HB31	0.0048324	-0.0018883	-5.77E-05	2.96E-05	-0.0003613	0.0001991	2.30E-05
HB32	-0.077669	0.053301	-0.0070711	0.01254	-0.0139	0.0014765	0.003813
HB33	-0.012841	-0.028204	0.038927	0.0047153	0.0053933	0.0039502	0.0019014
HB34	0.02722	0.038026	0.0043557	0.0017835	-0.015235	0.0070008	0.0022916
HB35	0.0062923	-0.020383	0.0011414	-0.0010411	0.0016444	0.017176	-0.0007966
HB36	-0.03306	0.023401	-0.0070964	-0.015335	0.0076504	-0.0048743	0.0067692
HB37	0.012944	-0.032405	0.01795	8.24E-05	-0.023488	-0.0069111	-0.019594
HB38	0.0004213	-0.012947	-0.019603	-0.003064	0.01334	0.0004643	0.0036998
HB39	0.0018594	0.04372	-0.018324	-0.003074	0.0075383	0.0050552	-0.019155
HB40	-0.035433	-0.031994	-0.018847	-0.022034	0.0066746	0.022788	0.016899
HB41	-0.047205	-0.026344	-0.016942	0.0042374	0.0096275	-0.0046972	-0.0080224
HB42	0.015822	0.053644	0.039947	-0.004326	-0.0061099	0.013483	0.0061984
HB43	0.0038436	-0.001731	0.0018204	-0.0005234	-0.0005065	9.83E-05	-8.91E-05

	AXIS 43	AXIS 44	AXIS 45	AXIS 46	AXIS 47	AXIS 48	AXIS 49
HB44	0.014956	0.003132	0.030884	0.01112	-0.0052839	-0.015679	0.0097509
HB45	0.012307	0.0092472	-0.017819	-0.010513	-0.0031338	0.0072339	-0.021235
HB46	-0.032037	-0.054581	-0.012235	0.0226616	-0.021987	-0.010629	0.011686
HB47	0.006934	-0.0047781	0.02407	-0.029603	0.015798	0.002083	-0.013807
HB48	0.040646	-0.0023182	-0.019467	0.0079114	0.019938	-0.0025828	0.0097421
HB49	0.024927	-0.0082179	0.0070162	0.0171	-0.010207	-0.013376	-0.00772
HB50	0.0082545	0.019083	-0.01229	0.01765	0.015543	-0.01197	0.011463
Taxon scores							
<i>Rogalskisporites cicaricosus</i>	0	0	0	0	0	0	0
<i>Neveissporites bigramulatus</i>	0.031325	0.094875	0.000417	0.010455	-0.0023588	0.011795	0.031138
<i>Amphicladisporites sp.</i>	0	0	0	0	0	0	0
<i>Densosporites velatus</i>	-0.11735	-0.029156	-0.020193	0.043241	0.0032047	-0.0072592	-0.029974
<i>Densosporites cf. velatus</i>	0	0	0	0	0	0	0
<i>Lycopodioidites cernitoides</i>	-0.025802	0.007571	0.0020478	0.0060721	-0.015005	-0.016291	-0.011757
<i>Lycopodioidites rugulatus</i>	0	0	0	0	0	0	0
<i>Neorasitriella truncans</i>	0.12856	-0.019719	-0.016103	-0.032607	-0.024153	-0.033184	0.012791
<i>Retriretiles astroclavoidites</i>	0.18565	-0.096768	-0.0038032	0.0020512	-0.036327	0.022621	0.0028595
<i>Retriretiles clavataoides</i>	-0.037947	-0.04167	0.040632	-0.0074249	0.0056247	0.0085947	-0.027611
<i>Retriretiles summuus</i>	-0.022223	0.077538	0.023503	0.018445	0.015101	0.05654	-0.0091716
<i>Lepidolepidites bosnus</i>	0.16733	-0.076355	0.081598	0.045758	-0.034047	-0.030761	0.011557
<i>Lepidolepidites equatibosus</i>	0.010183	-0.014567	0.033502	-0.018247	0.025717	-0.0092361	-0.018638
<i>Lepidolepidites major</i>	0.081532	0.016629	-0.040475	0.012196	9.89E-05	-0.028227	-0.019063
<i>Lepidolepidites crassibitens</i>	0	0	0	0	0	0	0
<i>Sesrosporites pseudoalveolatus</i>	0	0	0	0	0	0	0
<i>Staphisporites sp.</i>	0.0086973	0.041405	0.01355	-0.016803	-0.0047884	-0.021451	-0.033886
<i>Uvaeosporites argenteiformis</i>	0.14767	-0.088709	0.11994	-0.036286	-0.050927	0.011176	-0.011101
<i>Cátamospora mesozoa</i>	-0.020204	-0.022613	-0.010604	-0.0001014	-0.00713	0.0048511	0.00303882
<i>Marettisporites scabratus</i>	0.028048	0.015011	-0.010021	0.0001519	0.0032899	-0.0099309	0.0018436
<i>Baculatisporites comanensis</i>	-0.030343	0.06389	0.044827	0.0073807	-0.0017473	0.013478	-0.0013043
<i>Omnidacidites wellmani</i>	0.004723	0.013982	-0.080197	-0.0055085	-0.0030175	-0.0033658	0.011093
<i>Todisporites major</i>	0.030442	0.010136	-0.022654	0.092495	-0.022918	-0.013976	-0.0057747
<i>Todisporites minor</i>	0.057548	0.032851	0.012176	0.0001129	-0.014457	-0.013285	-0.01693
<i>Gleichenioidites senonensis</i>	-0.16289	0.066848	0.052227	-0.075436	-0.053927	-0.071284	0.0066198
<i>Conbaculatisporites mesozoius</i>	0.031786	0.0028786	0.0026708	0.0019867	-0.0062175	-0.0007268	-0.0050147
<i>Diclyophyllidites harrisi</i>	-0.0052554	-0.0011809	0.0075782	-0.0040163	-0.0056041	0.0035213	-0.010782
<i>Diclyophyllidites equisetinus</i>	-0.0051177	-0.0021156	0.0034192	0.0038648	-0.007202	-0.014702	-0.005387
<i>Concavosporites sp.</i>	-0.010589	-0.0039965	0.017712	-0.01295	0.016081	0.0093837	0.0020641
<i>Matonisporites phlebotrioides</i>	0	0	0	0	0	0	0
<i>Matonisporites cf. phlebotrioides</i>	0	0	0	0	0	0	0
<i>Contignisporites sp.</i>	-0.075076	-0.067697	0.0065476	-0.042911	0.01972	0.02682	-0.026785
<i>Duplexisporites problematicus</i>	-0.018898	0.0056839	0.047899	0.017807	-0.010132	0.0080601	0.01053
<i>Ischyrosporites sp.</i>	-0.05354	0.031748	-0.025559	0.020244	-0.0002973	-0.010013	-0.015243
<i>Cibicidespora jurtensis</i>	0.015698	0.061874	0.020486	0.027112	0.0073985	0.015653	-0.0006179
<i>Obusisporites canadensis</i>	0.030442	0.101316	-0.022654	0.092495	-0.022918	-0.013976	-0.0057747
<i>Concavissimiporites subgranulosus</i>	0.014925	-0.07158	0.011255	0.028964	-0.016638	0.008233	0.0013107
<i>Concavissimiporites variverrucatus</i>	0.015272	-0.039266	-0.034689	0.0050246	-0.0086996	-0.020482	-0.0006064
<i>Deltoidespora australis</i>	0.024586	-0.010624	0.020828	-0.0003054	0.020652	0.011064	0.0051988
<i>Deltoidespora concavus</i>	0.052349	0.030049	0.0008195	-0.0057816	-0.0063492	0.013967	-0.0029317
<i>Deltoidespora minor</i>	0.0047455	-0.019044	-0.017227	-0.006852	0.002239	0.0056804	0.00978
<i>Phloisporites brevipapillosum</i>	-0.16502	-0.063043	0.048071	0.071616	0.097924	-0.097221	0.0004675
<i>Alisporites danubienensis</i>	-0.16075	0.19674	0.056382	-0.22249	-0.20578	-0.048547	-0.012772

	Axis 43	Axis 44	Axis 45	Axis 46	Axis 47	Axis 48	Axis 49
<i>Alisporites thomasii</i>	-0.017834	-0.029019	0.014313	-0.002866	0.010852	0.0017204	0.0075958
<i>Vitreosporites pallidus</i>	-0.004109	-0.023647	-0.0073566	0.0092472	-0.0039092	-0.0076036	0.012198
<i>Pityosporites microalatus</i>	-0.011785	0.014978	-0.0076458	0.024752	-0.0070174	0.013396	-0.0014831
<i>Pityosporites minimus</i>	-0.069754	-0.0008945	-0.0071835	-0.013975	-0.0022048	0.010743	-0.0081833
<i>Podocarpidites ellipticus</i>	-0.019197	0.012394	-0.0035639	0.032004	-0.026679	-0.013306	-0.025359
<i>Quadræculina anellaformis</i>	0.10999	-0.035308	-0.042451	0.0034611	0.085057	0.017734	-0.055752
<i>Araucariacites australis</i>	-0.0049715	0.01747	0.0036978	-0.0057912	0.0012473	-0.0044577	0.0023623
<i>Callialasporites dampieri</i>	-0.02849	-0.011576	0.024663	-0.0061597	0.016021	-0.0071953	0.014649
<i>Callialasporites segmentatus</i>	-0.01809	0.0059841	0.020299	0.063009	0.03387	-0.014831	0.040058
<i>Callialasporites trilobatus</i>	-0.12135	0.055233	-0.13557	-0.010619	0.0005885	0.01196	-0.001265
<i>Callialasporites turbatus</i>	-0.040968	0.0091903	-0.0028887	0.0091932	0.0005505	0.0009235	-0.0050474
<i>Classopollis torosus</i>	0.0053504	0.0049192	0.008593	0.017584	0.013327	-0.0076279	0.002332
<i>Cerebropollenites mesozoicus</i>	-0.038537	-0.0035275	-0.014137	-0.029429	0.015599	-0.0066938	-0.0024023
<i>Spheripollenites scabratus</i>	0.032594	-0.0002587	-0.0072373	-0.0028241	-0.0035607	0.0031879	-0.0081074
<i>Spheripollenites subgranulatus</i>	-0.018607	-0.012553	0.015363	-0.0077517	-0.006506	-0.0030997	0.0035371
<i>Perinopollenites elatoides</i>	0.028894	-0.014065	0.0054559	-0.011971	-0.0024929	0.0017727	-0.0050507
<i>Chasmatosporites apertus</i>	0.000736	0.022115	-0.003041	-0.013011	-0.0042513	-0.0064751	0.011569
<i>Chasmatosporites hians</i>	-0.015589	-0.016197	0.0010635	0.018688	0.0051417	0.0051139	0.0076944
<i>Chasmatosporites major</i>	0.072233	-0.015379	-0.003002	0.04451	-0.026659	0.0027659	0.014588
<i>Cycadopites minimus</i>	0.0051822	0.022973	-0.0014106	-0.013029	0.0027553	0.015652	0.0020411
<i>Cycadopites carpentieri</i>	-0.0009165	0.0092096	-0.015387	0.029341	-0.015012	0.0028743	0.0051632
<i>Cycadopites subgranulosus</i>	0.038506	0.0008634	0.0085533	-0.0016324	0.0016427	0.0079642	0.014766
<i>Eucommiidites troedssonii</i>	-0.046064	-0.028429	-0.025432	0.018423	0.0034956	0.0037622	-0.014799
<i>Striate bisaccate sp.</i>	0	0	0	0	0	0	0

# Appendix 10





	AXIS 1	AXIS 2	AXIS 3	AXIS 4	AXIS 5	AXIS 6	AXIS 7	AXIS 8	AXIS 9	AXIS 10	AXIS 11	AXIS 12	AXIS 13	AXIS 14	AXIS 15	AXIS 16	AXIS 17	AXIS 18	AXIS 19	AXIS 20	AXIS 21
H844	-0.079016	-0.021003	-0.10977	-0.018885	-0.25051	0.17021	-0.1858	0.21145	-0.017182	-0.10006	-0.20237	-0.2269	-0.008318	-0.1461	-0.22762	-0.22004	-0.171265	0.097151	-0.044597	-0.13078	-0.11185
H845	-0.15523	-0.017053	-0.044166	-0.14791	0.062625	-0.088611	-0.12902	0.021534	0.19192	-0.01654	0.046723	0.17668	-0.1637	-0.1948	0.15763	-0.014304	-0.1	0.088157	-0.095016	-0.075867	-0.16059
H846	-0.27652	-0.20843	-0.032801	-0.056211	-0.098655	0.19757	-0.10645	0.035161	-0.07450	-0.18538	-0.13548	-0.019725	0.009466	0.006327	0.0065795	0.009556	0.0003271	0.054035	0.0003271	0.010566	0.013116
H847	-0.2414	-0.24261	0.055497	-0.096941	-0.021544	-0.11209	-0.16014	0.014195	0.078555	0.055458	0.17851	-0.26198	-0.004192	-0.19663	0.001284	0.043347	0.054035	0.054035	0.054035	0.04273	0.017116
H848	-0.3092	-0.34015	0.014989	-0.22209	0.11934	0.32396	0.066866	0.071862	0.027323	0.26167	0.18526	-0.058098	0.12115	0.075389	0.012282	0.035589	-0.152	0.11669	0.01669	0.10241	0.01472
H849	-0.23635	-0.29935	-0.076641	-0.040191	0.028733	-0.056388	-0.039971	-0.24246	0.007346	-0.032347	0.026167	0.0064989	0.19265	-0.023527	0.025957	0.052863	0.044745	0.12062	-0.060777	-0.10472	0.01472
H850	-0.25651	-0.08887	-0.093866	-0.038942	-0.025757	-0.12661	-0.17371	-0.19478	-0.39162	-0.000995	0.22031	0.048986	-0.11914	0.037774	-0.057939	0.16139	0.0099684	0.19392	0.22928	0.029529	-0.19006
Taxon scores																					
<i>Regaladisporites cicatricosus</i>	-1.1569	-1.2677	-0.35904	-0.65043	0.12723	2.3547	-0.19232	0.82709	-0.037799	0.41305	0.75431	1.9491	1.3835	-0.14888	0.69906	-0.51328	0.47892	-0.29262	-0.25789	0.1695	0.23898
<i>Neovestiporia bigrammatus</i>	-0.59848	-0.7636	-0.20685	0.38042	-0.3732	-0.05764	-0.2604	0.11832	-0.21689	0.21208	-0.2071	-0.059399	-0.4575	-0.21393	-0.39108	-0.003879	-0.028602	0.020577	-0.057953	-0.33587	0.046064
<i>Anpiculariopsis sp.</i>	-0.47911	-0.23361	-0.48681	-0.19522	-0.5419	1.2235	-0.38214	0.62401	-0.16459	-0.83515	-0.74822	0.79625	-0.06529	-0.34226	-0.028394	-0.028322	0.30269	-0.018299	0.088034	-0.32526	-0.26753
<i>Densosporites velatus</i>	-0.42457	-0.47133	0.050064	-0.42999	0.24615	-0.09424	0.3031	-0.29464	0.61139	-0.026632	0.18198	0.048416	0.38125	-0.038416	0.26942	-0.047294	0.06439	-0.24446	-0.04034	-0.49523	-0.37437
<i>Densosporites cf. velatus</i>	-0.50117	1.2063	-1.4689	-1.4483	1.2371	-0.72928	-3.0072	2.9006	0.59149	2.7537	0.096943	-0.037471	0.38633	3.1477	-0.02773	0.55266	-0.68233	-0.94525	0.65982	-0.34427	-0.17648
<i>Lycopodiaceae serritoides</i>	-0.01846	-0.067156	0.024931	-0.0020967	0.0066882	0.041142	-0.058018	0.051634	0.10774	0.045374	0.0665947	-0.12211	0.035976	0.038913	0.10297	0.004293	0.20172	0.24814	0.001942	-0.12416	0.001761
<i>Lycopodiaceae rugulatus</i>	-0.66005	-0.2176	0.0004056	3.8271	3.7524	-0.44668	-0.32518	1.1236	-0.35674	0.12338	-1.3676	0.28399	-1.0293	-1.0155	-0.86774	-0.65981	1.7122	-0.39519	-0.33	-0.01612	-0.28312
<i>Noorastria truncatus</i>	0.60335	1.5767	-2.6186	0.64326	0.44532	1.7669	0.68011	-2.5631	0.95538	0.91483	0.81458	-0.01402	-0.73821	0.18654	-0.977	-0.66199	-0.52417	-0.17688	0.091403	-0.062681	0.27155
<i>Retinella austroclavata</i>	-0.53922	0.19532	0.84214	-1.1186	0.46113	-0.62701	0.48152	-1.2874	3.169	-1.1282	-3.2677	2.9909	0.24237	1.4302	-0.242	0.94449	0.35435	1.0496	0.87223	-0.10088	-0.30227
<i>Retinella clavata</i>	-0.05128	-0.11795	0.048389	0.068174	-0.12929	0.070778	0.022662	0.54074	-0.041326	-0.1092	-0.036106	0.0994388	-0.13125	0.059615	-0.02482	0.063102	0.092422	-0.01312	-0.069719	0.084133	-0.09678
<i>Retinella semimaris</i>	-0.35359	-0.10967	-0.076924	0.012709	0.11013	0.056662	-0.22664	-0.16942	0.31212	0.21999	0.026614	-0.10126	0.07468	-0.17629	-0.12247	0.030059	-0.13876	0.029054	0.14688	-0.095296	-0.065044
<i>Leptopeltides bosus</i>	-0.51903	-0.17897	0.23084	1.3333	2.0374	-0.55776	0.30802	0.36664	0.51219	-0.561	0.43502	-0.59388	0.44609	-0.22771	0.45939	-0.16861	-0.61178	0.388	0.55219	-0.37473	0.047693
<i>Leptopeltides equitubosus</i>	0.35297	-0.34348	-0.040692	-0.38119	-0.026674	-0.18471	0.22296	0.53191	0.15148	0.31819	0.15388	-0.19318	0.05248	0.088967	-0.15152	-0.96668	-0.041541	0.13617	-0.34029	-0.15671	-0.01541
<i>Leptopeltides major</i>	-0.34703	-0.22153	-0.030148	-0.12492	0.25267	0.22193	-0.13397	-0.089397	0.11787	0.25835	-0.15979	-0.021264	-0.15439	0.30588	0.12128	0.10446	-0.041241	-0.028267	-0.041241	-0.028267	0.03636
<i>Leptopeltides crassibolus</i>	-0.54587	0.19746	-0.39448	3.9367	-3.9071	-1.7199	1.3862	0.25617	1.3862	0.95442	0.75281	1.1745	1.4103	-0.077646	0.095793	0.42198	-0.11675	0.10176	0.081843	0.097428	1.2515
<i>Sectosporites pseudotubulosus</i>	-0.37929	-0.2742	-0.051642	0.0070336	-0.51745	-0.07762	-0.043025	-0.23193	0.32963	0.051178	0.45721	-0.38069	-0.17143	-0.17847	0.06421	-0.07987	0.67108	-0.28794	0.45348	0.18403	-0.157
<i>Stapilinosporites sp.</i>	-0.10646	0.21729	0.3878	0.070075	-0.14837	0.1061	0.33059	-0.05609	0.15335	0.094887	0.23252	0.25718	0.46587	-0.0062783	-0.23651	0.071617	0.0083517	-0.12574	-0.013944	-0.16071	0.016392
<i>Uvaeosporites argemoneformis</i>	-0.31759	-0.099846	0.48992	-0.32269	0.06263	0.19019	-0.17794	-0.30229	-0.31827	-0.30916	0.09699	-0.39668	0.12588	0.4232	-0.10693	0.53914	-0.093089	0.2775	-0.10569	0.039549	0.39549
<i>Calamospora mesozata</i>	0.062961	0.048406	0.023802	0.01899	-0.0059893	-0.0038941	-0.0031931	-0.0071498	-0.042063	0.0154	0.0044164	0.056658	-0.38051	-0.02566	0.0009379	-0.02781	-0.11812	0.043284	0.0041748	0.018047	0.04576
<i>Marasmiopsis scaberrima</i>	0.049765	0.017707	0.093721	-0.032033	-0.04146	-0.07762	0.004749	0.1125	-0.075338	0.004212	0.019754	0.0064221	-0.053557	0.083734	0.032251	-0.060207	0.019398	-0.0024007	-0.016002	0.0055186	0.0055186
<i>Baculatisporites cananensis</i>	-0.32322	-0.22175	-0.075019	0.14761	-0.50719	-0.10717	0.30885	0.018519	0.15817	0.052854	0.065841	0.22338	-0.028861	0.014957	-0.14033	-0.094454	0.0083438	-0.214	0.068236	0.092655	-0.0099064
<i>Osmundacillales wetmannii</i>	0.063043	-0.05243	-0.24658	-0.044773	-0.16756	-0.10124	0.058231	0.026346	0.053963	0.025606	0.23182	-0.22091	0.016769	0.053336	-0.2239	0.11089	-0.040261	-0.10764	-0.16259	0.065961	-0.14227
<i>Isidiosporites major</i>	-0.31759	-0.099846	0.48992	-0.32269	0.06263	0.19019	-0.17794	-0.30229	-0.31827	-0.30916	0.09699	-0.39668	0.12588	0.4232	-0.10693	0.53914	-0.093089	0.2775	-0.10569	0.039549	0.39549
<i>Isidiosporites minor</i>	-0.033741	0.19784	-0.1515	0.11737	0.07812	0.05842	-0.092699	-0.14193	0.02732	0.17207	-0.3497	-0.17184	0.35957	0.07898	0.086884	-0.11278	0.074888	0.086884	0.11017	0.14668	-0.10068
<i>Gleicheniales senonicus</i>	1.7622	-1.6755	-0.27599	-0.22026	0.1367	-0.80421	-0.15	-0.82141	-0.49211	0.63426	-0.83898	0.031228	0.59982	-0.57242	0.24361	-0.12772	-0.28486	-0.74639	-0.32428	-0.46434	0.88976
<i>Cambacillales sporites mesozata</i>	-0.26015	-0.08677	-0.063702	0.0045684	-0.082398	-0.0012451	-0.08827	0.10613	0.064417	-0.047021	-0.017675	0.11417	-0.17676	0.047607	0.059112	-0.07248	-0.034181	-0.042962	0.13095	-0.1928	0.040072
<i>Dicycopillidiales burrii</i>	0.071908	0.080606	-0.014772	-0.05021	-0.021989	-0.003841	-0.011914	0.005475	-0.034298	-0.0098602	0.018548	-0.023635	-0.043954	0.041305	0.0044819	-0.026926	0.011547	0.0033515	-0.01787	0.01616	0.01616
<i>Dicycopillidiales equinatus</i>	0.088216	0.1099	-0.033329	-0.065117	0.050007	0.070035	0.025015	0.023835	-0.0085177	-0.05311	-0.073704	-0.016449	-0.049469	-0.033488	0.091857	-0.024801	-0.024801	-0.052625	-0.018514	0.026345	-0.027192
<i>Concavosporites sp.</i>	0.039293	0.091648	-0.015952	-0.0069886	0.020607	0.022733	-0.0059091	0.0033566	0.066175	-0.015491	0.070115	-0.0027957	-0.045247	-0.047636	0.01171	0.13351	0.045208	0.061013	0.035907	0.042673	0.021447
<i>Metanosporites phleboteroides</i>	5.6747	-3.5653	0.63807	0.80188	0.094464	1.0851	-0.78088	0.0099991	1.3358	-0.4048	0.42567	0.01296	-0.21054	0.17144	-0.096312	0.7048	0.095292	-0.015481	-0.48194	0.37688	-0.70719
<i>Metanosporites cf. phleboteroides</i>	0.16675	-0.89921	-0.92155	-0.30542	-0.38806	-0.987	2.8072	0.59264	-0.44582	2.2929	-1.3086	-0.69586	0.45246	-0.41111	0.43007	0.56746	0.071285	0.79543	-0.029188	0.80829	-0.18095
<i>Contigiosporites sp.</i>	-0.66887	-0.73162	0.01942	-0.050688	-0.030396	0.34249	0.3059	0.016544	-0.20514	-0.14112	0.12906	-0.061287	0.19113	0.45039	0.45882	-0.43724	-0.14872	-0.15965	0.54888	0.099431	0.091069
<i>Duplexosporites problematicus</i>	0.026369	0.045109	-0.054008	-0.058576	-0.11734	0.05418	-0.022121	-0.0087008	0.092867	-0.0079445	0.028572	-0.11126	0.0045735	0.0046258	0.011525	0.081238	-0.057454	-0.0032093	-0.035547	0.10649	-0.057456

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	Axis 11	Axis 12	Axis 13	Axis 14	Axis 15	Axis 16	Axis 17	Axis 18	Axis 19	Axis 20	Axis 21
<i>Alloporites thomasi</i>	0.047854	0.042399	0.10176	-0.069748	-0.12254	0.049818	0.05079	0.11016	0.0078039	-0.034612	0.037353	0.008667	0.031329	0.061979	0.011962	0.018103	-0.063037	0.10487	0.018068	0.0056384	-0.015897
<i>Vireosporites pallidus</i>	0.13803	0.10248	-0.12017	0.026503	-0.065772	-0.048709	0.032024	0.0008219	-0.024828	-0.083132	-0.11881	-0.0076863	-0.038756	0.067175	0.038801	-0.022491	-0.025657	-0.10816	-0.018828	0.054633	0.029645
<i>Ptyosporites microcladus</i>	0.071908	0.080066	-0.014772	-0.005021	-0.021989	-0.003841	-0.011914	0.005475	-0.034109	-0.033298	-0.0098602	0.018548	-0.023363	0.043954	0.041305	0.0044819	-0.026926	0.011547	0.0013515	-0.01787	0.01616
<i>Ptyosporites minimus</i>	-0.12847	0.078151	-0.085665	0.026528	-0.026566	0.025958	-0.14912	-0.11647	-0.042817	0.039572	-0.066079	0.024906	0.056105	-0.027923	-0.061648	-0.030909	0.025972	-0.15608	0.063874	0.017925	-0.01046
<i>Podocarpoidites ellipticus</i>	-0.20111	-0.088435	0.26176	-0.071457	0.18906	-0.1943	0.36491	0.079202	-0.074511	-0.10605	0.10198	0.024796	0.050153	-0.057847	-0.36156	0.23568	-0.15623	-0.083337	0.20762	0.11902	0.1208
<i>Quadracutina anellaciformis</i>	0.072239	-0.48387	-0.513	0.34531	0.24137	0.52192	0.45957	-0.1095	-0.21941	0.30107	0.13973	0.18915	-0.11218	0.21231	0.096961	0.12133	0.028541	0.2028	-0.02207	-0.035061	-0.25668
<i>Araucarioxites australis</i>	0.071908	0.080066	-0.014772	-0.005021	-0.021989	-0.003841	-0.011914	0.005475	-0.034109	-0.033298	-0.0098602	0.018548	-0.023363	-0.043954	0.041305	0.0044819	-0.026926	0.011547	0.0013515	-0.01787	0.01616
<i>Callialasporites dampieri</i>	-0.098413	0.11351	0.034394	-0.096034	0.05832	0.0638	0.1123	0.058652	-0.014835	-0.014981	0.045778	-0.043947	-0.08963	0.023893	-0.056677	0.014613	0.026311	0.0040766	-0.030393	-0.016234	-0.024582
<i>Callialasporites segmentatus</i>	-0.30659	0.19099	0.7	1.3936	-0.12194	0.09367	0.014047	-0.056977	-0.15744	0.039853	-0.089532	-0.13033	0.32097	0.61871	0.27354	0.12628	-0.17905	-0.51367	-0.68285	0.1585	-0.34584
<i>Callialasporites trilobatus</i>	-0.33248	-0.12141	0.15999	-0.23343	0.63247	-0.095687	-0.5734	0.16678	-0.10562	0.37255	0.49338	0.33445	0.06731	-0.38128	-0.2617	0.21639	0.051446	0.11284	-0.19272	0.31026	-0.062504
<i>Callialasporites turbatus</i>	0.057588	0.055967	0.0005388	-0.005653	-0.018963	0.0026887	0.0034308	0.0012234	-0.031478	-0.018476	0.009679	0.016464	-0.027891	-0.038156	0.010813	0.026977	-0.028567	-0.011322	-0.017036	-0.031489	0.011579
<i>Classopollis torus</i>	0.071908	0.080066	-0.014772	-0.005021	-0.021989	-0.003841	-0.011914	0.005475	-0.034109	-0.033298	-0.0098602	0.018548	-0.023363	-0.043954	0.041305	0.0044819	-0.026926	0.011547	0.0013515	-0.01787	0.01616
<i>Cerebropollenites mesozoicus</i>	0.071908	0.080066	-0.014772	-0.005021	-0.021989	-0.003841	-0.011914	0.005475	-0.034109	-0.033298	-0.0098602	0.018548	-0.023363	-0.043954	0.041305	0.0044819	-0.026926	0.011547	0.0013515	-0.01787	0.01616
<i>Spheripollenites scabratus</i>	0.071908	0.080066	-0.014772	-0.005021	-0.021989	-0.003841	-0.011914	0.005475	-0.034109	-0.033298	-0.0098602	0.018548	-0.023363	-0.043954	0.041305	0.0044819	-0.026926	0.011547	0.0013515	-0.01787	0.01616
<i>Spheripollenites subgranulatus</i>	0.071908	0.080066	-0.014772	-0.005021	-0.021989	-0.003841	-0.011914	0.005475	-0.034109	-0.033298	-0.0098602	0.018548	-0.023363	-0.043954	0.041305	0.0044819	-0.026926	0.011547	0.0013515	-0.01787	0.01616
<i>Perinopollenites etaloides</i>	0.071908	0.080066	-0.014772	-0.005021	-0.021989	-0.003841	-0.011914	0.005475	-0.034109	-0.033298	-0.0098602	0.018548	-0.023363	-0.043954	0.041305	0.0044819	-0.026926	0.011547	0.0013515	-0.01787	0.01616
<i>Chasmatosporites aperius</i>	0.022368	0.055594	0.023122	0.0033727	-0.03043	0.049158	0.036424	0.05423	0.038494	-0.016643	0.053037	-0.0076898	-0.076925	-0.015571	-0.014459	0.03053	0.05867	-0.015892	0.011124	-0.01542	-0.016503
<i>Chasmatosporites huans</i>	-0.41615	-0.37196	0.18497	0.14952	-0.11994	0.036145	0.081095	0.0053388	-0.08949	0.071995	-0.083163	0.11211	-0.16927	0.16529	0.033053	-0.086058	-0.054694	0.16144	-0.072536	-0.072016	-0.021629
<i>Chasmatosporites major</i>	0.78977	0.30743	1.1245	-0.02209	-0.20251	0.22481	0.29209	0.066471	-0.4491	0.18387	0.34735	0.27775	-0.20773	0.2662	-0.26675	-0.2876	0.35298	0.038538	0.15542	-0.38347	0.10757
<i>Cycadopolites minimus</i>	0.071908	0.080066	-0.014772	-0.005021	-0.021989	-0.003841	-0.011914	0.005475	-0.034109	-0.033298	-0.0098602	0.018548	-0.023363	-0.043954	0.041305	0.0044819	-0.026926	0.011547	0.0013515	-0.01787	0.01616
<i>Cycadopolites carpenteri</i>	-0.025431	-0.16047	-0.22483	-0.016797	0.014426	-0.037794	-0.28719	-0.14047	0.090362	-0.057331	-0.028564	0.053821	-0.050281	-0.061247	0.0703	-0.17552	-0.082567	0.13419	-0.06656	0.0065899	0.0008579
<i>Cycadopolites subgranulosus</i>	0.54938	0.41314	-0.38591	0.26808	0.17194	-0.15488	0.086921	0.097143	-0.020703	-0.055054	0.2274	0.008069	0.37324	0.076642	0.011634	-0.051816	0.21305	0.19648	-0.012399	-0.11162	0.13239
<i>Eucommiidites troedsonii</i>	0.06747	0.079018	-0.033959	0.0023282	-0.013779	-0.0013034	-0.032996	-0.0068326	-0.032021	-0.023001	-0.025185	0.013137	-0.019749	0.0765465	0.069964	0.06008	-0.012634	0.019497	-0.0030367	-0.028145	-0.0051261
<i>Striate bisaccate sp.</i>	0.097725	1.3375	3.052	0.051385	-0.037411	1.3986	-0.59398	-0.89649	0.075235	2.2902	-0.63278	-0.93464	0.10305	-0.90139	0.43944	0.37075	-0.23705	0.11244	0.63264	-0.25204	-0.4419

	Axis 23	Axis 24	Axis 25	Axis 26	Axis 27	Axis 28	Axis 29	Axis 30	Axis 31	Axis 32	Axis 33	Axis 34	Axis 35	Axis 36	Axis 37	Axis 38	Axis 39	Axis 40	Axis 41	Axis 42	
HB1	-0.04999	-0.03168	-0.09536	-0.07449	-0.13712	-0.02478	-0.01346	-0.04503	-0.02973	-0.02686	-0.12742	-0.03878	-0.02675	-0.02876	-0.03216	-0.04982	-0.007195	-0.042592	-0.048485	-0.03091	-0.0034285
HB2	-0.16052	0.04886	0.051733	0.08526	0.13708	0.20572	0.09377	0.11616	-0.01156	0.02023	-0.16033	-0.10034	0.1547	-0.0071518	0.03992	0.09679	-0.02571	-0.026175	-0.030358	0.01205	0.0007997
HB3	0.21624	-0.20804	-0.25093	0.14299	0.25881	-0.09308	-0.13013	-0.11826	0.1267	0.0025231	-0.085489	-0.03329	-0.02547	-0.029825	-0.082667	0.050122	-0.04703	0.009786	-0.0085764	-0.043947	-0.0008444
HB4	0.021555	-0.013407	-0.072936	0.011491	-0.011642	-0.19286	-0.034094	0.05719	-0.052692	0.055536	-0.025897	0.006992	0.020567	-0.09771	0.0099775	-0.026605	0.061648	0.008988	0.011179	0.018121	-0.0001993
HB5	0.069456	0.036867	0.12545	-0.10312	-0.026253	0.15146	0.060079	-0.058789	0.04183	-0.0037329	0.025248	-0.023445	0.08399	0.069606	0.033485	0.005731	-0.015782	-0.0089951	-0.014222	-0.0013352	-0.0069773
HB6	-0.006716	0.16007	0.049158	-0.021852	-0.063857	-0.047093	-0.095451	-0.071913	0.012403	-0.018075	0.021782	0.080006	0.029076	-0.010465	-0.0028681	0.062535	0.023705	0.066912	-0.066973	-0.029837	-0.006973
HB7	-0.082311	-0.035539	0.18788	0.023439	0.053856	-0.058901	0.10302	-0.15229	0.016466	0.0358	0.08186	-0.069691	0.024064	-0.088165	-0.013248	0.015181	0.019856	-0.014512	-0.017797	0.016129	0.032048
HB8	0.006312	-0.013239	-0.013101	0.012739	-0.0034116	0.024783	-0.0034529	-0.014902	-0.0074198	-0.0026355	-0.0095434	-0.002641	0.004310	0.002341	0.000665	-0.0033494	-0.0009316	-0.0004724	-0.0021011	0.0021011	0.0021011
HB9	-0.13255	-0.088428	0.0049954	0.12729	-0.002087	-0.087116	-0.090516	0.001752	0.12823	-0.059222	0.10109	0.17384	-0.018046	-0.019483	-0.059902	0.01526	-0.016884	-0.023549	0.044482	-0.0072245	-0.027787
HB10	0.10861	0.030765	-0.007025	0.024844	-0.013336	-0.0043289	-0.0070525	-0.018952	-0.027938	0.0012423	0.015404	-0.0022423	-0.0067748	0.0043803	-0.0013892	0.0034656	0.0027878	0.0025689	0.0011023	0.0021011	0.0021011
HB11	-0.088175	0.0052591	-0.01212	0.035074	0.057944	0.13534	-0.078436	0.16326	-0.0404	0.024747	0.010041	-0.049371	0.036762	-0.053703	-0.0014893	0.09524	-0.0089409	-0.032018	0.0026078	0.0021011	0.0021011
HB12	0.1168	-0.10791	0.081355	-0.039004	-0.18773	-0.0011229	-0.001595	-0.047941	-0.0085708	-0.059416	-0.10672	0.024867	0.032056	-0.0052387	0.025043	0.034747	-0.041149	-0.0045192	0.0072848	0.0077033	0.0077033
HB13	-0.17447	0.082396	0.11067	0.084132	-0.049091	-0.0047099	-0.12157	-0.037141	-0.002626	0.039916	-0.10672	0.024867	0.032056	-0.0052387	0.025043	0.034747	-0.041149	-0.0045192	0.0072848	0.0077033	0.0077033
HB14	-0.033063	-0.047983	-0.022529	0.0574	0.096397	0.04355	-0.05779	-0.02139	0.069612	0.075415	0.013484	0.036264	-0.049878	0.049657	0.11142	0.0065942	-0.039835	0.0085755	0.0074425	0.035784	0.035784
HB15	0.068515	-0.11027	-0.02967	-0.10965	-0.045915	-0.023779	-0.055415	-0.03735	-0.01938	-0.02542	0.028889	0.0061023	0.025436	0.024939	0.13606	0.037764	-0.021135	0.035866	-0.058665	0.048166	0.048166
HB16	-0.004821	-0.10414	0.029256	-0.035201	0.053188	0.093265	0.073465	-0.10607	0.051667	-0.098287	-0.019874	-0.0032926	-0.14908	-0.037638	-0.047557	0.020906	-0.03463	-0.013774	-0.0067783	-0.0042003	0.015439
HB17	-0.023871	-0.094913	0.24587	-0.027272	-0.061359	0.0065479	-0.073035	0.00137	-0.06055	0.087285	0.053907	-0.083077	-0.048032	0.13021	-0.04423	-0.013997	-0.031827	0.041422	-0.0014948	0.0028241	-0.062891
HB18	-0.082015	-0.34245	-0.021083	-0.25532	-0.0081907	-0.038685	-0.001119	0.031404	0.024224	0.017987	-0.11868	0.015439	-0.038603	0.018789	0.05578	0.02442	0.05343	0.045492	0.044575	0.0005615	0.0005615
HB19	-0.015093	0.02702	-0.056398	-0.027367	0.0069524	-0.10438	0.0093797	0.035664	-0.086504	0.049333	-0.046092	-0.058088	-0.017101	-0.02553	0.0044069	0.018028	0.0069513	-0.020584	-0.056771	0.0051802	0.003427
HB20	0.32092	0.050133	0.16515	0.07724	0.14124	-0.04586	0.029571	0.27517	0.030261	-0.061021	0.063003	0.017459	0.058801	-0.016091	-0.095886	-0.058139	-0.0052043	0.0044675	-0.0085179	-0.017369	0.0005605
HB21	0.045072	0.0014257	-0.11159	0.13242	-0.057411	-0.029142	0.059467	0.021554	-0.047667	0.023465	-0.046634	0.11834	-0.01866	0.0058564	0.0087352	0.075928	-0.0098311	0.0055485	0.073578	-0.021881	-0.021881
HB22	-0.14107	0.18075	0.045408	0.0093371	-0.025489	0.039265	0.073465	-0.10607	0.051667	-0.098287	-0.019874	-0.0032926	-0.14908	-0.037638	-0.047557	0.020906	-0.03463	-0.013774	-0.0067783	-0.0042003	0.015439
HB23	-0.19632	0.023758	-0.056511	-0.022388	-0.29352	-0.18839	-0.028516	-0.027678	0.12391	-0.040447	-0.014197	-0.06099	-0.01325	0.033367	0.0091393	-0.057025	-0.032076	-0.037689	-0.033222	-0.063347	-0.0099699
HB24	-0.075398	-0.10536	-0.061919	0.069466	-0.12385	0.066019	0.048229	0.040756	0.043687	0.046268	-0.048882	-0.046469	0.088418	0.012701	-0.037243	-0.03067	0.0040654	-0.022008	-0.0003274	-0.0012213	0.0078205
HB25	0.19868	0.069638	-0.086897	-0.23592	0.030072	0.19323	-0.10031	-0.096742	-0.057948	0.072849	0.012179	0.039152	0.011578	-0.13365	0.081663	0.046793	0.028463	-0.00304	-0.021481	-0.00412	-0.00412
HB26	-0.017754	0.15995	-0.05052	0.14883	-0.044595	-0.03463	-0.073902	-0.14358	-0.065132	-0.05282	0.031206	-0.069043	0.038359	0.037803	0.0013644	0.03131	0.008862	0.089411	0.0087934	0.02715	0.040658
HB27	-0.02585	-0.048766	0.034541	0.051591	-0.007621	-0.01793	0.083921	0.0041445	0.012684	0.02288	0.12911	-0.031398	0.035413	0.04813	0.002188	0.082304	0.034721	0.030485	-0.025562	-0.0042381	-0.010634
HB28	0.052494	0.0041893	-0.023236	-0.09923	0.077515	0.011607	0.004002	-0.039437	-0.025813	0.10676	-0.035856	0.030244	-0.0082257	0.039963	-0.085951	-0.0016484	-0.0064666	-0.030448	0.009837	-0.006547	-0.022445
HB29	-0.10669	0.018075	-0.087399	-0.047626	-0.0066219	-0.0056513	0.075073	-0.082586	-0.085787	-0.052177	-0.073992	-0.029446	-0.0038066	-0.054781	0.022868	-0.055116	-0.05809	-0.051272	-0.012272	-0.028397	-0.0098936
HB30	-0.041726	-0.033233	0.040237	-0.05078	-0.0084573	-0.065561	-0.059671	-0.034726	-0.017552	0.0062468	0.0017225	-0.33E-05	0.0092803	0.0099755	-0.0046408	-0.0037265	0.0003884	-0.0036655	0.0062387	0.0021908	0.0024409
HB31	0.032259	-0.026206	0.0014127	0.076738	-0.070651	-0.022986	0.10587	-0.01261	0.028465	0.016062	-0.005603	-0.0021556	-0.00012663	-0.0054957	0.0059004	-0.0015648	-0.0017631	0.0037849	0.0029591	0.0001613	-0.0002386
HB32	0.044987	0.028218	0.036055	0.032582	0.044513	0.0057128	-0.082335	-0.0042843	-0.017537	0.016857	0.0056933	0.0057278	-0.012063	0.0086389	0.012147	0.013713	-0.0054275	0.0070587	0.0030745	0.0011951	0.0003657
HB33	0.008957	0.11022	-0.093209	-0.095834	-0.097668	0.021583	-0.20045	0.10815	0.089062	0.043536	0.01187	-0.05623	0.022028	-0.0092845	-0.056731	0.032971	-0.020341	-0.019147	-0.019162	0.014603	0.013526
HB34	-0.13064	-0.041669	0.004486	0.0081497	0.013954	0.13007	-0.023999	0.037697	0.013859	0.025773	0.03925	0.03647	-0.056562	0.025566	-0.045511	-0.041361	0.044994	0.0062372	0.001794	-0.048919	-0.048919
HB35	-0.009107	-0.072014	-0.12791	-0.055041	-0.008905	0.035635	0.094434	-0.020902	-0.032697	0.10634	0.011005	0.031526	-0.022356	-0.011885	-0.0523369	0.049075	-0.015322	-0.0015322	0.0052761	-0.039805	0.044018
HB36	0.27847	0.17838	0.15807	0.005164	0.07289	-0.048525	0.0019653	0.0070988	0.11835	0.045503	-0.008392	0.015401	-0.084886	-0.0064367	0.030862	-0.054477	0.04889	-0.038199	0.0051045	0.049858	-0.013462
HB37	-0.029059	-0.04311	0.048788	0.071094	-0.086153	0.12651	-0.068556	-0.14374	-0.05092	0.0048919	0.024569	-0.0039089	-0.011831	-0.030449	-0.056498	-0.035939	0.0012919	0.032595	0.014599	0.049609	0.049609
HB38	-0.13957	0.13183	-0.20279	-0.011429	0.12821	-0.15777	-0.0081846	-0.020635	-0.047004	-0.019563	-0.005923	-0.028167	0.08135	-0.019277	-0.064329	0.0572	0.0070343	-0.019233	0.02606	-0.019395	-0.019395
HB39	0.078821	-0.051345	-0.0077386	-0.031984	-0.12174	0.022072	0.11177	0.075346	-0.0032733	-0.054007	-0.012466	-0.01107	-0.039508	-0.033808	-0.0013794	-0.0015178	0.020401	-0.0005908	0.0087022	0.0087258	0.0087258
HB40	0.16701	0.056386	0.080609	-0.0013843	0.012321	0.082023	0.016823	-0.071395	0.050464	0.033981	-0.057723	0.028938	0.04781	-0.017281	-0.010774	-0.013846	-0.024986	0.025407	0.061209	-0.0071405	-0.0004618
HB41	0.1045	0.039832	-0.11114	0.15868	-0.063876	-0.027641	0.080043	0.050313	-0.13406	0.02448	-0.036308	0.09771	-0.024312	0.078665	0.040855	-0.02478	-0.068075	-0.014817	-0.056018	-0.029307	-0.0092046
HB42	0.018719	-0.084523	0.034222	0.003785	0.039362	0.048314	-0.043568	0.000275	-0.03376	-0.16103	-0.0059469	-0.02036	-0.01773	0.0222576	0.093914	-0.0028838	0.024135	-0.0067568	-0.016129	-0.0036236	-0.019188
HB43	-0.14854	0.090459	0.095614	-0.092754	-0.048853	-0.046094	0.01841	-0.054772	0.046888	0.05317	-0.051235	0.075229									

	Axis 22	Axis 23	Axis 24	Axis 25	Axis 26	Axis 27	Axis 28	Axis 29	Axis 30	Axis 31	Axis 32	Axis 33	Axis 34	Axis 35	Axis 36	Axis 37	Axis 38	Axis 39	Axis 40	Axis 41	Axis 42
HB44	0.063405	-0.045639	0.035268	-0.013738	0.068336	0.025008	0.123999	-0.093726	0.066407	0.049199	0.030313	0.018973	0.009478	-0.014258	-0.037946	-0.051584	-0.005948	0.003892	-0.063613	0.032348	0.018174
HB45	-0.071003	0.022975	-0.090049	-0.202296	-0.135755	-0.16655	0.084292	0.008875	-0.006715	-0.039888	0.075157	-0.032288	0.06311	0.071816	0.032398	0.003393	-0.060436	0.008886	0.053998	0.022991	0.053635
HB46	-0.021043	0.062864	-0.033104	-0.038633	-0.139223	-0.083054	0.040331	-0.12771	-0.049626	-0.007701	-0.043817	-0.038103	-0.007692	-0.039192	-0.007692	-0.032565	0.081134	0.002513	-0.030409	-0.050246	-0.050246
HB47	-0.040873	-0.021997	-0.069974	0.074148	0.026668	-0.010538	0.11594	0.040697	0.035471	0.066866	0.035471	0.05622	0.003508	-0.006453	0.004191	-0.032565	0.081134	0.002513	-0.030409	-0.050246	-0.050246
HB48	-0.020034	-0.091458	0.06762	0.10192	0.13937	-0.002588	0.1751	-0.037011	-0.038413	-0.0076159	-0.003526	-0.007377	0.019839	-0.036468	0.0071865	-0.08134	0.032594	0.038604	-0.011913	-0.002365	0.013759
HB49	-0.077405	-0.1022	0.13937	-0.002588	0.1751	-0.037011	-0.038413	-0.0076159	-0.003526	-0.007377	0.019839	-0.036468	0.0071865	-0.08134	0.032594	0.038604	-0.011913	-0.002365	0.013759	0.027785	0.027785
HB50	0.087538	0.011592	0.13182	0.087678	-0.10719	-0.040892	-0.014834	0.035552	0.17315	0.022785	-0.0071884	0.0664109	0.018952	0.0057071	0.10223	0.039656	0.016125	0.052106	0.001108	-0.014717	0.011965
Taxon scores																					
<i>Rogalskisporites crenatosus</i>	0.27682	-0.71206	0.33012	0.40393	-0.12306	0.036264	0.24695	0.15148	-0.52132	0.54428	0.1819	-0.051353	0.10895	-0.077432	0.077389	0.055357	0.0090354	0.014024	-0.07164	-0.016845	-0.034403
<i>Neveskisporites bigrammus</i>	0.088684	-0.14474	0.22508	0.22264	-0.16381	0.058005	0.13801	0.14577	-0.11443	-0.19212	-0.15922	-0.011674	-0.2832	-0.08762	-0.073773	-0.042745	-0.010292	0.013633	0.031825	0.012483	0.006411
<i>Angulatisporites sp.</i>	0.14325	0.32123	-0.15948	-0.27461	-0.27116	-0.21911	0.03302	0.038359	0.082203	0.051318	-0.10586	0.018558	-0.038021	-0.10711	0.028310	-0.054034	-0.022804	0.0098063	0.012483	0.006411	0.006411
<i>Densokisporites viduus</i>	-0.16073	0.0654859	0.27569	-0.24369	-0.29126	-0.073508	0.007928	0.070077	-0.047822	-0.023124	0.029842	0.005067	0.078874	-0.097997	0.010547	-0.01359	0.059631	0.010547	-0.01359	0.059631	0.059631
<i>Densokisporites viduus</i>	0.0228	0.31508	-0.077556	0.28697	-0.15926	-0.054219	-0.093502	0.23746	-0.38837	0.27099	0.29826	0.28476	-0.044721	-0.034848	-0.13027	0.11063	-0.04005	-0.10547	0.08991	0.099085	0.046262
<i>Lycopodioides cernitoides</i>	-0.046827	0.049468	0.09173	0.015934	0.05293	0.024134	0.097188	0.096454	0.015638	0.028103	-0.073556	0.075166	-0.020494	0.023997	0.020538	0.022236	-0.018079	0.062247	0.016195	0.033576	-0.032151
<i>Lycopodioides rugulatus</i>	0.42367	0.289	0.39753	0.37635	0.33272	0.071554	-1.09116	-0.058202	0.24859	0.26461	0.10091	0.10588	-0.2406	0.18454	0.26944	0.34635	-0.15647	0.21482	0.099157	0.04662	0.015346
<i>Neovratiscia truncatus</i>	0.42856	0.12013	0.28952	-0.52918	-0.22676	-0.258	0.17225	-0.018665	-0.081571	0.24969	-0.0057438	-0.12428	-0.02878	-0.099449	0.18785	0.086884	-0.084515	-0.11689	0.035219	0.061707	-0.022202
<i>Retrioides auroleavaldites</i>	0.30381	-0.26839	0.0115576	0.88663	-0.84553	-0.2879	0.14036	-0.1713	0.04349	0.25213	-0.089733	-0.039848	-0.025238	-0.11739	0.13088	-0.039522	-0.05829	0.11518	0.095434	0.0062198	-0.089756
<i>Retrioides clavuloides</i>	-0.052107	0.010822	0.032253	-0.11181	-0.037113	-0.002562	0.88999	-0.1384	0.030404	0.0049001	0.11204	0.082784	-0.032845	0.09359	0.033847	0.056666	0.075107	0.0011302	0.015499	0.022945	-0.025606
<i>Retrioides seminaris</i>	0.079591	-0.063445	-0.13466	-0.013295	0.12482	-0.075123	-0.057993	0.07016	0.093758	0.036111	-0.006904	0.013516	-0.036403	0.069832	0.013117	-0.016292	-0.034287	0.070431	-0.082734	-0.00797	-0.011386
<i>Leptolepidites bosius</i>	0.0519	-0.49511	-0.22953	-0.13057	-0.58182	0.043846	0.47645	-0.32986	-0.19504	0.115	-0.053759	0.094845	0.027053	-0.02127	-0.11032	-0.01116	-0.020268	-0.033622	0.03208	-0.042308	0.033235
<i>Leptolepidites equatibosus</i>	-0.17604	-0.29852	-0.067866	0.055387	0.008028	-0.086166	-0.081399	0.2031	0.099971	-0.039712	-0.07428	-0.05074	0.051663	0.10823	-0.0018311	0.051628	-0.052047	0.023189	-0.047018	-0.0056993	0.0077459
<i>Leptolepidites major</i>	-0.065899	-0.20495	-0.013375	-0.21186	-0.039985	0.082554	0.012792	-0.091783	-0.18005	0.049749	-0.15252	-0.040187	0.086121	-0.077155	0.0252067	-0.013332	-0.014194	-0.051802	-0.024135	0.0077459	0.0077459
<i>Serpentisporites crassiballus</i>	-0.39296	-0.34056	0.44364	-0.58656	-0.10121	-0.82116	-0.79112	-0.47176	-0.2488	0.09806	0.030529	-0.001724	0.18509	0.21309	-0.10294	-0.074516	-0.01108	-0.11155	0.20282	0.084501	0.10244
<i>Serpentisporites pseudobivallus</i>	0.21053	-0.10121	-0.15163	0.091743	-0.17652	0.12092	0.023603	0.069982	0.1581	0.04803	0.069071	0.021232	0.028061	-0.071109	0.052667	-0.024516	-0.008618	-0.0024948	-0.017438	-0.01425	-0.006151
<i>Staphisporites sp.</i>	0.13247	0.07029	-0.069724	0.030381	-0.011086	0.33108	-0.022004	-0.018714	-0.0012158	-0.10113	-0.0654798	-0.023663	-0.10665	0.022667	0.05574	-0.0052106	-0.052414	-0.01174	0.022985	-0.028324	0.04985
<i>Uvaeosporites argenteiformis</i>	-0.32256	0.0056328	-0.13804	0.054059	0.10726	0.069618	-0.090283	0.07655	-0.019318	0.24819	-0.0008716	-0.017248	-0.053872	-0.11562	0.06257	0.041667	-0.050991	0.059877	0.051581	-0.0031338	0.034648
<i>Calamospora mesozoaica</i>	0.051252	-0.040238	-0.050479	0.013613	0.020201	0.021273	-0.030935	0.085601	0.030673	-0.0087856	-0.0074815	-0.0025334	-0.037403	0.02496	0.0059596	0.012894	-0.066032	-0.0043835	-0.032214	0.043701	0.0064937
<i>Manatisporites scabratus</i>	0.015928	-0.018672	-0.008938	0.056044	0.026657	0.004567	-0.0019819	0.015939	0.017703	-0.0066885	0.01631	-0.015806	0.007377	-0.0016427	-0.012825	-0.002236	0.006613	0.0063158	-0.0006812	0.0002728	0.0081941
<i>Baculatisporites conamensis</i>	-0.23136	0.15346	-0.26298	0.042498	0.049006	-0.16992	0.07368	-0.17386	-0.14457	-0.011574	-0.042392	0.020838	-0.12714	0.016913	-0.094596	0.018409	0.060028	-0.007929	0.012854	-0.024127	0.0011925
<i>Osmundacidites waldmanni</i>	0.0028699	-0.04902	0.15083	0.099472	-0.106	-0.01572	-0.0020251	-0.099872	-0.12606	-0.042223	0.064096	0.012742	0.027461	-0.013863	-0.019157	0.03229	-0.038951	0.044273	-0.013323	-0.021978	-0.038744
<i>Taliopterites minor</i>	0.0018463	0.13991	-0.11553	0.064781	-0.22586	-0.026474	-0.18775	0.072258	-0.15774	-0.09242	0.054728	0.035394	0.019557	-0.007776	-0.0097065	-0.07866	-0.078315	-0.041156	0.016202	0.000101	-0.014609
<i>Taliopterites major</i>	-0.11179	-0.1381	-0.092914	-0.14398	0.05077	0.16503	0.01203	0.074256	-0.073672	-0.075111	-0.028872	0.057004	0.02771	-0.0086666	0.016423	-0.046316	0.064889	0.012105	0.020453	0.0058061	-0.034594
<i>Gluchonidites xenonius</i>	-0.059562	0.32898	-0.013675	-0.094807	-0.48143	0.17943	0.081422	0.084752	0.1888	0.15052	0.071342	0.25901	-0.048663	0.011043	0.025419	0.033949	0.035581	0.075134	0.036506	0.025197	-0.078833
<i>Conbaulatisporites mesozoicus</i>	-0.10219	0.27186	0.18853	-0.032273	0.0042271	0.15908	0.024921	-0.091053	-0.026623	0.1372	-0.045103	-0.09121	-0.006099	0.023234	-0.018763	-0.071743	-0.011737	-0.001494	0.020009	-0.04873	-0.0212
<i>Dicypophylloides harrisi</i>	0.032433	-0.01312	0.0038107	0.013435	-0.016521	-0.006129	0.0049875	0.014867	0.013733	0.0035857	0.015428	-0.020145	-0.05605	-0.0055549	-0.0047982	0.0032607	0.0029679	0.0013874	0.0007548	0.0027302	0.0065783
<i>Dicypophylloides equitatus</i>	-0.0094175	-0.040744	-0.099402	0.0091122	0.024408	0.047388	-0.013066	-0.080637	-0.056795	-0.0033303	0.014306	-0.061684	-0.030175	0.014562	0.004128	-0.022004	-0.02177	-0.053554	0.04409	0.04494	-0.003676
<i>Concavosporites sp.</i>	0.051578	-0.0092475	0.041783	-0.055447	0.089845	-0.028786	-0.018435	0.069090	0.01191	-0.037201	0.039717	-0.041471	-0.036228	0.014892	0.05871	-0.008873	-0.017481	0.036087	-0.071492	-0.050502	0.050502
<i>Manonisporites phillopteroides</i>	0.059445	0.1426	-0.14664	-0.15133	0.15245	-0.04273	0.032857	-0.046907	0.21124	-0.11647	-0.041889	-0.17276	-0.091883	-0.008576	0.056607	0.0071755	0.019171	-0.10193	-0.030045	-0.011822	0.088182
<i>Manonisporites phillopteroides</i>	0.171535	0.42711	-0.15622	-0.16605	0.11533	-0.14004	0.1737	-0.2427	-0.25544	0.1205	-0.11548	-0.26943	-0.088107	-0.070617	0.052819	-0.25996	0.074756	0.01558	-0.037805	0.062223	
<i>Concavosporites sp.</i>	0.12179	0.12617	0.16025	0.09947	-0.091933	-0.12709	-0.18239	-0.082626	0.14442	-0.20266	-0.11331	-0.039274									

	Axis 22	Axis 23	Axis 24	Axis 25	Axis 26	Axis 27	Axis 28	Axis 29	Axis 30	Axis 31	Axis 32	Axis 33	Axis 34	Axis 35	Axis 36	Axis 37	Axis 38	Axis 39	Axis 40	Axis 41	Axis 42
<i>Alloporicia thomasi</i>	0.013396	0.050784	0.070737	-0.078994	-0.045174	0.085461	0.017945	0.055689	-0.025277	-0.053283	-0.050976	0.10542	0.022934	0.11239	0.017017	0.022314	-0.018877	0.025594	-0.05328	-0.018288	0.01546
<i>Lineosporites pallidus</i>	-0.067333	-0.029889	-0.02199	0.008829	0.052818	0.080571	-0.121	-0.13272	-0.076569	0.080301	-0.089057	0.06708	-0.03041	-0.029255	-0.057871	-0.046916	-0.011718	-0.028559	-0.071912	-0.0068873	-0.015039
<i>Physosporites microdinus</i>	0.032433	-0.01312	0.0038107	0.013435	0.016521	-0.006129	0.0049875	0.014867	0.013732	0.0035857	0.015428	-0.020145	0.005606	-0.0055549	-0.0047982	0.0032607	0.0029679	0.0013874	0.0007548	0.0027302	0.0065783
<i>Physosporites minimus</i>	-0.12026	0.046289	-0.12099	0.14574	0.043747	-0.063863	0.097874	-0.11268	0.10214	-0.037382	0.0017943	0.043655	0.12704	0.026107	-0.026952	0.080754	-0.046909	-0.046568	0.001769	0.047676	0.02281
<i>Podocarpites ellipticus</i>	0.030642	0.020716	0.08102	0.004083	-0.013523	0.073481	-0.15017	0.020271	0.017916	0.020621	0.044879	-0.040727	0.060235	0.030731	-0.045048	0.065299	-0.087761	-0.0064935	0.047559	-0.042325	
<i>Quadracaulina meliogramis</i>	-0.19468	-0.059024	0.013402	0.1378	-0.087899	0.01511	-0.20588	0.090855	0.20133	-0.05167	0.059008	0.12129	0.11646	0.0060646	-0.14875	-0.10071	-0.085472	-0.012565	0.015321	0.0034872	0.014541
<i>Araneosporites australis</i>	0.032433	-0.01312	0.0038107	0.013435	0.016521	-0.006129	0.0049875	0.014867	0.013732	0.0035857	0.015428	-0.020145	0.005606	-0.0055549	-0.0047982	0.0032607	0.0029679	0.0013874	0.0007548	0.0027302	0.0065783
<i>Callialosporites dampieri</i>	0.04225	0.025192	0.069799	-0.066366	-0.051604	-0.025861	0.066978	0.015083	-0.0015991	-0.013025	0.064026	0.064617	-0.041273	-0.0069973	0.0001789	-0.048878	0.047395	0.025886	0.021431	0.003576	0.0063124
<i>Callialosporites segmenianus</i>	0.18201	0.0019452	-0.01593	-0.080201	-0.10865	-0.015396	0.10412	0.21575	0.21222	0.067609	-0.052029	-0.15234	0.057904	-0.051523	0.054186	0.0048038	0.011829	-0.05E-05	-0.024017	-0.021373	-0.049385
<i>Callialosporites trilobatus</i>	-0.044014	0.29021	-0.018169	-0.20168	-0.073308	-0.06364	0.10741	-0.10084	0.20222	-0.08326	-0.15663	-0.045507	0.039784	-0.015523	-0.0065216	-0.046602	0.0014591	0.014289	0.016808	0.038241	-0.022011
<i>Callialosporites turbatus</i>	0.063947	-0.03113	-0.007523	-0.0063909	-0.01622	-0.058839	-0.020282	-0.017034	0.017355	-0.0030118	0.073735	0.017298	-0.057246	-0.0025505	-0.022592	-0.046506	0.0169	0.017673	0.020752	-0.0060342	0.0060276
<i>Classopollis tonsus</i>	0.032433	-0.01312	0.0038107	0.013435	0.016521	-0.006129	0.0049875	0.014867	0.013732	0.0035857	0.015428	-0.020145	0.005606	-0.0055549	-0.0047982	0.0032607	0.0029679	0.0013874	0.0007548	0.0027302	0.0065783
<i>Cerebropollenites mesozoicus</i>	0.032433	-0.01312	0.0038107	0.013435	0.016521	-0.006129	0.0049875	0.014867	0.013732	0.0035857	0.015428	-0.020145	0.005606	-0.0055549	-0.0047982	0.0032607	0.0029679	0.0013874	0.0007548	0.0027302	0.0065783
<i>Sphaeripollenites scabratus</i>	0.032433	-0.01312	0.0038107	0.013435	0.016521	-0.006129	0.0049875	0.014867	0.013732	0.0035857	0.015428	-0.020145	0.005606	-0.0055549	-0.0047982	0.0032607	0.0029679	0.0013874	0.0007548	0.0027302	0.0065783
<i>Sphaeripollenites subgranulatus</i>	0.032433	-0.01312	0.0038107	0.013435	0.016521	-0.006129	0.0049875	0.014867	0.013732	0.0035857	0.015428	-0.020145	0.005606	-0.0055549	-0.0047982	0.0032607	0.0029679	0.0013874	0.0007548	0.0027302	0.0065783
<i>Perinipollenites etadoides</i>	0.032433	-0.01312	0.0038107	0.013435	0.016521	-0.006129	0.0049875	0.014867	0.013732	0.0035857	0.015428	-0.020145	0.005606	-0.0055549	-0.0047982	0.0032607	0.0029679	0.0013874	0.0007548	0.0027302	0.0065783
<i>Chamaesporites aperius</i>	0.075088	-0.025064	0.013985	-0.02443	0.017219	-0.006532	-0.017074	-0.0030134	0.026332	-0.011769	0.032822	0.032593	-0.047334	-0.015906	-0.037909	-0.02126	0.01682	0.045045	0.017928	-0.030381	0.0091508
<i>Chamaesporites hians</i>	0.13548	-0.063093	-0.23148	-0.15386	-0.065126	-0.10182	-0.038749	-0.065203	-0.10408	0.088185	-0.13902	0.053771	0.14711	-0.11259	-0.09886	0.034082	-0.053318	0.085048	0.025169	0.022797	-0.053826
<i>Cycadites major</i>	0.032433	-0.01312	0.0038107	0.013435	0.016521	-0.006129	0.0049875	0.014867	0.013732	0.0035857	0.015428	-0.020145	0.005606	-0.0055549	-0.0047982	0.0032607	0.0029679	0.0013874	0.0007548	0.0027302	0.0065783
<i>Cycadites minimus</i>	0.20323	0.11132	-0.1274	0.0024855	0.010713	0.12594	-0.11424	-0.043452	-0.037627	-0.036332	-0.012302	-0.019234	0.08692	-0.028268	-0.0065477	0.056026	0.082286	0.022082	0.028941	0.002702	0.0049833
<i>Cycadites carpentieri</i>	-0.16997	0.24602	-0.02167	0.261	0.032491	-0.028394	0.071474	-0.052064	-0.025241	-0.14694	0.091415	-0.052726	-0.020226	-0.027568	0.055183	-0.030694	0.012268	0.026256	-0.063889	0.022322	-0.046365
<i>Cycadites subgranulatus</i>	0.036507	-0.04682	0.011776	-0.021374	0.02775	0.0025978	0.025085	0.054978	0.032855	0.020728	0.0044553	0.0054913	-0.0098939	-0.022148	-0.005137	-0.012811	-0.0080687	-0.054116	-0.0050175	-0.018586	-0.028111
<i>Eucommioidites troidsonii</i>																					
<i>Straatbuxcateae sp.</i>	-0.87609	0.17211	0.41968	0.4951	-0.3402	-0.14178	-0.2562	-0.22413	-0.09173	0.13996	0.19844	-0.077007	-0.19436	-0.078915	0.031589	0.11326	0.15512	-0.045172	-0.032173	-0.026529	0.025538

	Axis 43	Axis 44	Axis 45	Axis 46	Axis 47	Axis 48	Axis 49
HB1	-0.010739	0.013972	-0.0006226	-0.0016441	-0.010061	0.0003481	-0.0029868
HB2	0.041777	-0.019853	-0.0020337	-0.0072139	0.0025206	-0.0042752	0.0008441
HB3	-0.039011	-0.0033053	-0.0001821	0.0077112	0.011515	-0.0011554	-0.0008441
HB4	0.033063	-0.025277	-0.014943	-0.020401	0.013141	-0.0037023	0.0027045
HB5	-0.033442	0.025427	0.014244	0.019273	-0.012811	0.004122	-0.0027526
HB6	-0.0004156	0.013113	0.0009358	-0.0016581	-0.0030044	0.017084	-0.0086738
HB7	-0.038718	-0.010248	0.014671	-0.0034743	-0.0023259	-0.012626	0.008614
HB8	-0.0013127	0.0001544	0.0001005	-0.0006223	0.0004416	-0.0001457	-3.48E-06
HB9	-0.024065	-0.0076513	0.0038268	-0.00015127	0.016673	-0.0099605	0.0029931
HB10	-0.0007197	-0.0014723	0.0002364	-0.0003954	-0.0001874	0.0001585	-1.00E-05
HB11	0.015125	0.031383	0.011309	0.0015949	0.0027569	0.0082074	0.0043805
HB12	0.02741	0.010542	0.002163	0.0099288	-0.0033912	-0.0067756	0.0036272
HB13	-0.030149	0.0101	-0.0019483	0.020066	0.0040177	-0.0028205	-0.0006678
HB14	0.018202	-0.037628	0.033185	-0.0038083	0.0094072	0.0029186	0.0011365
HB15	0.037093	0.0070553	0.024742	-0.0004933	-0.0069665	0.0082716	-0.0028103
HB16	-0.0019835	0.0075521	-0.021691	0.025783	-0.02171	-0.010371	0.0076096
HB17	0.011415	-0.034572	-0.018906	0.0078233	0.033698	-0.0017542	0.0053227
HB18	-0.021884	0.013321	-0.0040871	-0.014218	-0.0090454	-0.01414	-0.0093914
HB19	-0.031155	0.0021523	0.0031201	0.0068914	-0.0086548	0.007702	-0.0029698
HB20	-0.02549	-0.0005184	-0.0051928	-0.019667	0.0024574	-0.0042622	-0.0055746
HB21	0.017194	0.02882	-0.01556	0.023512	0.0003165	0.018591	0.0052068
HB22	0.026028	0.013563	-0.0078369	-0.046355	-0.0051677	-0.0027128	-0.010008
HB23	0.051535	0.0007449	-0.0081397	0.015181	-0.0072284	0.0016163	0.0038552
HB24	-0.023274	0.018057	0.036334	-0.023153	0.014658	0.010328	0.002228
HB25	0.027595	-0.0012252	0.010839	0.011123	0.004225	-0.0054876	0.0008197
HB26	-0.021009	-0.020662	-0.0002314	0.014613	-0.0057953	-0.0067891	-0.0024877
HB27	0.034179	-0.0089296	3.54E-05	-0.019483	-0.0035689	0.0032736	0.0005873
HB28	0.0044681	-0.039345	0.004302	-0.012765	-0.028289	5.00E-05	0.0033783
HB29	-0.0098132	-1.27E-06	-0.01351	0.0057509	0.028993	-0.0008857	0.0017788
HB30	0.0016491	-5.20E-05	0.0001029	-0.0002852	-6.91E-06	-0.0002231	0.0001038
HB31	0.0022209	0.0010745	-0.0004075	-0.0005172	3.66E-05	-2.07E-05	-2.90E-05
HB32	-0.0006394	0.0003436	-0.0011165	-0.001272	-3.91E-05	-5.54E-06	7.13E-05
HB33	-0.0012015	-0.0001874	-0.019082	0.0043661	0.0027981	-0.0085438	-0.0078119
HB34	-0.0050274	-0.017549	0.0005598	0.0079417	-0.015505	-7.59E-05	-0.0062353
HB35	-0.019223	0.006386	-0.00018525	-0.017377	0.018218	0.007024	0.0024831
HB36	0.0048844	0.0077176	0.022151	0.0023651	-0.0038436	0.0064492	0.0014934
HB37	0.02348	-0.028816	-0.020089	-0.0069894	-0.029461	0.012648	0.0009993
HB38	-0.023388	-0.0019992	-0.0046373	0.0029688	0.0020865	-0.0066183	0.0062068
HB39	-0.007299	-0.036773	0.013671	0.015982	0.0026042	0.002806	0.0014754
HB40	0.028927	-0.0005846	-0.0020954	-0.0073112	0.0096122	-0.0075645	0.0029387
HB41	-0.0053892	-0.0073608	0.01723	0.0073818	0.0033093	-0.026458	-0.0093339
HB42	-0.040637	-0.028104	-0.026413	-0.0098739	0.0093012	0.016375	-0.0037264
HB43	-0.014261	-0.013789	0.003275	0.0096585	-0.0013348	0.0068979	0.0002519

	Axis 43	Axis 44	Axis 45	Axis 46	Axis 47	Axis 48	Axis 49
HB44	0.011242	0.032457	-0.046668	0.0036073	0.0040524	-0.0040853	0.0022336
HB45	-0.017062	0.0064532	-0.0015131	-0.0043546	0.0014036	0.0063136	0.0018111
HB46	-0.015772	0.028479	0.018254	-0.019904	-0.017912	-0.0096038	0.011805
HB47	0.020304	0.0030384	0.0008691	0.025275	0.0003767	-0.0015171	-0.00721
HB48	0.0063035	0.057273	-0.012562	-0.015796	-0.0016151	-0.0028224	-0.0015172
HB49	0.032345	0.01942	0.024763	0.018236	0.016333	0.0010671	-0.0057462
HB50	-0.014456	0.0073111	-0.011978	-0.010935	-0.0075508	-0.004165	0.0036304
Taxon scores							
<i>Regalsia</i> sp. <i>creaticosa</i>	-0.021841	0.013303	0.036627	0.0066305	0.046852	-0.009926	-0.0044045
<i>Nevesia</i> sp. <i>bigranulata</i>	-0.011224	-0.024222	0.029437	0.0021266	0.023105	0.0021497	-0.0042035
<i>Anapicalia</i> sp. sp.	0.036243	-0.0047812	0.0032613	-0.016801	-0.028098	0.011643	0.005814
<i>Densia</i> sp. <i>velata</i>	-0.0003629	-0.014989	-0.0052406	-0.01297	0.015231	0.0045015	-0.0010462
<i>Densia</i> sp. cf. <i>velata</i>	-0.031579	-0.078328	0.015619	-0.02818	-0.01538	0.019228	-0.0021141
<i>Lycopodiaceae</i> <i>cernuities</i>	-0.046155	0.03305	-0.016153	0.036611	-0.011135	-0.0016425	0.0013334
<i>Lycopodiaceae</i> <i>rigulatus</i>	-0.028038	0.018278	-0.07375	-0.090657	-0.0032119	-0.0006716	0.015052
<i>Neorisotria</i> <i>truncata</i>	-0.052182	0.0039986	-0.0231	-0.040185	0.013523	0.025451	-0.0050864
<i>Retrirea</i> <i>anselavandites</i>	0.097456	0.057164	-0.026919	-0.036862	0.0030026	-0.0025063	-0.0061271
<i>Retrirea</i> <i>clavata</i>	-0.015159	-0.020197	0.014397	0.0096915	-0.0013219	0.0021042	-0.0086144
<i>Retrirea</i> <i>sommaris</i>	0.0044668	0.007778	0.052059	0.021429	-0.005159	-0.0091106	-0.0012694
<i>Leptolpidia</i> <i>bosius</i>	0.027643	-0.0036986	-0.0040643	-0.013871	-0.014711	0.0050627	-0.002836
<i>Leptolpidia</i> <i>equatibosius</i>	0.012676	-0.0003391	-0.0050452	-0.01071	0.007918	0.0030585	-0.0034372
<i>Calamospira</i> <i>mesozoea</i>	0.015137	0.028191	0.0026048	-0.001338	-0.0079704	-0.0004821	0.0005974
<i>Leptolpidia</i> <i>major</i>	0.072362	-0.0027651	0.0067958	-0.020329	-0.0005671	-0.027067	0.021913
<i>Scirpopsis</i> <i>psuedobrevilata</i>	0.017331	-0.007268	-0.018576	-0.002112	0.0097801	0.010918	-0.002548
<i>Staphisporites</i> sp.	-0.028179	-0.021652	-0.012171	0.011549	-0.015897	0.00553	0.0058651
<i>Uvaeopsis</i> <i>argenteiformis</i>	-0.0077919	0.0079281	-0.013742	-0.0033579	0.030512	0.0006717	-0.0037082
<i>Calamospira</i> <i>mesozoea</i>	0.033127	-0.0031688	-0.024613	0.0010208	0.0048312	-0.013531	-0.0019859
<i>Marattiasporites</i> <i>scabratus</i>	-0.0004737	-0.0001594	-0.0021726	-0.0049254	-0.0048448	-0.0033242	-0.0020366
<i>Baculatisporites</i> <i>comataensis</i>	0.01957	0.025731	-0.010257	5.71E-05	-0.011169	-0.0002243	-0.0044209
<i>Obanulacidae</i> <i>welhamii</i>	0.038456	0.019557	-0.033498	0.012378	-0.014052	-0.009318	-0.0021971
<i>Tetrasporites</i> <i>major</i>	-0.047881	-0.013345	0.033495	-0.027371	-0.0066929	-0.0096974	-4.88E-05
<i>Tetrasporites</i> <i>minor</i>	-0.02788	-0.023358	-0.01722	-0.018224	0.013097	-0.014102	-0.007605
<i>Gleichenioides</i> <i>senonensis</i>	0.028682	-0.0032966	0.010859	0.0044435	-0.027535	-0.014079	0.010575
<i>Conbaulacisporites</i> <i>mesozoeus</i>	-0.0057478	-0.0003823	0.01196	-0.0044226	0.0060083	-0.011343	-0.0076208
<i>Dicropophyllidites</i> <i>harrisii</i>	-0.0025421	6.88E-06	-0.0030097	-0.0063357	-0.0041101	-0.0021732	-0.0021586
<i>Dicropophyllidites</i> <i>equatius</i>	0.047373	0.0081596	0.016535	0.026004	0.0070122	-0.007626	0.0049447
<i>Concisporites</i> sp.	0.038999	-0.050678	0.012794	0.003302	-0.0095577	-0.0018396	0.0023025
<i>Maionisporites</i> <i>phleboteroides</i>	-0.057603	0.0082167	0.0066359	-0.04435	0.036237	-0.017676	-0.0007355
<i>Maionisporites</i> cf. <i>phleboteroides</i>	-0.048877	0.041703	0.033847	-0.01496	0.039281	0.0083427	-0.0032864
<i>Concisporites</i> sp.	-0.0014531	0.014208	-0.015019	-0.013767	-0.003682	-0.0044647	0.0025485
<i>Duplexporites</i> <i>proharmaticus</i>	-0.02802	-0.023896	0.0052051	-0.0061738	-0.010992	0.0016034	0.0071632
<i>Ischyrosporites</i> sp.	0.034736	0.016608	0.030568	-0.012917	-0.023409	0.0040936	0.0012438
<i>Cibicidespora</i> <i>jerriensis</i>	-0.024231	0.0032737	0.0019829	0.024246	-0.0038632	0.010468	0.0066951
<i>Obusisporites</i> <i>canadensis</i>	0.028714	-0.014021	-0.0038784	0.013658	-0.011892	0.0071619	-0.0022048
<i>Concisissimporites</i> <i>subgranulosus</i>	0.0031073	-0.030519	0.0023462	0.030838	0.014871	-0.0013671	-0.0029042
<i>Concisissimporites</i> <i>verruccatae</i>	0.012871	-0.021582	-0.0018059	-0.0028284	0.018983	0.022403	-0.0002069
<i>Deltoispora</i> <i>australis</i>	-0.0040944	0.00259845	0.0028585	0.0049548	-0.015519	0.0023208	0.007708
<i>Deltoispora</i> <i>conceaus</i>	-0.01217	-0.014107	-0.0061303	0.015348	0.0098348	0.0041652	-0.0057471
<i>Deltoispora</i> <i>minor</i>	-0.0025421	6.89E-06	-0.0030097	-0.0063357	-0.0041101	-0.0021732	-0.0021586
<i>Pilosporites</i> <i>brevipapillosus</i>	0.015842	0.01443	0.039032	-0.019342	-0.0094504	0.0039574	0.0023025
<i>Alisporites</i> <i>dunbariensis</i>	-0.057603	0.0082167	0.0066359	-0.04435	0.036237	-0.017676	-0.0007355

	Axis 43	Axis 44	Axis 45	Axis 46	Axis 47	Axis 48	Axis 49
<i>Alisporites thomastii</i>	0.032754	0.025976	-0.0015817	-0.017234	0.01772	0.014038	-0.0026338
<i>Vireisporites pallidus</i>	-0.020902	0.023363	-0.0006646	-0.0019736	-0.014251	-0.0008958	0.005607
<i>Ptyosporites microalatus</i>	-0.0025421	6.89E-06	-0.0030097	-0.0063357	-0.0041101	-0.0021732	-0.0021586
<i>Ptyosporites minimus</i>	-0.036163	-0.0001747	-0.0060884	-0.0047648	0.017052	-0.010121	0.0041453
<i>Podocarpidites ellipticus</i>	-0.012477	0.0095058	0.025943	-0.0026483	0.01058	0.0046078	-0.0005891
<i>Quadraeculina anellaiformis</i>	0.021667	-0.024892	0.0076752	0.011942	-0.021811	0.0030963	0.000824
<i>Araucariacites australis</i>	-0.0025421	6.89E-06	-0.0030097	-0.0063357	-0.0041101	-0.0021732	-0.0021586
<i>Callialasporites dampieri</i>	0.0046219	0.010747	0.0005238	-0.003786	0.032275	-0.021874	0.012605
<i>Callialasporites segmentatus</i>	-0.0059774	0.04109	0.027772	0.01595	0.016181	-0.0007255	-0.0041031
<i>Callialasporites trilobatus</i>	0.01117	0.0081547	-0.025291	-0.013001	-0.013284	-0.000621	0.0001086
<i>Callialasporites turbatus</i>	-0.040006	0.021562	-0.0003296	0.0040277	-0.0084151	0.0083662	-0.0058397
<i>Classopollis torosus</i>	-0.0025421	6.89E-06	-0.0030097	-0.0063357	-0.0041101	-0.0021732	-0.0021586
<i>Cerebropollenites mesozoicus</i>	-0.0025421	6.89E-06	-0.0030097	-0.0063357	-0.0041101	-0.0021732	-0.0021586
<i>Spheripollenites scabratus</i>	-0.0025421	6.89E-06	-0.0030097	-0.0063357	-0.0041101	-0.0021732	-0.0021586
<i>Spheripollenites subgranulatus</i>	-0.0025421	6.89E-06	-0.0030097	-0.0063357	-0.0041101	-0.0021732	-0.0021586
<i>Perinopollenites elatoides</i>	-0.0025421	6.89E-06	-0.0030097	-0.0063357	-0.0041101	-0.0021732	-0.0021586
<i>Chasmatosporites apertus</i>	-0.031023	0.0065257	0.0005203	0.0065527	0.0086098	0.0076608	0.0071761
<i>Chasmatosporites hians</i>	-0.0004151	-0.063241	-0.033458	0.0032604	-0.0004673	0.0059964	0.0078932
<i>Chasmatosporites major</i>	0.0074551	0.0022864	0.016195	0.0020091	0.0080778	-0.0067917	-0.0047636
<i>Cycadopites minimus</i>	-0.0025421	6.89E-06	-0.0030097	-0.0063357	-0.0041101	-0.0021732	-0.0021586
<i>Cycadopites carpentieri</i>	0.019784	0.022377	-0.012519	0.036656	0.014012	0.01158	-0.0013153
<i>Cycadopites subgranulosus</i>	0.0077273	-0.0062336	0.030531	-0.0020257	0.016463	0.0089142	-0.0016493
<i>Eucommiidites troedssonii</i>	0.01622	0.022441	-0.0027593	-0.02772	0.0055112	0.01459	0.0085164
<i>Siriate bisaccate sp.</i>	0.088413	0.03113	-0.06318	0.020779	0.018414	0.027483	-0.0084959



# Appendix 11

Appendix 11: Nonmetric multidimensional scaling data of samples using logarithmically transformed sporomorph relative abundances (refers to Fig. 5.4C).

Analyzing 67 taxa, 50 samples

Bray-Curtis dissimilarity metric

Stress = 0.207

Name	Axis 1	Axis 2
HB1	-0.075372925	-0.27557846
HB2	-0.108572107	-0.181884926
HB3	0.001571249	-0.183735918
HB4	-0.116814005	-0.087823341
HB5	-0.188038635	-0.057465128
HB6	-0.0101676	-0.07285434
HB7	-0.112083598	0.022006214
HB8	-0.231712407	-0.105364911
HB9	-0.220712007	-0.00926147
HB10	-0.076878225	-0.092335034
HB11	0.001525829	-0.03186641
HB12	-0.090630054	-0.000475915
HB13	-0.097163105	0.0554047
HB14	-0.078626911	0.011427117
HB15	-0.003661366	0.013480342
HB16	-0.127072597	0.077818097
HB17	-0.036881583	0.048692877
HB18	-0.071820029	0.094176163
HB19	-0.026118005	0.033665125
HB20	-0.092085158	0.113677202
HB21	-0.113400848	0.101769476
HB22	-0.069676073	0.072497556
HB23	-0.050843469	0.009046193
HB24	0.00869223	0.050106041
HB25	-0.06039358	0.17557341
HB26	-0.029011933	0.147198868
HB27	-0.034094456	0.087502703
HB28	0.018018784	0.151538929
HB29	0.045003599	0.058112
HB30	0.137792065	0.026814596
HB31	0.065991142	0.050574736
HB32	0.057292895	0.018104865
HB33	0.044463015	0.01606857
HB34	0.08637896	0.061780463
HB35	0.084992344	0.029145074
HB36	0.101124932	0.006791007
HB37	0.141295899	-0.017305986
HB38	0.169597643	-0.020962349
HB39	0.09174043	-0.058514271
HB40	0.070974913	-0.048918581
HB41	0.102529541	-0.048533229
HB42	0.097439206	-0.023349951
HB43	0.072067142	-0.024052817
HB44	0.145273232	-0.085188646
HB45	0.09299745	-0.028549604
HB46	0.102273043	-0.006397242
HB47	0.083919057	-0.048293862
HB48	0.084554162	-0.028870309
HB49	0.08008052	-0.004335932
HB50	0.134241398	0.008946309

# Appendix 12

Appendix 12: Nonmetric multidimensional scaling data of samples using sporomorph presence-absences (refers to Fig. 5.4D).

Analyzing 67 taxa, 50 samples

Bray-Curtis dissimilarity metric

Stress = 0.225

Name	Axis 1	Axis 2
HB1	-0.252620993	-0.09616866
HB2	-0.1370748	-0.059699197
HB3	-0.131399343	-0.174761349
HB4	-0.092898946	-0.097846554
HB5	-0.035558994	-0.064529336
HB6	-0.061379337	-0.042128572
HB7	-0.077347455	-0.06123237
HB8	-0.17530865	0.032559178
HB9	-0.064221478	-0.02364627
HB10	-0.037286478	-0.028295186
HB11	-0.030770376	-0.012449847
HB12	-0.099410923	0.132509196
HB13	-0.019171392	0.040282285
HB14	-0.037761657	0.014377066
HB15	-0.002159516	-0.013415532
HB16	-0.033215258	0.032868708
HB17	-0.089570241	0.046605275
HB18	-0.085816285	0.007946407
HB19	-0.04660292	0.079502846
HB20	-0.192113955	0.175736985
HB21	-0.054509255	0.040314247
HB22	-0.03717111	0.054309609
HB23	0.000441368	0.073286854
HB24	0.052205632	0.099996371
HB25	0.007051892	0.154615788
HB26	0.023205239	0.100114916
HB27	0.059487857	-0.121544585
HB28	0.042263882	0.030946158
HB29	-0.000462913	-0.039910535
HB30	0.102242077	-0.095567783
HB31	0.033837983	0.007157184
HB32	0.093962257	0.055235057
HB33	0.066805263	0.000984003
HB34	0.061273886	0.043628358
HB35	0.064394341	-0.016537872
HB36	0.015397248	-0.107356372
HB37	0.040349658	-0.062099787
HB38	0.036211069	-0.003145635
HB39	0.130426659	-0.035464607
HB40	0.095058962	0.012677746
HB41	0.045217822	-0.038578644
HB42	0.065864416	0.00716407
HB43	0.0846182	0.026869448
HB44	0.065471955	-0.080989209
HB45	0.091962897	-0.038230275
HB46	0.070462575	-0.009903812
HB47	0.122385196	-0.003231706
HB48	0.088819067	0.019348751
HB49	0.082935646	0.003339857
HB50	0.151479226	0.03435733

# Appendix 13

Appendix 13: Correspondence analysis data of taxa and samples using logarithmically transformed sporomorph relative abundances (refers to Fig. 5.5A).

Analyzing 16 taxa, 50 samples

Eigenvalues		Axis 1	Axis 2										
Eigenvalues		0.0364127	0.0178371										
Percentage of total		29.242	14.324										
Taxon scores													
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	Axis 11	Axis 12	Axis 13
<i>Calamospora mesozoica</i>	-0.11575	-0.14186	0.0152	0.09847	0.37843	0.021659	-0.047377	-0.0062558	-0.025806	0.050448	-0.019427	0.014975	0.0044776
<i>Marattisporites scabratus</i>	0.033763	-0.29233	0.2208	-0.029699	-0.07948	-0.030532	0.016415	-0.063368	0.088122	0.078064	0.024928	-0.034134	0.020152
<i>Dictyophyllidites harrisii</i>	0.048474	-0.19509	-0.036913	0.050317	-0.05975	-0.0009826	-0.024024	0.16193	-0.055865	0.0014874	-0.0012303	0.032728	-0.075718
<i>Dictyophyllidites equitinus</i>	0.45983	0.12967	-0.14317	-0.42218	0.10027	-0.080378	-0.099029	0.017526	-0.029639	0.093209	0.11815	-0.046798	-0.030159
<i>Deltoidospora minor</i>	0.16211	-0.10677	-0.096355	-0.0015543	0.0030315	0.090975	0.017918	0.0074121	-0.029085	-0.030678	0.018982	0.027141	0.087974
<i>Pityosporites microalatus</i>	0.25749	0.041425	-0.026667	-0.0071925	0.032566	-0.2156	0.26442	0.078898	0.031224	0.016526	-0.07116	0.036724	0.011628
<i>Araucariacites australis</i>	0.10093	0.04904	-0.030948	0.022864	0.045812	0.01629	0.037589	-0.1137	0.082416	-0.085498	0.022226	0.023285	-0.04645
<i>Callialasporites turbatus</i>	-0.092452	0.20252	0.17448	-0.097607	0.036309	0.22237	0.11417	0.084005	0.016037	0.032264	-0.038296	-0.049244	-0.020398
<i>Classopollis torosus</i>	-0.070248	0.012962	-0.026324	-0.017883	-0.013215	-0.047493	-0.0034824	0.0090749	-0.048508	-0.066197	-0.022466	-0.070361	0.031594
<i>Cerebropollenites mesozoicus</i>	0.099226	-0.023017	-0.26708	0.2573	-0.082281	0.11404	0.07763	-0.051875	-0.014183	0.075302	0.053643	-0.091987	-0.035382
<i>Spheripollenites scabratus</i>	0.028233	0.128	0.13142	0.037329	-0.062611	-0.0043404	0.027555	-0.12385	-0.16104	0.052789	0.013952	0.065186	-0.0021041
<i>Spheripollenites subgranulatus</i>	-0.08513	0.010577	0.048839	0.0080697	-0.0081866	-0.086767	-0.083281	-0.039461	-0.019862	-0.02001	-0.044151	-0.03604	-0.029003
<i>Perinopollenites elatoides</i>	-0.23297	0.02397	0.049256	-0.023504	-0.022803	-0.0030657	-0.0046221	0.0625	0.020051	-0.050495	0.081426	0.035413	0.0075682
<i>Chasmatosporites apertus</i>	0.29856	0.30259	0.090861	0.24573	-0.024338	-0.046092	-0.17082	0.099133	0.09476	0.0482	0.0005187	0.0092232	0.041902
<i>Cycadopsis minimus</i>	0.030399	-0.037885	-0.10751	-0.12102	-0.078209	0.095455	-0.090364	-0.030449	0.041744	0.011879	-0.10454	0.052106	0.0010521
<i>Cycadopsis carpentieri</i>	-0.70873	0.14128	-0.28613	-0.037372	-0.034703	-0.10911	0.034659	-0.02568	0.074556	0.14952	0.0042623	0.028865	0.022519
Sample scores													
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	Axis 11	Axis 12	Axis 13
HB1	-0.1589	-0.24581	-0.36738	-0.089556	-0.1024	0.12421	0.023315	0.20467	0.0053492	0.080175	0.087916	0.1256	0.022032
HB2	-0.086004	-0.39457	-0.18385	-0.046629	-0.1801	-0.0061832	-0.089148	-0.083965	0.095811	0.011944	-0.015175	-0.041506	0.028692
HB3	0.016547	-0.20286	-0.031085	-0.2135	-0.112	0.028211	-0.17247	0.06312	-0.027292	-0.038977	-0.1598	-0.10265	-0.024872
HB4	0.081857	0.32132	-0.097606	-0.15607	0.12514	-0.089577	-0.14936	0.1049	0.016796	0.037799	-0.035639	0.020987	-0.032873
HB5	0.0049497	0.38042	-0.14323	0.16994	-0.03697	-0.10531	-0.086142	-0.044791	0.022558	0.063427	-0.039247	0.0010788	-0.037457
HB6	-0.022042	0.060808	0.074384	-0.01098	-0.22766	-0.028479	0.099867	-0.14562	-0.041459	-0.02368	0.056446	0.11449	-0.04321
HB7	0.31852	0.058402	0.081576	-0.10686	-0.13991	-0.16149	-0.099058	0.04075	0.069764	-0.039478	0.092715	0.023148	-0.015429
HB8	0.077309	-0.071878	-0.27834	-0.078432	0.077117	-0.082671	0.25461	-0.010107	-0.01497	-0.011736	-0.062937	-0.032619	-0.051937
HB9	0.19485	0.21496	-0.1838	-0.057149	-0.024407	-0.020031	0.10403	-0.02554	0.10382	-0.025505	0.038332	-0.0065511	0.016945
HB10	0.034393	-0.27201	-0.026354	-0.042076	0.10593	-0.0934	-0.016159	-0.023175	0.14545	-0.062325	-0.0026993	0.033308	-0.058677
HB11	-0.091133	-0.067252	0.0079655	0.15574	0.15944	-0.048662	0.063113	0.030685	0.086208	-0.0034641	-0.068831	0.05722	-0.019752
HB12	0.12199	0.006601	0.008414	0.16848	-0.042167	-0.084328	-0.024812	-0.0074584	0.081862	0.096549	0.040405	-0.046688	-0.018267
HB13	0.068974	-0.11632	-0.03791	0.30159	0.11326	0.13507	-0.074089	-0.040124	-0.012804	-0.092754	0.0097695	-0.030296	-0.090736
HB14	0.19462	-0.033526	0.040711	0.046446	0.053877	-0.010105	-0.036435	0.019188	-0.036674	0.015607	0.05803	-0.055432	-0.030277
HB15	0.031815	-0.057257	0.16879	-0.1969	0.14096	-0.023632	0.085077	-0.05547	0.040113	-0.013144	0.024567	0.056158	-0.0009368
HB16	0.31498	0.018021	-0.069128	0.041806	0.066358	-0.062139	-0.14692	-0.060966	-0.054838	0.0074466	0.0065824	0.019254	0.0099384
HB17	0.28303	-0.10793	0.042905	-0.0791	-0.019391	-0.025703	-0.051692	-0.046004	-0.019805	0.071764	0.029203	0.021575	-0.013517
HB18	0.20781	0.051274	-0.058425	0.03754	0.12722	0.15047	-0.085274	0.13972	0.021962	-0.078206	-0.037093	0.019027	0.039546
HB19	0.21191	-0.027242	-0.018707	0.059047	-0.029032	0.007111	-0.027979	0.038794	-0.0087231	-0.10706	-0.017202	0.044276	0.038345
HB20	0.20765	-0.017311	0.050225	0.21456	-0.12834	0.11651	0.062563	0.033187	0.091949	-0.0083236	-0.091136	-0.011469	0.036838
HB21	0.30509	0.067909	-0.045097	-0.023261	0.036107	-0.03033	0.10046	-0.066954	-0.0043003	-0.015647	-0.021935	-0.032621	0.06822
HB22	0.2229	-0.23894	0.10758	-0.071741	0.066914	-0.033735	0.096593	-0.11252	-0.047987	0.082177	0.0063098	-0.083647	0.019433
HB23	0.16222	-0.028549	0.15765	0.085557	-0.03486	-0.061949	-0.052615	0.051049	-0.036098	0.078059	-0.018691	0.027062	0.018883
HB24	0.080962	-0.086713	0.13189	0.0061635	-0.023049	0.15373	-0.032397	-0.016618	0.063571	-0.033433	0.10766	-0.05265	0.005723
HB25	0.19973	0.12357	-0.20722	0.068247	-0.002655	0.088566	-0.047378	-0.16956	-0.12127	-0.051741	0.013828	0.018261	0.098326
HB26	0.13311	0.065227	-0.086258	-0.084232	0.019973	0.18925	0.1139	-0.021804	0.030972	-0.0058449	0.030765	0.014444	-0.08069
HB27	0.26652	0.025778	-0.070564	-0.040875	-0.023347	0.048308	0.051085	-0.04923	-0.1365	0.009155	-0.056889	0.021197	-0.075762
HB28	0.055531	0.0035685	0.15235	-0.037188	0.10229	0.10753	-0.0071725	0.027531	0.10634	0.038819	-0.01151	0.041202	0.048413
HB29	0.0071074	0.0074411	0.12547	-0.12102	-0.0080206	0.038813	0.027908	0.045115	-0.088546	0.11393	-0.07122	0.050959	0.026299
HB30	-0.2358	-0.0027132	0.20349	0.013606	0.0025037	0.15666	-0.10153	-0.053341	-0.0099664	0.058407	-0.055349	0.087611	-0.033696
HB31	0.050967	0.11796	0.049776	-0.17286	-0.088637	0.084621	0.081375	0.075214	0.018848	0.0061297	-0.028025	-0.054326	0.010157
HB32	-0.097575	0.1721	0.12772	-0.006599	-0.047554	0.047485	0.060114	-0.038064	0.068659	-0.0012247	0.0037542	-0.014092	0.011755
HB33	0.020775	0.060754	0.10313	0.038772	-0.23187	0.0013626	0.026786	0.059654	-0.058289	-0.01436	-0.018944	-0.031492	-0.045693
HB34	0.089655	-0.072552	0.16037	0.049809	0.075272	-0.083378	0.082723	0.15078	-0.13794	-0.007843	0.043149	-0.017947	0.015405
HB35	-0.089309	0.076692	0.021729	0.030368	0.084476	0.12494	-0.041572	-0.0017236	-0.010249	0.040821	0.068064	-0.014446	0.030943
HB36	-0.20359	0.092066	0.12801	0.040931	-0.027062	-0.0066301	0.075997	-0.0092557	0.092105	0.0093791	-0.068357	-0.023377	0.0071998
HB37	-0.29235	0.10756	-0.025145	-0.062075	0.1336	0.0775	0.035691	0.0095825	-0.042212	0.022685	0.081556	-0.065965	-0.041144
HB38	-0.39321	0.11595	0.0017027	-0.004962	-0.09187	0.089744	-0.02602	0.0022507	-0.074212	-0.10812	0.024815	-0.022084	-0.034334
HB39	-0.2279	0.109	-0.051886	-0.030773	-0.13162	0.024403	0.014612	0.09026	0.0094601	-0.017129	0.025433	-0.046932	0.056373
HB40	-0.29788	-0.094338	-0.029106	0.095986	-0.014953	0.048553	0.007516	-0.021645	-0.060721	0.069167	0.01333	-0.038687	-0.010144
HB41	-0.22379	0.0042662	-0.040848	-0.13489	0.088457	-0.032037	-0.085726	-0.1162	0.017311	0.026017	0.044805	-0.044924	0.038633
HB42	-0.26616	0.0271	-0.069787	-0.02662	0.030798	-0.05493	-0.12723	-0.020368	0.034314	0.09322	0.0085519	-0.01865	-0.034729
HB43	-0.18532	0.0094185	-0.002656	0.13748	-0.10201	-0.11393	0.0017986	-0.07718	0.017677	-0.0006526	0.012805	0.0066809	0.033283
HB44	-0.33473	0.053479	0.048091	-0.18627	0.095376	-0.013263	-0.04215	-0.14496	-0.016953	-0.12906	-0.053199	0.015882	0.04571
HB45	-0.24035	-0.092263	0.02808	0.037279	-0.027321	-0.076175	0.025797	-0.076889	-0.026684	-0.0040563	-0.036563	0.062923	0.0001936
HB46	-0.17132	0.020913	0.10948	0.13587	0.050212	-0.11217	0.1006	0.11256	-0.0003628	-0.045644	0.025231	-0.0191	0.015449
HB47	-0.061833	-0.039608	0.10808	-0.11358	-0.042658	-0.13964	-0.055303	0.084044	-0.029587	-0.16797	0.035866	0.013988	-0.029322
HB48	-0.23484	0.055155	-0.16302	0.026918	0.023838	-0.083416	0.068467	0.022635	0.017195	0.011805	-0.030115	-0.0051022	0.012664
HB49	-0.11814	-0.041672	-0.016762	0.005808	0.040002	-0.10592	0.015542	0.10035	-0.05705	0.019983	0.0045619	-0.022629	0.022211
HB50	-0.15588</												

	Axis 14	Axis 15
<i>Calamospora mesozoica</i>	0.0011765	-0.024692
<i>Marattisporites scabratus</i>	-0.015479	-0.0049168
<i>Dictyophyllidites harrisii</i>	-0.038755	0.018754
<i>Dictyophyllidites equiexinus</i>	0.0015995	-0.0024336
<i>Deltoidospora minor</i>	0.011312	0.052387
<i>Pityosporites microalatus</i>	0.034285	-0.016007
<i>Araucariacites australis</i>	-0.030325	0.012539
<i>Callialasporites turbatus</i>	-0.0019876	0.021757
<i>Classopollis torosus</i>	-0.038721	-0.024351
<i>Cerebropollenites mesozoicus</i>	0.049324	-0.033378
<i>Spheripollenites scabratus</i>	-0.014581	-0.010118
<i>Spheripollenites subgranulatus</i>	0.055756	0.042667
<i>Perinopollenites elatoides</i>	0.036997	-0.027673
<i>Chasmatosporites apertus</i>	-0.022772	-0.0016883
<i>Cycadopites minimus</i>	0.014835	-0.043514
<i>Cycadopites carpentieri</i>	-0.05515	0.048743

	Axis 14	Axis 15
HB1	0.013597	-0.005636
HB2	0.033717	0.030261
HB3	-0.053445	0.0065791
HB4	0.0058289	-0.015468
HB5	0.019029	0.036456
HB6	0.0031048	-0.021008
HB7	-0.039749	0.0169
HB8	-0.07247	0.0010294
HB9	-0.042535	-0.047012
HB10	0.055881	-0.0043469
HB11	0.017142	0.027047
HB12	-0.047047	0.010875
HB13	0.027616	-0.0088083
HB14	0.050265	0.030523
HB15	0.0017979	0.027979
HB16	0.0082574	0.015208
HB17	-0.017056	0.0080219
HB18	-0.023478	0.0042168
HB19	-0.02098	0.0083669
HB20	-0.020755	-0.036092
HB21	0.083189	0.011459
HB22	-0.035836	0.030691
HB23	0.044337	-0.066428
HB24	0.0023727	-0.03336
HB25	-0.024728	0.0071282
HB26	0.0064095	0.0026733
HB27	0.013162	-0.01117
HB28	-0.037345	0.011921
HB29	-0.0060874	0.035703
HB30	-0.0082381	0.018016
HB31	0.081129	-0.050679
HB32	-0.0040845	0.045789
HB33	0.043914	0.021291
HB34	-0.021877	-0.057369
HB35	-0.0066298	0.021382
HB36	-0.030641	-0.048523
HB37	-0.027646	0.0017822
HB38	-0.036632	0.0074525
HB39	0.011485	0.063221
HB40	0.0049493	-0.0015478
HB41	0.024769	-0.047889
HB42	-0.020418	-0.049764
HB43	-0.019955	-0.018868
HB44	0.028977	-0.019423
HB45	-0.016965	-0.0043677
HB46	0.011992	0.05129
HB47	-0.016735	0.0075322
HB48	0.041382	0.010258
HB49	0.016887	0.0010099
HB50	-0.014373	-0.025846

# Appendix 14





## A quantitative comparison of dispersed spore/pollen and plant megafossil assemblages from a Middle Jurassic plant bed from Yorkshire, UK

Sam M. Slater and Charles H. Wellman

**Abstract.**—Detailed quantitative data has previously been collected from plant megafossil assemblages from a Middle Jurassic (Aalenian) plant bed from Hasty Bank, North Yorkshire, UK. We conducted a similar analysis of palynological dispersed sporomorph (spore and pollen) assemblages collected from the same section using the same sampling regime: 67 sporomorph taxa were recorded from 50 samples taken at 10 cm intervals through the plant bed. Basic palynofacies analysis was also undertaken on each sample. Both dispersed sporomorph and plant megafossil assemblages display consistent changes in composition, diversity (richness), and abundance through time. However, the dispersed sporomorph and plant megafossil records provide conflicting evidence for the nature of parent vegetation. Specifically, conifers and ferns are underrepresented in plant megafossil assemblages, bryophytes and lycopsids are represented only in sporomorph assemblages, and sphenophytes, pteridosperms, Caytoniales, Cycadales, Ginkgoales and Bennettitales are comparatively underrepresented in sporomorph assemblages. Combined multivariate analysis (correspondence analysis and nonmetric multidimensional scaling) of sporomorph occurrence/abundance data demonstrates that temporal variation in sporomorph assemblages is the result of depositional change through the plant bed. The reproductive strategies of parent plants are considered to be a principal factor in shaping many of the major abundance and diversity irregularities between dispersed sporomorph and plant megafossil data sets that seemingly reflects different parent vegetation. Preferential occurrence/preservation of sporomorphs and equivalent parent plants is a consequence of a complex array of biological, ecological, geographical, taphonomic, and depositional factors that act inconsistently between and within fossil assemblages, which results in notable discrepancies between data sets.

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### Introduction

Understanding the causes of temporal variation in paleofloras is a fundamental objective of paleobotany. Extracting these causes is, however, frequently problematic as it is often difficult to determine the dominant controls on the constituents of fossil assemblages. Such controls include ecological, climatic, depositional, and preservational factors. Establishing the causes of paleofloristic temporal variation is clearly enhanced when a multidisciplinary approach is used, as the overreliance on singular lines of evidence can often lead to over interpretation. Comparing data from the plant megafossil and terrestrial palynological records can provide important insight into ecological and preservational biases that can

shape diversity (richness) and abundance patterns of these fossil assemblages. Thus, such comparisons can help to determine the reliability of paleofloristic interpretations based on the spore and pollen (sporomorph) and plant megafossil records in isolation.

The sequences of North Yorkshire, UK offer a rare example of extensive Middle Jurassic terrestrial deposits. The sedimentary successions have previously been studied in detail for their paleontological significance (e.g., Romano and Whyte 2003) and particularly for the famous plant beds that are scattered throughout these sequences (e.g., Black 1929; van Konijnenburg-van Cittert 1968, 1975, 1996, 2008; Crane and Herendeen 2009; Spicer and Hill 1979; van Konijnenburg-van Cittert and Morgans 1999). Although plant megafossil studies from these

deposits are common in the literature (e.g., Harris 1941, 1944, 1952, 1953, 1961a,b, 1964, 1969, 1978, 1979; van Konijnenburg-van Cittert 1972, 1975, 1978, 1981, 1989, 1996, 2008; Harris et al. 1974; Spicer and Hill 1979; Hill 1990; Morgans 1999; van Konijnenburg-van Cittert and Morgans 1999), published dispersed spore and pollen investigations remain comparatively sparse (e.g., Couper 1958; Chaloner 1968; Chaloner and Muir 1968; Riding 1984; Riding and Wright 1989; Gowland and Riding 1991; Boulter and Windle 1993; Hubbard and Boulter 1997; Butler et al. 2005; Srivastava 2011).

This study provides a detailed palynological assessment of a plant bed from Hasty Bank, North Yorkshire, UK that was previously analyzed for its plant megafossil contents. Spicer and Hill (1979) carried out a comprehensive quantitative study of this plant bed in which they sampled contiguous plant megafossil census counts through a through a 5 m outcrop section. Plant megafossil counts were carried out on rock blocks of either 50 or 25 cm<sup>2</sup> parallel to bedding and 10 or 20 cm in depth, perpendicular to bedding. Counts were then multiplied accordingly so that all abundances correspond to a 50 × 50 × 20 cm<sup>3</sup> block of sediment. The histogram of their results is provided in Supplementary Figure 1. Sporomorph quantitative data was analyzed here from the same section discussed in Spicer and Hill (1979) in order to compare this with the quantitative plant megafossil data. Palynofacies analysis was also carried out in order to aid environmental reconstructions (Tyson 1995). Paleofloristic comparisons of sporomorph and plant megafossil data are possible due to comprehensive in situ spore/pollen (e.g., van Konijnenburg-van Cittert 1968, 1971, 1978, 1981, 1989, 1993, 2000; Pedersen et al. 1989; Hill 1990; Osborn and Taylor 1993; Balme 1995; Friis and Pedersen 1996; Yang et al. 2008) and ultrastructural transmission electron microscope (TEM) studies (e.g., Batten and Dutta 1997) which means that the majority of Middle Jurassic sporomorphs can now be assigned at least to family level plant classification.

By comparing dispersed spore/pollen assemblages with plant megafossil data in association with palynofacies analysis it was anticipated that a more realistic paleofloristic

and paleoenvironmental interpretation would be possible and potential discrepancies in data sets would help to explain preservational biases between sporomorph and plant megafossil records. Since sporomorph and plant megafossil assemblages undergo different transportation and depositional processes, it was expected that the respective fossil assemblages would be notably dissimilar in composition (e.g., Bercovici et al. 2008, 2009), with the anticipation that our analyses may shed light on the reasons behind these differences.

### Geological Setting

The Mesozoic sequences of the Cleveland Basin, northeast England (Fig. 1) have been intensively studied since the early nineteenth century (e.g., Young and Bird 1822) and offer important insight into both terrestrial and marine environments of this time. Middle Jurassic sediments of the Cleveland Basin are dominated by the chiefly terrestrial sequences of the Ravenscar Group (Fig. 2). Regional uplift and associated relative sea level fall led to the deposition of extensive fluviodeltaic sequences derived from upland areas surrounding the Cleveland Basin. Marine beds occur sporadically throughout the Ravenscar Group as a result of marine incursions from the south and east (Hemingway and Knox 1973; Knox 1973; Hemingway 1974; Nami and Leeder 1978; Leeder and Nami 1979; Hancock and Fisher 1981;

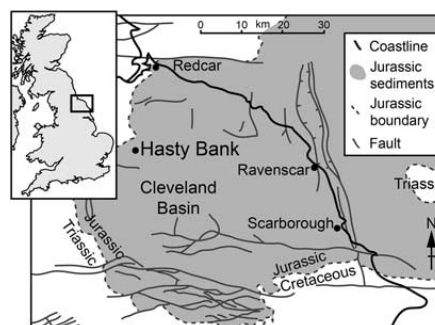


FIGURE 1. Location and geological setting of Hasty Bank, northeast England. Modified from Milsom and Rawson (1989); Mjos and Prestholm (1993); Cox and Sumbler (2002); Palliani and Riding (2000); Slater et al. (2015).

Livera and Leeder 1981; Fisher and Hancock 1985; Kantorowicz 1985; Alexander 1989, 1992; Riding and Wright 1989; Gowland and Riding 1991; Rawson and Wright 2000; Powell 2010). The Ravenscar Group provides an exceptional example of extensive Middle Jurassic terrestrial sequences and the plethora of plant fossils

(e.g., van Konijnenburg-van Cittert and Morgans 1999) and dinosaur footprints (Whyte and Romano 1993, 2001a,b; Romano et al. 1999; Romano and Whyte 2003; Whyte et al. 2006, 2007, 2010) make the Cleveland Basin an important region for paleontology.

The plant bed under investigation is located on the northern slope of Hasty Bank (NZ 567 037), situated within the northwest region of the North York Moors National Park, northeast England. The plant bed occurs at the base of the Aalenian Saltwick Formation, stratigraphically located at the base of the Ravenscar Group (Fig. 2) and lies unconformably above the marine Dogger Formation. The bed is approximately 7 m thick and has previously yielded a varied flora of 90 species (Hill and van Konijnenburg-van Cittert 1973; Hill 1974; Spicer and Hill 1979). Two lithologies dominate the plant bed (Fig. 3), a claystone that forms the lower part of the section and a siltstone that occupies the majority of the upper part of the section. An erosional surface is present between the claystone and the siltstone. A thin lens of dark gray clay is also present at the top of the section (Hill and van Konijnenburg-van Cittert 1973; Hill 1974).

The claystone is uniform dark gray in color. Grain size is homogeneous through the unit and

Epoch	Stage	Lithostratigraphical Division	Age (Ma)	
Middle Jurassic	Lower Callovian	Cornbrash Formation (25 m)	166	
	Bathonian	Ravenscar Group (~200 m)	Scalby Formation (60 m)	168
			Long Nab Member (45 m)	
	Upper Bajocian	Ravenscar Group (~200 m)	Moor Grit Member (15 m)	170
			Scarborough Formation (30 m)	
	Lower Bajocian	Ravenscar Group (~200 m)	Gristhorpe Member (26 m)	174
			Cloughton Formation (85 m)	
			Leberston Member (9 m)	
			Sycarham Member (50 m)	
	Aalenian	Ravenscar Group (~200 m)	Eller Beck Formation (4 m)	174
Saltwick Formation (40 m)				
Dogger Formation (2 m)				

FIGURE 2. Subdivision of Middle Jurassic sequences of the North Yorkshire Coast. Marine units shaded. The arrow indicates the stratigraphic position of the plant bed. Modified from Rawson and Wright (2000); Slater et al. (2015).

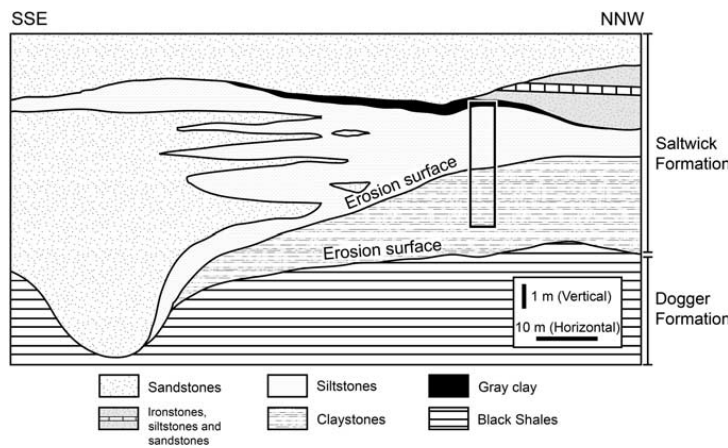


FIGURE 3. Cross section of the geology of the main plant bed at Hasty Bank. Vertical and horizontal scales provided (vertical scale exaggerated four times). The section discussed is shown by the rectangle. Adapted from Hill and van Konijnenburg-van Cittert (1973); Spicer and Hill (1979); van Konijnenburg-van Cittert and Morgans (1999).

thin (1–3 mm scale) horizontal laminae are abundant. The rock is relatively soft and breaks apart easily along laminae, which often reveal highly abundant fragmentary plant megafossils.

The siltstone is a homogeneous medium gray color. Grain size is uniform through the unit and larger, more prominent horizontal laminae (5–10 mm scale) are present. The rock is harder than the claystone and fragmentary plant megafossils are abundant, although less so than in the claystone. Horizontal roots occur in low abundance within the basal ~1 m of the siltstone, these are typically less than 2 cm in length and ~2 mm in width.

The gray clay at the top of the section is a homogeneous very dark gray color. Grain size is uniform through the unit and no sedimentary structures are visible. The rock is very soft and not fully lithified. Plant megafossils are less common in the gray clay than in the claystone and siltstone.

*Previous Interpretations of the Depositional Environments at Hasty Bank.*—The Hasty Bank plant bed was first recognized as an important fossil locality by Black (1929). Subsequent paleobotanical and paleoecological studies have commented on possible environments of deposition for the plant bed, most notably by Harris (1964), Hill and van Konijnenburg-van Cittert (1973), Hill (1974), and van Konijnenburg-van Cittert and Morgans (1999).

Harris (1964) postulated that the claystone at the base of the plant bed (Fig. 3) was deposited in a coastal environment periodically flooded by seawater. These interpretations were based on the occurrence of the pteridosperm *Pachypteris papillosa* in association with rare marine microfossils thought to be derived from marine flooding events. Harris (1983) reconstructed *P. papillosa* as a large shrub that formed mangrove-like thickets along tidal rivers. Spicer and Hill (1979) showed that *P. papillosa* is markedly more abundant within the claystone deposit compared to the rest of the section.

The siltstone is interpreted as the peripheral fringes of a large channel sandstone deposit immediately adjacent to the southeast of the plant bed (Fig. 3). Hill and van Konijnenburg-van Cittert (1973) concluded that the siltstone was deposited in the slower flowing region of

the channel. It is possible that the siltstone could however represent a levee or floodplain deposit peripheral to the sandstone. The channel has cut into the underlying sediments forming an erosional surface between the claystone and the siltstone and thus there is a time gap between these deposits.

Previous depositional environmental interpretations for the gray clay are lacking. However, sedimentological, sporomorph and palynofacies evidence from this study suggests that this deposit represents a swamp or an abandoned channel.

### Materials and Methods

*Collection.*—A total of 50 samples (HB1–HB50, numbered in reverse stratigraphic order, i.e., HB1 is at the top of the section) were collected at 10 cm vertical intervals from the main Hasty Bank plant bed (NZ 567 037) for palynological processing. Samples were taken from the identical section of that discussed by Spicer and Hill (1979), shown in Figure 3. Christopher R. Hill (of Spicer and Hill [1979]) was present during collection of samples to ensure the exact position of the section was located. Sampling required the excavation of approximately 50 cm of modern deposits to access the outcrop. The exterior of the outcrop was weathered between 5 and 20 cm deep into the rock. The section was therefore excavated a further ~30 cm into the outcrop to ensure fresh exposure. Samples HB1–HB3 are from the gray clay at the top of the section; HB4–HB28 are from the siltstone unit; and HB29–HB50 are from the claystone unit.

*Processing.*—Dry rock samples were weighed at 20 g before being dissolved in 40% hydrochloric acid for at least 24 hours to remove carbonates, followed by two week maceration in 40% hydrofluoric acid to remove silicates. Samples were agitated every two days to ensure full break down of rock material. Samples were then decanted and fresh water added, repeating the process until neutral. One day was left between decants to ensure minimal loss of palynomorphs. Two *Lycopodium* tablets (produced by the University of Lund, Sweden; batch 1031) were added before sieving at 10 µm. Centrifuging residues in zinc chloride was then

undertaken to remove heavy minerals. Residues were then sieved again at 10 µm to remove the heavy liquid and final residues were spread across cover slips and gently heated on a hot plate to remove excess water. Cover slips were then mounted onto slides using epoxy resin on a hot plate. All materials (rock samples and slides) are housed in the collections of the Centre for Palynology at the University of Sheffield.

*Counting.*—Slides were examined under a Meiji Techno (MA151/35/50) light microscope. A minimum of 200 indigenous Jurassic sporomorphs were counted from each sample in addition to any *Lycopodium* spores from tablets in order to assess the relative organic richness of samples. The *Lycopodium* tablets contain a known quantity of spores (20,848 ± 1546 spores per tablet). This allows the palynomorph productivity of each sample to be assessed when counting sporomorphs, as numbers of *Lycopodium* spores can be compared with numbers of indigenous Jurassic sporomorphs to assess the palynomorph richness of samples. In this study, increased numbers of *Lycopodium* correspond to a decrease in palynomorph productivity per unit of sediment. Counts were carried out in systematic traverses across slides to ensure no grains were missed. For presence/absence data, the remainder of the slide was then examined in the same fashion to identify species that were not present in the count data. The complete raw data set is provided in Supplementary Table 1. For sporomorph images that refer closely to the taxonomic identifications used in this study, see Couper (1958), Boulter and Windle (1993) and Srivastava (2011).

*Palynofacies Analysis.*—The term palynofacies typically refers to all of the visible organic particles (usually 2–250 µm in size) that occur within palynological maceration residues (Traverse 2007). Palynofacies analysis is commonly used to assess depositional environments (e.g., Parry et al. 1981; Boulter and Riddick 1986; Van der Zwan 1990; Brugman et al. 1994; Oboh-Ikuenobe and Yepes 1997; Oboh-Ikuenobe et al. 2005; Carvalho et al. 2006). In this study, palynofacies analysis attempts to provide a more in depth interpretation of the depositional environments at Hasty Bank. A similar palynofacies classification scheme to Tyson (1995) and Batten and Stead (2005) was

used to categorize organic matter. Categories for palynofacies debris are: spores; pollen; algae; dinoflagellate cysts; acritarchs; humic debris; amorphous organic matter (AOM); *Botryococcus*; structured vitrinite; unstructured vitrinite; cuticle; and inertinite. Counts of 200 palynodebris were carried out on all samples, the complete raw data set is provided in Supplementary Table 2.

*Statistical Analysis.*—Correspondence analysis (CA) and nonmetric multidimensional scaling (NMDS) were performed on sporomorph data sets to further understand the causes of floral variation through the Hasty Bank plant bed. Correspondence analysis and NMDS are ordination methods that plot complex multivariate data onto a minimal number of axes (e.g., Jardine et al. 2012). Correspondence analysis is an eigenvector method of ordination that produces a graphical representation of a contingency table (Spicer and Hill 1979). Nonmetric multidimensional scaling is a nonparametric ordination technique that uses ranked distances between samples to assess the degree of similarity between samples (Chatfield and Collins 1980; ter Braak 1995; Legendre and Legendre 2012; Hammer and Harper 2006; Jardine et al. 2012), hence clustering of samples in ordination space indicates high compositional similarity between those samples. For comprehensive descriptions of CA and NMDS see Greenacre (2007) and Cox and Cox (2001), respectively. Correspondence analysis and NMDS are becoming increasingly used in palynological analysis of quantitative paleoecological studies (e.g., Kovach 1989, 1993; Wing and Harrington 2001; Hammer and Harper 2006; Bonis and Kürschner 2012; Jardine et al. 2012; Stukins et al. 2013) as such methods allow the user to extract information on the major causes of variation from complex data sets. Correspondence analysis was chosen over detrended correspondence analysis (DCA) as this method was employed by Spicer and Hill (1979) on megafossil data, thus to allow comparison of ordinations we used the same technique here. Furthermore, CA ordinations do not indicate the need for DCA. Both CA and NMDS are used here to assess abundance and presence/absence data. For NMDS ordinations, the Bray-Curtis dissimilarity metric was used

to generate distances between samples as this method is considered to perform well in ecological analyses (e.g., Minchin 1987; Harrington 2008; Bowman et al. 2014). Repeated runs were carried out for two dimensions until a convergent solution was established. Principal components rotation and centering was then applied to the final ordination. Nonmetric multidimensional scaling ordinations were performed using R, version 3.1.2 (R Core Team 2014), within the package “vegan”, version 2.2-1 (Oksanen et al. 2015). Sporomorph relative abundances have been transformed logarithmically for CA and NMDS. This procedure condenses the differences in scores between abundant and rare species between samples, thus reducing the impact of highly abundant taxa on the data set and also reducing statistical noise. Spicer and Hill (1979) suggested that the most effective way to assess megafossil data in ordinations was to logarithmically transform abundances. Species that are present in samples but not in counts have been excluded from logarithmically transformed relative abundance ordinations. For taxonomic CA the same data has been used with the exclusion of species that contribute less than 1% of the total count to eliminate statistical noise. Presence/absence CA and NMDS were performed to assess co-occurrence and compositional variation between samples. For presence/absence analyses all species are included; species that are present are scored as 1, species that absent are scored as 0. Spiked *Lycopodium* data has been excluded from all ordinations. The statistical program PAST (Hammer et al. 2001) was used to create CA plots.

## Results

*Sporomorph Diversity (Richness) and Abundance Variation.*—A total of 67 sporomorph taxa were recognized from 50 samples; the entire taxonomic list with associations between sporomorphs and parent plant groups is provided in Supplementary Table 3. The commonly used Chao2 species richness estimator (Colwell and Coddington 1994) gave a species estimate of 69.94 taxa (standard deviation = 3.36) for the entire data set, which suggests the data set was not severely

undersampled. Diversities (richness) using presence/absence data (Fig. 4B) are highest within the claystone; diversity (richness) is slightly lower within the siltstone assemblage and lower again in gray clay samples. This indicates that the claystone was deposited at a time of increased floral diversity and/or claystone samples are capturing more sporomorph taxa due to preservational biases.

Relative abundances of all taxa are displayed graphically in Supplementary Figure 2. Relative abundances of the ten most abundant sporomorph taxa are provided in Figure 4A. Sporomorphs have been grouped into their botanical affinities in Figure 5A to extract information on higher taxonomic level temporal floral variations. Spiked *Lycopodium* spores exhibit the most prominent abundance variation through the sequence. Abundant spiked *Lycopodium* in gray clay (HB1–HB3) and siltstone (HB4–HB28) samples indicates that claystone samples (HB29–HB50) preserve far greater numbers of indigenous Jurassic sporomorphs.

Bryophytes (Fig. 5A) are represented by two species and are in low abundance throughout the section. Lycopods are highly diverse (16 taxa) and abundances are low throughout the plant bed, but slightly higher in the siltstone compared to the claystone and gray clay. Sphenophytes are represented by *Calamospora mesozoica* and abundances are low and relatively constant throughout the section. Ferns are the most diverse group (23 taxa) and are highly abundant through the plant bed. Abundances increase from the claystone into the siltstone and increase again into the gray clay. Pteridosperms are represented by two species of *Alisporites*; diversity and abundances are low throughout the section, but slightly higher in the siltstone compared to the claystone and gray clay. Caytoniales are represented by the single species *Vitreisporites pallidus*; similarly to pteridosperms, abundances are low throughout the section, but slightly higher in the siltstone compared to the claystone and gray clay. Conifers constitute the most abundant group and are highly diverse (14 taxa). Abundances decrease markedly from the claystone into the siltstone and decrease again within the gray clay. Relative abundance variation within the conifers is

most apparent within the three most abundant species: *Classopollis torosus*, *Perinopollenites elatoides*, and *Araucariacites australis* (Fig. 4A). *Classopollis torosus* and *P. elatoides* are considerably more abundant within claystone samples, whereas *A. australis* contrasts the overall abundance pattern of the conifers and is more abundant within siltstone samples. Cycadopsida/Ginkgopsida pollen is moderately diverse (four taxa) and displays little change in abundance (Fig. 5A) through the plant bed. *Chasmatosporites hians* exhibits the most pronounced abundance variation within the Cycadopsida/Ginkgopsida group; *C. hians* is relatively common in the claystone, but becomes increasingly rare within siltstone samples and is absent above sample HB19. Bennettitales are low in abundance and diversity throughout the plant bed (two taxa). The largest relative abundance variation within the Bennettitales is displayed by *Cycadopites carpentieri*, which occurs frequently in the basal and upper samples of the

section, but is absent from samples HB26 to HB16.

*Sporomorph Sample Ordination*.—CA and NMDS (Fig. 6) reveal samples from claystone, siltstone, and gray clay units are well separated in ordination space, with only minimal overlap. This illustrates that lithology and apparent floristic composition are correlated and perhaps both are responding to the same principal factors of deposition and/or environment. Logarithmically transformed relative abundance (Figs. 6A,C) and presence/absence sample multivariate plots (Figs. 6B,D) demonstrate little clustering of stratigraphically adjacent samples within lithological point clouds, suggesting little temporal floral change and habitat partitioning within each of the three depositional settings. For logarithmically transformed relative abundance CA (Fig. 6A) the variance is 14% for axis one and 9% for axis two. For presence/absence CA (Fig. 6B) the variance is 11% for axis one and 8% for axis two. Gray clay samples display

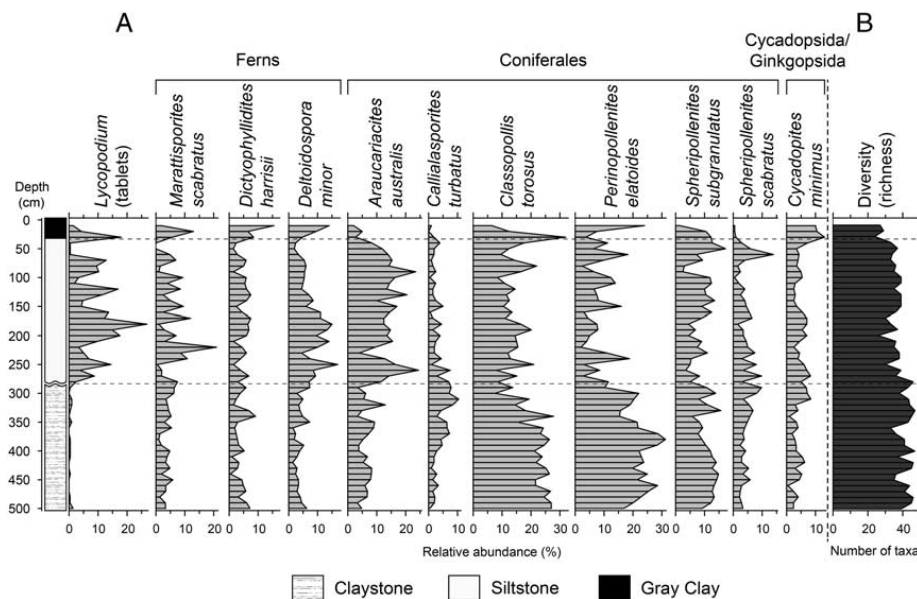


FIGURE 4. A, Relative abundance chart of the ten most abundant sporomorph taxa in addition to spiked *Lycopodium*. Relative abundances of Jurassic taxa are calculated from counts of at least 200 grains. Spiked *Lycopodium* count data is shown as a percentage of the indigenous Jurassic taxa plus the spiked *Lycopodium* itself. B, Sporomorph diversity (richness) for all samples.

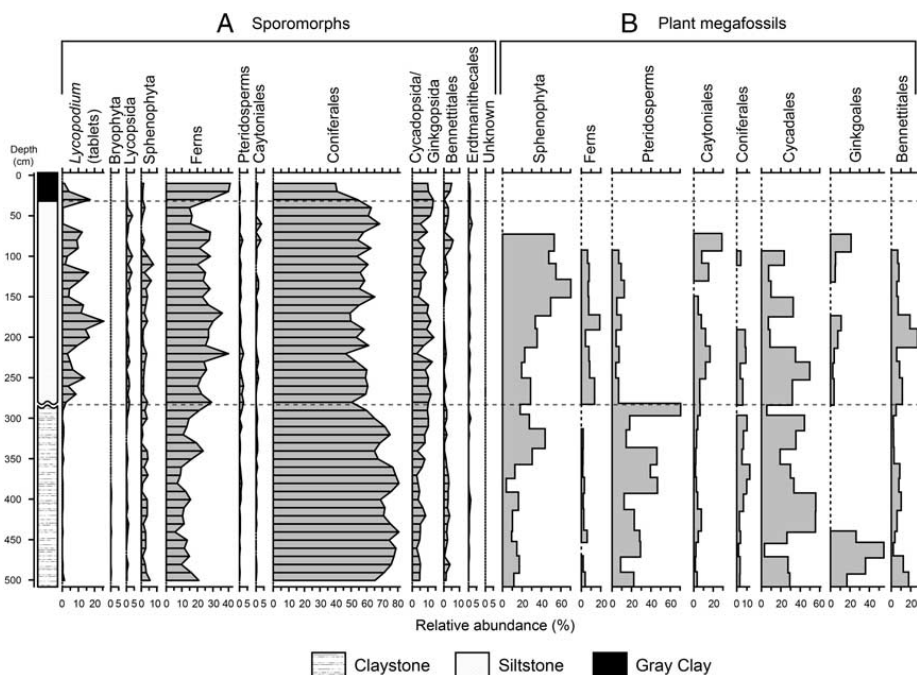


FIGURE 5. Relative abundance charts of (A) sporomorphs and (B) plant megafossils (Spicer and Hill 1979) grouped into their respective botanical affinities. Relative abundances of Jurassic sporomorph taxa are calculated from counts of at least 200 grains. Spiked *Lycopodium* count data is shown as a percentage of the indigenous Jurassic taxa plus the spiked *Lycopodium* itself.

some volatility between relative abundance and presence/absence CA (Figs. 6A,B), which potentially reflects the comparatively low abundance of conifers and low overall diversities within the gray clay. However, in all ordinations (Fig. 6) gray clay samples are consistently more similar to siltstone samples than claystone samples. In NMDS ordinations (Figs. 6C,D) samples of different lithologies are separated predominantly on axis one, suggesting this corresponds to depositional setting. Data for Figure 6 is provided in Supplementary Tables 4–7.

*Taxon Correspondence Analysis.*—The scatter plot of the first two CA axes (43% cumulative variation) of logarithmically transformed relative abundances of taxa reveals four groupings, labeled A–D (Fig. 7A). Eigenvalues and percentage variance data for Figure 7 is provided in Supplementary Table 8. Relative abundances of taxa from clusters A–D have been grouped and plotted in Figure 7B.

Cluster A (Fig. 7A) is occupied by *P. elatoides* (Taxodiaceae [van Konijnenburg-van Cittert and van der Burgh 1989; Boulter and Windle 1993; Balme 1995; Couper 1958; Mander et al. 2010; Mander 2011]), *Callialasporites turbatus* (Araucariaceae [Boulter and Windle 1993]), *C. torosus* (Cheirolepidiaceae [Harris 1979; Boulter and Windle 1993; Balme 1995; Couper 1958; Ziaja 2006; Mander et al. 2010; Mander 2011]), *Spheripollenites subgranulatus* (Taxodiaceae [Couper 1958; Boulter and Windle 1993]), and *Spheripollenites scabratus* (Taxodiaceae [Couper 1958; Boulter and Windle 1993]). Taxa from cluster A are considerably more abundant within claystone samples (Fig. 7B). Cluster B (Fig. 7A) is occupied by *C. mesozoica* (Sphenophyta [Harris 1978; Boulter and Windle 1993; Balme 1995]), *Dictyophyllidites harrisii* (Dipteridaceae/Matoniaceae [Couper 1958; Boulter and Windle 1993; van Konijnenburg-van Cittert 1993; Guignard et al. 2009]), and



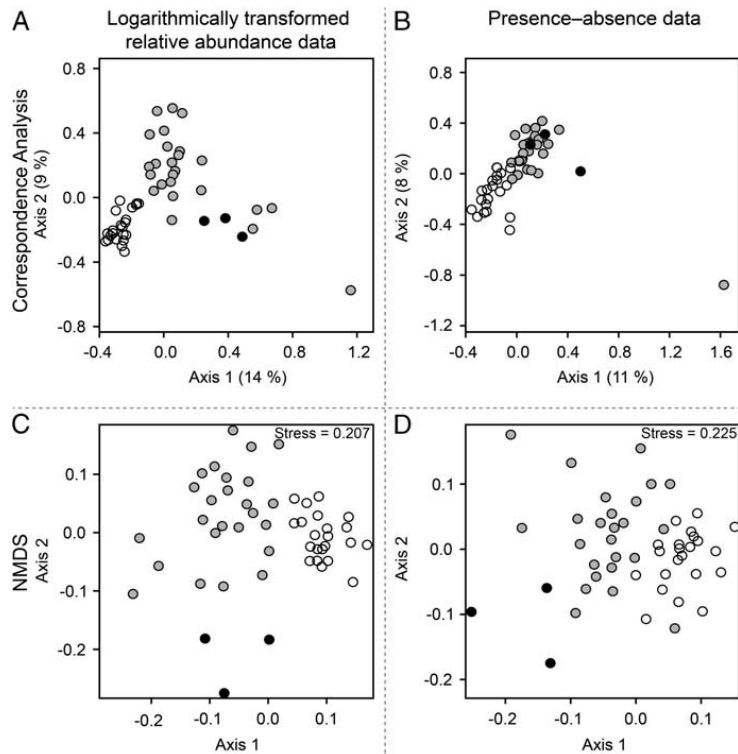


FIGURE 6. Combined ordination plots of samples (spiked *Lycopodium* excluded). A, B, correspondence analysis; C, D, nonmetric multidimensional scaling. A, C, logarithmically transformed relative abundance data; B, D, presence/absence data. White circles represent claystone samples; gray circles represent siltstone samples; black circles represent gray clay samples.

*Marattisporites scabratus* (Marattiaceae [Couper 1958; Filatoff 1975; Boulter and Windle 1993; Balme 1995]). Taxa from cluster B display little change in relative abundances through the section (Fig. 7B). Cluster C (Fig. 7A) is occupied by *A. australis* (Araucariaceae [Couper 1958; Boulter and Windle 1993; Balme 1995; Mander et al. 2010; Mander 2011; Bonis and Kürschner 2012]), *Pityosporites microalatus* (Pinaceae [Couper 1958; Boulter and Windle 1993]), *Cerebropollenites mesozoicus* (Coniferales [van Konijnenburg-van Cittert and van der Burgh 1989; Boulter and Windle 1993; Balme 1995]), *Cycadopites minimus* (Cycadales/Ginkgoales [Boulter and Windle 1993; Balme 1995; Mander et al. 2010]), and *Deltoidospora minor* (Cyatheaceae/Dicksoniaceae/Dipteridaceae/Matoniaceae [Couper 1958; Boulter and Windle 1993; van Konijnenburg-van

Cittert 1993; Guignard et al. 2009]). Taxa from cluster C are considerably more abundant within siltstone and gray clay samples (Fig. 7B). Cluster D is occupied by *Chasmatosporites apertus* (?Cycadales/?Ginkgoales/?Gnetales [Boulter and Windle 1993; Balme 1995]) and *Dictyophyllidites equixinus* (Dipteridaceae/Matoniaceae [Boulter and Windle 1993; van Konijnenburg-van Cittert 1993]). Taxa from cluster D are more abundant within siltstone samples compared to claystone and gray clay samples (Fig. 7B). *Cycadopites carpentieri* (Bennettitales [Boulter and Windle 1993]) plots separately in ordination space from clusters A–D. Figure 7B demonstrates that *C. carpentieri* is considerably more abundant within claystone samples. Relative abundances of clusters (Fig. 7B) reveal each point cloud (Fig. 7A) has a

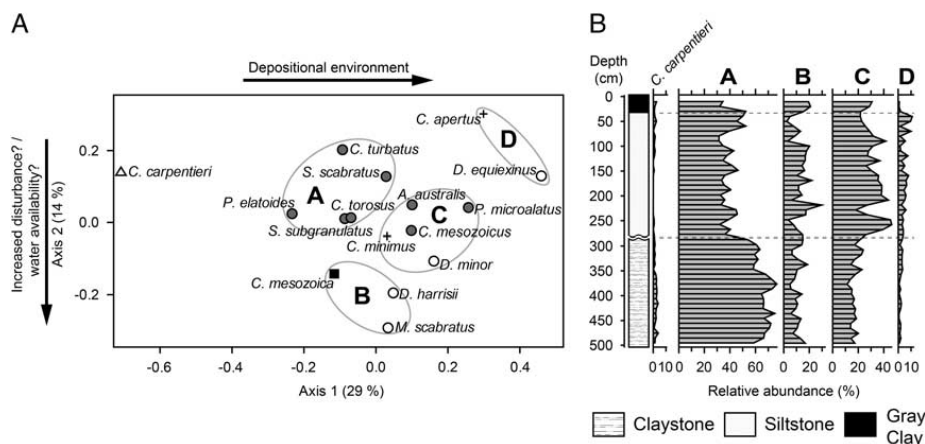


FIGURE 7. A, Correspondence analysis of taxa using logarithmically transformed sporomorph relative abundance data (excluding spiked *Lycopodium*). Squares represent sphenophytes; white circles represent ferns; gray circles represent conifers; crosses represent Cycadopsida/Ginkgopsida; triangles represent Bennettitales. Ellipses A–D show clustering of plots. B, Relative abundances of grouped taxa from clusters A–D from Figure 7A.

distinct abundance pattern between different lithological/depositional units that correlate with variation on axis one (29% variation), signifying axis one corresponds to depositional setting.

The conifer dominated clusters A and C represent possible upland communities, as conifers are typical of upland and well-drained settings (e.g., Stukins et al. 2013). Megafloral studies have hypothesized that Mesozoic ferns were typical of areas of high disturbance and water supply (Harris 1961b; van Konijnenburg-van Cittert and van der Burgh 1989; Stukins et al. 2013). The co-occurrence of Sphenophyta and fern spores in cluster B is suggestive of such a community. Ascribing a specific control for axis two (14% variation) with confidence is problematic as this could be one of a myriad of possible factors related to the principal driving mechanisms of vegetation dynamics; differential site availability, species availability and species performance (Pickett and Cadenasso 2005; Stukins et al. 2013).

**Palynofacies Analysis.**—Two palynofacies are recognized that correspond directly with lithological variation, herein referred to as palynofacies 1 and 2. Palynofacies 1 represents the gray clay and siltstone assemblage (samples HB1–HB28) and palynofacies 2

represents the claystone assemblage (samples HB29–HB50). Relative abundances of organic debris are provided in Figure 8. Palynofacies 1 is dominated by inertinite (~43%) and unstructured vitrinite (~31%). Palynofacies 2 comprises a more heterogeneous mixture of organic debris and is co-dominated by AOM (~23%), pollen (~23%), inertinite (~21%) and unstructured vitrinite (~17%).

**Comparison of Sporomorph and Plant Megafossil Assemblages.**—A direct comparison of sporomorph and plant megafossil abundance variation through the plant bed is provided in Figure 5. A comparison of the sporomorph and plant megafossil diversity (richness) data is provided in Figure 9. Sporomorph assemblages are more diverse (67 taxa) than megafossil assemblages (49 taxa in Spicer and Hill 1979).

Bryophytes are represented by two species in sporomorph assemblages and are very low in abundance through the section (Figs. 5, 9). Bryophytes are absent from megafossil assemblages (Spicer and Hill 1979).

Lycopods are highly diverse (16 taxa) within the sporomorph assemblage, however they are absent from megafossil counts (Fig. 9) (Spicer and Hill 1979). Abundances are low through the section within sporomorph assemblages (Fig. 5).

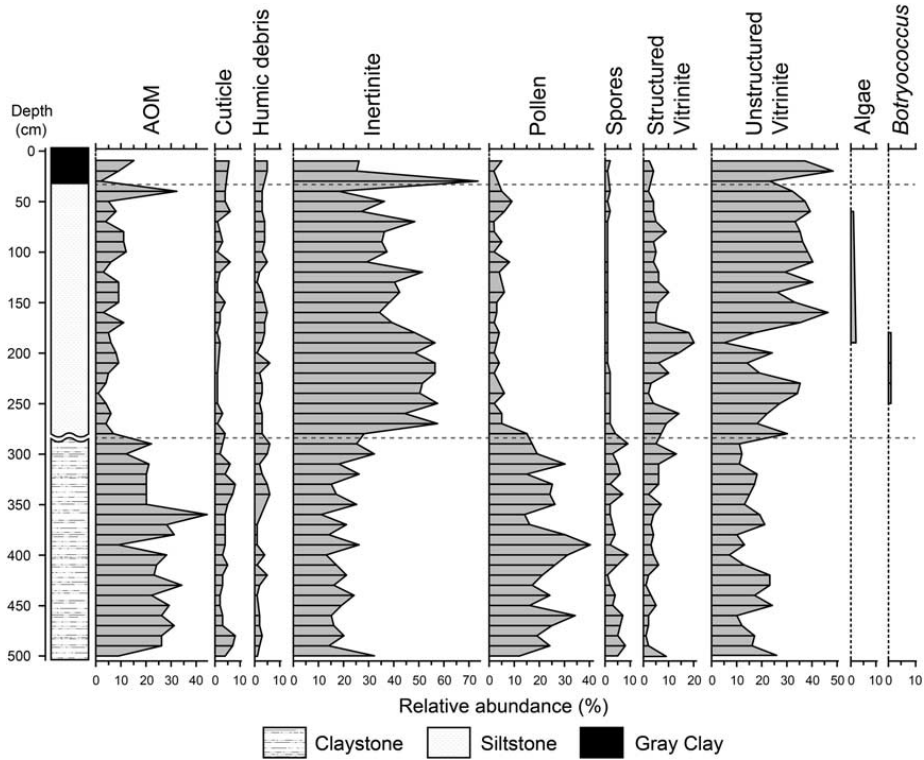


FIGURE 8. Relative abundance chart of palynofacies categories.

Sphenophytes are markedly more abundant within the megafossil assemblage (Fig. 5B) and diversity is the same (one species) in both sporomorph and megafossil assemblages (Fig. 9). Abundances are relatively constant through the section within sporomorph assemblages, however, megafossil assemblages record an increase in abundance within the siltstone compared to the claystone (Fig. 5).

Ferns are the most diverse plant group within sporomorph assemblages at Hasty Bank. Abundances (Fig. 5) and diversities (Fig. 9) are considerably higher within sporomorph assemblages (23 taxa) compared to megafossil assemblages (nine taxa). Abundances increase through the section in both sporomorph and plant megafossil assemblages (Fig. 5).

Pteridosperms are considerably more abundant (Fig. 5) and diverse (Fig. 9) within

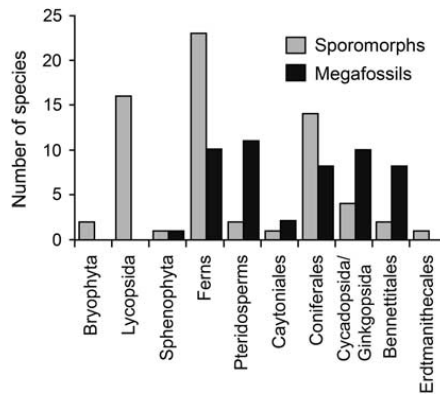


FIGURE 9. Comparative diversities (richness) of the dominant plant groups within sporomorph and plant megafossil assemblages.

megafossil assemblages (11 taxa) compared to sporomorph assemblages (two taxa). Interestingly, sporomorph and megafossil assemblages display conflicting records for pteridosperm temporal abundance variation. Specifically, megafossil assemblages record a large decrease in pteridosperm abundances across the claystone–siltstone boundary, however in sporomorph samples, pteridosperm abundances are slightly higher within the siltstone unit.

Caytoniales are more abundant (Fig. 5) and diverse (Fig. 9) in megafossil assemblages (two taxa) compared to sporomorph assemblages (one taxa). Both sporomorph and megafossil assemblages document a slight increase in Caytoniales abundance within the siltstone unit (Fig. 5).

Coniferales are the most abundant plant group within sporomorph assemblages (Fig. 5A) and diversity is high (14 taxa) (Fig. 9). Abundance (Fig. 5B) and diversity (eight taxa) (Fig. 9) in megafossil assemblages is considerably lower. Abundances decrease through the section in both sporomorph and megafossil assemblages (Fig. 5).

Cycadopsida/Ginkgopsida are considerably more abundant (Fig. 5) and diverse (Fig. 9) within megafossil assemblages (10 taxa), compared to sporomorph assemblages (four taxa). Abundances of Cycadopsida/Ginkgopsida display little change through the section within sporomorph assemblages (Fig. 5A). Conversely, abundances of Cycadales and Ginkgoales decrease through the section within megafossil assemblages (Fig. 5B).

Bennettiales are notably more abundant (Fig. 5) and diverse (Fig. 9) in megafossil assemblages (eight taxa), compared to sporomorph assemblages (two taxa). Abundances are slightly higher in the siltstone unit within both sporomorph and plant megafossil assemblages (Fig. 5).

### Discussion

*Depositional Environments.*—The sedimentology and palynofacies of the claystone indicates a low energy, low oxygen and high nutrient depositional environment. The occurrence of *Tasmanites* spp. and *Crassosphaera* spp. from samples HB50 to HB4 reveals a

marine component through the plant bed and suggests periodic flooding by seawater, as described by Harris (1964). However, *Tasmanites* spp. and *Crassosphaera* spp. are very rare (typically less than one specimen per 1000 palynomorphs) and the presence of *Botryococcus* and absence of dinoflagellates in palynofacies counts demonstrates dominantly fresh water conditions (Gray 1960; Tyson 1995). The possibility that the rare marine palynomorphs could be reworked, potentially from the underlying marine Dogger Formation, cannot be discounted. Abundant AOM in claystone samples indicates relatively low oxygen and high nutrient levels within the original water during deposition (Tyson 1995; Roncaglia 2004; Traverse 2007; Paction et al. 2011). It is difficult to state with certainty a definitive depositional setting for the claystone, however the results of this study agree with Harris' (1964) interpretations and are suggestive of a coastal plain periodically flooded by seawater, occupied by mangrove-like vegetation.

Interpretations of the depositional environment for the siltstone are consistent with previous studies that indicate this unit represents the slow moving part of a fluvial channel (Hill and van Konijnenburg-van Cittert 1973; van Konijnenburg-van Cittert and Morgans 1999). Decreased abundances of AOM signify lower nutrient levels than the claystone (Tyson 1995).

The absence of marine palynomorphs in the gray clay demonstrates marine influence is negligible to absent. Sample ordination (Fig. 6) reveals that the gray clay is compositionally more similar to the siltstone than the claystone. Sporomorph assemblages of the gray clay contain higher abundances of ferns and lower abundances of wind blown taxa, suggesting a smaller catchment area and reduced sporomorph transportation distances compared to the claystone and siltstone (Chaloner and Muir 1968). These combined factors are suggestive of a swamp or an abandoned channel environment for the gray clay.

Taphonomical models of time-averaging verses catchment area for multiple depositional environments demonstrate that the components of fossil assemblages can be used to indicate their temporal and spatial

representations (Behrensmeyer and Kidwell 1985; Behrensmeyer et al. 2000). Fossil assemblages that contain transported plant megafossils are typical of floodplain, pond and lake deposits. Such deposits generally represent time periods of ~100–10,000 years and source areas of ~100,000 m<sup>2</sup>. Sporomorphs are generally representative of larger source areas, frequently in excess of 1,000,000 m<sup>2</sup> (Behrensmeyer et al. 2000). Estimates of source areas and time-averaging for floodplain and channel environments are highly variable (Behrensmeyer et al. 2000). Channels generally represent increased time-averaging and source area sizes compared to floodplain deposits, although there is significant overlap in source area sizes and the degree of time-averaging between channels and floodplains. Interestingly, the claystone unit (coastal plain) at Hasty Bank is interpreted to represent a longer time interval and a larger source area than the siltstone (fluvial channel) due to slower sedimentation rates and the probability that numerous rivers potentially flowed into the coastal plain environment.

*Explanations for Temporal Sporomorph Variation.*—Variation in sporomorph and plant megafossil assemblages through the section can be correlated strongly with depositional change. The depositional environment is a primary control on parent vegetation, thus a change in depositional setting typically results in a change in sporomorph and megafossil assemblages. The erosional surface between the claystone and siltstone separates two distinct depositional environments by a period of unknown duration; therefore a change in floral composition between the claystone and the upper part of the section (siltstone and gray clay) is not particularly surprising. Although the claystone and gray clay are more similar to each other in terms of lithology than they are to the siltstone, the reason for their differing sporomorph assemblages is attributed to their different depositional environments and associated variable catchment areas.

The higher number of sporomorphs within the claystone unit is a result of a combination of ecological and non-ecological variables. Non-ecological variables include lithological factors, sedimentation rates and the depositional

environment. Although governed by the depositional environment, the lithology itself can impact on the preservation of sporomorphs and therefore result in apparent temporal floral variation. Spores and pollen can be considered as sedimentary particles during transportation and depositional processes; hence certain taxa are preferentially preserved based on factors such as particle size, particle shape and durability (Traverse 2007). Thus, changes in transportation and depositional processes between claystone, siltstone and gray clay units would have presumably resulted in the preferential preservation of particular taxa based on these physical factors. The preservation potential of sporomorphs is generally increased when sediment grain size is reduced and sedimentation rates are slower (Traverse 2007). Therefore, the high number of sporomorphs and high diversities within the claystone are probably a result of the relatively small grain size and slow sedimentation rates of this unit. Conversely, the siltstone is considered to have been deposited more rapidly than the claystone, thus the lower abundances and diversities of coniferous pollen within the siltstone are probably a result of faster sedimentation rates, as there would have been less time for such pollen “rain” to accumulate. The lower diversities within the siltstone compared to the claystone are also a consequence of the smaller catchment area supplying this deposit with sporomorphs. Specifically, the channel environment of the siltstone would have presumably had fewer tributaries feeding this deposit compared to the numerous rivers that would have potentially flowed into the coastal plain setting of the claystone.

Spicer and Hill (1979) postulated that differential rates of compaction could have affected floral compositions between lithologies. This could have had some influence on abundances; however, there is no conclusive sedimentological evidence that suggests compaction was vastly different between lithologies. The differential sedimentation rates and sediment grain sizes between depositional environments are considered to be far larger contributors to such abundance differences. For example, diversity is likely to be lower

TABLE 1. Sporomorph dispersal methods, sporomorph production levels, and relative parent plant heights of modern equivalents of the major plant groups in the Hasty Bank plant bed.

Plant group	Typical sporomorph dispersal method	Typical sporomorph production level	Typical modern equivalent parent plant heights	References
Bryophyta	Mostly wind	Relatively high	Very low (Some epiphytic)	Pohjamo et al. 2006
Lycopsida	Mostly wind	High	Low (Some epiphytic)	Brack-Hanes 1981; Traverse 2007
Sphenophyta	Wind	High	Relatively small	van Konijnenburg-van Cittert and Morgans 1999
Ferns	Mostly wind	Very High	Variable, mostly low (Some epiphytic)	Durand and Goldstein 2001
Pteridosperms	Mostly wind, some potentially insect	–	–	Labandeira et al. 2007
Caytoniales	Wind and ?insect	–	–	Harris 1933, 1945; Schwendemann et al. 2007; Ren et al. 2009; Labandeira 2010
Coniferales	Wind	Very high	Variable, mostly very tall	Critchfield 1985; van Konijnenburg-van Cittert and Morgans 1999
Cycadales	Wind and insect	Variable (Relatively high in wind pollinated taxa, low in wind and insect pollinated taxa)	Variable, low to moderately tall	Norstog 1987
Ginkgoales	Wind and ?insect	High	Very tall	Del Tredici 1989; van Konijnenburg-van Cittert 2010; Crane 2013; Bhowmik and Parveen 2014
Bennettitales	Wind and ?insect	–	–	Crepet et al. 1991

within the fluvial siltstone (compared to the same unit of claystone), because it was deposited more rapidly.

*Ecological Causes for Variation between Sporomorph and Plant Megafossil Assemblages.*—Table 1 shows the generalized sporomorph dispersal methods of the dominant plant groups through the Hasty Bank plant bed. The majority of plant groups in Table 1 rely on wind to disperse sporomorphs. The life habits and reproductive methods of wind dispersed taxa result in abundance and diversity discrepancies between the sporomorph and megafossil assemblages. Pollen and spore production in wind dispersed species is typically very high as the efficiency of wind pollination increases as the concentration of airborne pollen increases (Regal 1982; Whitehead 1983; Allison 1990; Friedman and Barrett 2009). The sporomorph and megafossil records at Hasty Bank reflect this bias; conifers and ferns that produce vast numbers of pollen and spores are considerably more abundant

(Fig. 5) and diverse (Fig. 9) within sporomorph assemblages.

The nature of wind pollination means that sporomorph assemblages capture spores and pollen from a significantly larger geographic area compared to plant megafossil assemblages, which are more representative of the local paleoflora (e.g., Prentice 1985). Many of the coniferous species within the sporomorph assemblage are therefore potentially not representative of the flora close to the site of deposition and are possibly more indicative of upland communities.

The physical size of parent plants also impacts on the composition of sporomorph assemblages. Pollen released at elevated heights increases dispersal distances as: (1) wind speeds are greater, (2) pollen remains within the airstream longer, and (3) there is usually less intervening vegetation to intercept pollen (Levin and Kerster 1974; Okubo and Levin 1989; Friedman and Barrett 2009). Many coniferous sporomorph taxa from the Hasty Bank plant

bed originate from large trees; this is a principal factor contributing to their high abundances within sporomorph assemblages.

Harris (1964) described the pollen organ *Pteroma thomasi* from Hasty Bank and associated this with the pteridosperm *P. papillosa* based on their similar cuticles and co-occurrence. The pollen of *P. thomasi* is most similar to the wind dispersed pollen of *Alisporites thomasi* (Harris 1964; Ziaja 2006). Spicer and Hill (1979) demonstrated that the parent plant, *P. papillosa* is markedly more abundant within the claystone, however the dispersed pollen, *A. thomasi* does not record this abundance change and is low in abundance throughout the section. Temporal changes in local vegetation are generally less well recorded among wind dispersed taxa in the sporomorph record as such taxa are captured from larger geographic areas than corresponding megafossils.

Animal-plant interactions could also be a cause of inconsistencies between sporomorph and plant megafossil assemblages. Potential insect assisted pollination in Caytoniales (Harris 1945; Labandeira 2010) could be a cause of the underrepresentation of such pollen in sporomorph assemblages (Figs. 5 and 9) as pollen production in insect pollinated plants is typically very low compared to wind dispersed taxa (e.g., Norstog 1987).

Cycads and Bennettiales display markedly lower abundances (Fig. 5) and diversities (Fig. 9) within the sporomorph record. The reproductive methods of these plants differ considerably from the exclusively wind dispersed conifers and ferns. Some modern cycads rely on a combination of wind and insect pollination (Niklas and Norstog 1984; Clark and Clark 1987; Tang 1987; Norstog and Fawcett 1989; Ornduff 1990; Pellmyr et al. 1991; Wilson 2002; Kono and Tobe 2007; Terry et al. 2007), and both fossil cycads and Bennettiales display early evidence of possible insect pollination (Crepet et al. 1991; Klavins et al. 2005; Labandeira et al. 2007). Pollen production varies greatly among modern cycads, depending on whether wind or insect pollination is dominant (Norstog 1987). Kono and Tobe (2007) demonstrated that the pollen of the modern cycad, *Cycas revoluta* occurs only in

abundance within very close proximity (~2 m) to the cones from which it is released. If Jurassic cycads share such a characteristic, cycad pollen would almost certainly be underrepresented in the sporomorph assemblage. *Nilssonina kendalliae* is the most common species within megafossil counts, constituting ~29% of the total assemblage (Spicer and Hill 1979). Harris (1964) presumed *N. kendalliae* to be of cycad or pteridosperm affinity. In situ pollen studies have associated the pollen *Androstrobus* with *N. kendalliae* (van Konijnenburg-van Cittert 1968) and more generally Nilssoniaceae (Hill 1990). In situ *Androstrobus* pollen is considered to be equivalent to dispersed *Chasmatosporites* pollen (Balme 1995). As a genus *Chasmatosporites* constitutes only ~2.9% of the total sporomorph assemblage. This abundance discrepancy is interpreted to be due to low pollen production and small dispersal ranges of cycads compared to many of the wholly wind pollinated plants. Hence, the specialized reproductive nature of cycads, Bennettiales and potentially Caytoniales (Delevoryas 1963; Harris 1974; Labandeira 2010; Mander et al. 2010) is probably the principal factor contributing to their underrepresentation in sporomorph assemblages.

The underrepresentation of cycads, Bennettiales and ginkgos in the sporomorph diversity record is potentially compounded by recognition biases. The leaves of these groups typically possess distinctive morphological features that enable easy differentiation to generic and species level (Lidgard and Crane 1990), thus the diversity of such taxa in the megafossil assemblage is high. However, the pollen of these groups is often simple and monosulcate, with little morphological and sculptural variation visible under light microscopy (Frederiksen 1980). Sporomorph species therefore potentially represent numerous parent plant species, thus diversity in the dispersed sporomorph record is underrepresented.

The high diversities of lycopsids, ferns and bryophytes in sporomorph assemblages compared to megafossil assemblages (Fig. 9) could be related to epiphytic communities. Epiphytes are generally poorly represented in the megafossil record as the burial and subsequent fossilization of such species is unlikely

compared to most other plants (Schneider and Kenrick 2001; Frahm and Newton 2005; Tstutsumi and Kato 2006; Schuettpelz and Pryer 2007, 2009; Dubuisson et al. 2009; Pšenička and Opluštil 2013). In contrast, sporomorphs released from epiphytes do not experience this bias, thus diversities of epiphytic groups are comparatively unaffected in the sporomorph record.

The absence of lycopsids and low diversity of ferns in megafossil assemblages could also be linked to the relatively low preservation potential of many non-arborescent species. Scheihing (1980) demonstrated that non-arborescent taxa are frequently underrepresented in the megafossil record as a result of: (1) the increased biomass of arborescent species, (2) difficulty in recognition of non-arborescent plant parts, and (3) shielding of the non-arborescent understory by the arborescent canopy during high energy transport and depositional processes.

*Variation in Plant and Sporomorph Durability Causing Megafossil–Sporomorph Inconsistencies.*—Many of the inconsistencies between the plant megafossil and sporomorph assemblages are interpreted to be a result of differences in durability between parent plants and associated sporomorphs.

*Equisetum columnare* is the second most abundant plant species in megafossil assemblages, constituting ~19% of the megaflorea (Spicer and Hill 1979). However, its corresponding microspore, *C. mesozoica* represents only ~2.5% of the sporomorph assemblage. This discrepancy is probably due to the highly durable nature of *Equisetum*, which means that this genus is overrepresented compared to other megafloreal taxa. Conversely, *C. mesozoica* has a low preservation potential due to its thin wall and low sporopollenin content (Traverse 2007; Grauvogel-Stamm and Lugardon 2009), thus this species is underrepresented in the sporomorph assemblage. These combined factors give rise to a notable differential preservation potential between the parent plant and sporomorph.

The high diversity of lycopsids (16 taxa) in sporomorph assemblages and their absence from megafossil assemblages suggests an extremely low preservation potential for

lycopsid remains within this deposit. The same pattern is also present within Triassic–Jurassic plant beds from East Greenland (Mander et al. 2010, 2013) and Lower Jurassic deposits of Odrowąż, central Poland (Ziaja 2006). Lycopsids are notable both for their diversity in the megaspore record of the Middle Jurassic deposits of Yorkshire (reviewed in Slater et al. 2015) and for their lack of megafossils within these deposits. Harris (1961b) summarizes studies on the lycopsid megafossil *Selaginellites falcatus*. With the exception of this species there are no other convincing reports of lycopsid megafossils from the Middle Jurassic of Yorkshire (Lindley and Hutton 1833; Hill et al. 1985; Schweitzer et al. 1997). The absence of lycopsid megafossils may also be exacerbated by the lack of recognition of delicate lycopsid remains (Skog and Hill 1992).

*Are Sporomorphs or Plant Megafossils More Informative regarding Paleofloristic Reconstructions?*—Comparison of palynological and plant megafossil records demonstrates that respective data sets reflect different aspects of the paleoflora as they preferentially preserve certain taxa based on a multitude of ecological and non-ecological variables. Such variables include spore/pollen and plant durability, absolute abundances of plant species in life, proximity of parent plants to depositional location, spore/pollen dispersal methods, spore/pollen dispersal distances, absolute numbers of spores/pollen released from parent plants, transportation distances, transportation processes, climatic variations, and the depositional environment. This study illustrates that sporomorphs preserve some aspects of the paleoflora more completely (mostly wind dispersed taxa) than megafossil assemblages. However, megafossil assemblages equally preserve other aspects of the paleoflora (mostly reproductively specialized taxa) more completely than sporomorph assemblages.

Direct quantitative comparative studies of dispersed sporomorph and plant megafossil assemblages from pre-angiosperm Mesozoic floras are relatively uncommon in the literature due to the rarity of such fossil sites (e.g., Pedersen and Lund 1980; Ziaja 2006; Mander et al. 2010). Most previous studies that incorporate dispersed sporomorphs and plant



megafossils are confined to Paleozoic (e.g., Looy and Hotton 2014), Cretaceous (e.g., Lidgard and Crane 1990; Bercovici et al. 2008, 2009) and Cenozoic (e.g., Tinner et al. 1996; Wing and Harrington 2001) floras. These floras are fundamentally different to pre-angiosperm Mesozoic communities, thus comparison of such floras with those at Hasty Bank is highly problematic. Rare examples where combined sporomorph and megafossil data have been used in vegetation reconstructions from pre-angiosperm Mesozoic floras demonstrate consistency with findings from Hasty Bank. Specifically, conifers and ferns are typically well represented in sporomorph assemblages (Jana and Hilton 2007), cycads, Bennettitales and pteridosperms are generally well represented in megafossil assemblages (Pedersen and Lund 1980; Götz et al. 2011), and bryophytes and lycopsids are often confined to sporomorph assemblages (Ziaja 2006; Mander et al. 2010, 2013). Such large discrepancies between parent plant and dispersed sporomorph assemblages questions the reliability of local vegetation reconstructions based on megafossil or sporomorph evidence in isolation and suggests that where possible a combined approach is considerably more informative.

### Conclusions

Variation in sporomorph assemblages through the Hasty Bank plant bed is the result of a change in depositional setting between the three lithological units. Changes in the depositional environments consequently influence the vegetation, catchment areas, and preservation potential of sporomorphs and plant megafossils; hence the fossil assemblages vary notably between lithologies. Discrepancies between sporomorph and plant megafossil assemblages are primarily a result of the different life habits and reproductive strategies employed by parent plants. Such differences often cause large variation in sporomorph production and dispersal distances. Differential preservation potentials between parent plants and associated spores/pollen also has a substantial impact on generating inconsistencies between sporomorph and plant megafossil data sets. This is particularly apparent

regarding the absence of lycopsids and the elevated abundances of *E. columnare* in plant megafossil assemblages (Spicer and Hill 1979). Based on the results at Hasty Bank and similar studies (e.g., Ziaja 2006; Mander et al. 2010; 2013), explaining discrepancies between sporomorph and plant megafossil assemblages requires considerable analysis and there is no "best" method of reconstructing paleofloras. Assemblage compositions are the product of a complex array of biological, geographical, and depositional factors that act inconsistently between and within sporomorph and megafossil assemblages, resulting in notable disparities between respective data sets. Refining parent plant affinities with spore and pollen in situ studies will aid in future reconstructions of paleofloras using dispersed sporomorphs.

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# Appendix 15



## Morphology and wall ultrastructure of a new and highly distinctive megaspore from the Middle Jurassic of Yorkshire, UK



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Long Nab Member

### ABSTRACT

We describe a new and rather unusual megaspore recovered from Middle Jurassic terrestrial deposits of Yorkshire, England that we name *Reticuspinosporites whytei* gen. et sp. nov. The contact area is non-trilete and is formed where an outer sculptured layer has not developed. This outer layer covers the remainder of the megaspore and bears novel sculpture consisting of a highly irregular reticulum with areas 'infilled' to form plateaus that bear long spines. Analysis of wall ultrastructure reveals a four-layered wall comprising from inside to outside: (i) innermost, separated lamina; (ii) inner homogeneous layer; (iii) central spongy layer; and (iv) outermost homogeneous layer that forms the sculpture. Wall ultrastructure is not entirely diagnostic but is most suggestive of lycopsid affinities. Unusually the megaspores commonly occur in pairs. They are not attached at their contact faces but by their equatorial or distal surfaces through entanglement of their spines. We interpret this feature as possibly an adaptation for floating and transport by water.

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### 1. Introduction

The Middle Jurassic sequence of Yorkshire contains some of the first non-marine deposits of this age to be studied in detail by geologists and palaeontologists, and thus provides an important historical context in terms of understanding terrestrial ecosystems from this time period (Young and Bird, 1822; van Konijnenburg-van Cittert and Morgans, 1999). These deposits are particularly important because they represent a relatively rare example of an extensive development of predominantly non-marine Middle Jurassic sediments and they contain abundant, often exquisitely preserved, fossil plant material. However, there are only a small number of reports of megaspores from the Middle Jurassic of Yorkshire and nearby East Midlands (Black, 1929; Murray, 1939; Kendall, 1942; Gilbert and Harris, 1953; Harris, 1961) and none for at least half a century. In this paper we report on a newly discovered megaspore which has novel wall structure and ornament, and describe it as *Reticuspinosporites whytei* gen. et sp. nov. on the basis of its morphology, gross structure and wall ultrastructure as determined by detailed observation of specimens under a light microscope (LM), scanning electron microscope (SEM) and transmission electron microscope (TEM). We also compare it with other fossil megaspore taxa and with the megaspores of extant megaspore-producing plants in order to

shed light on its biological affinities and on the ecology of its parent plant, thus adding to our knowledge of the classic Middle Jurassic flora of Yorkshire.

### 2. Previous work on megaspores from the Middle Jurassic of Yorkshire and the East Midlands

Megaspores from the Middle Jurassic of Yorkshire and elsewhere in eastern England were first recognised by Black (1929) but not described in detail. Subsequently Murray (1939), Kendall (1942), Gilbert and Harris (1953) and Harris (1961) provided more detailed descriptions of megaspores. Table 1 outlines the taxa reported within the context of a modern taxonomic and nomenclatural framework (Batten and Kovach, 1990). These early descriptions of megaspores were undertaken prior to the widespread use by palynologists/palaeobotanists of SEM and TEM technology. Therefore they were limited to LM studies of basic morphology, with illustrations largely confined to line drawings.

### 3. Geological setting

The geology of the Mesozoic deposits of the Cleveland Basin of northeast England has been intensively studied since the time of the pioneering geologists of the early nineteenth century (reviewed in Rawson and Wright, 2000). The sediments of the Middle Jurassic (Aalenian to Bathonian) Ravenscar Group represent a predominantly

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**Table 1**

Previously described megaspores from the Middle Jurassic of Yorkshire and related strata arranged in chronological order of reporting. Updated taxonomy is from Batten and Kovach (1990) and their probable affinities are from selected observations in the literature.

Taxon	Publication	Affinities
<i>Triletes (Triletes) murrayi</i> (Harris, 1961) Marcinkiewicz, 1971 (as <i>Selaginellites</i> sp.; see Harris, 1961 for synonymy)	Black (1929)	Selaginellalean based on wall ultrastructure (Kempf, 1971a).
<i>Echitriletes (Triletes) polysceles</i> (Murray, 1939) Potonié, 1956 (as <i>Triletes polysceles</i> sp. nov.)	Murray (1939)	Genus lycopsid based on in situ reports (Balme, 1995) and selaginellalean or isoetalean based on wall ultrastructure (Batten, 2012).
<i>Erlansonisporites (Triletes) sparassis</i> (Murray, 1939) Potonié, 1956 (as <i>Triletes sparassis</i> sp. nov.)	Murray (1939)	Selaginellalean based on wall ultrastructure (Taylor and Taylor, 1988).
<i>Horstisporites (Triletes) harrisi</i> (Murray, 1939) Potonié, 1956 (as <i>Triletes harrisi</i> sp. nov.)	Murray (1939)	Selaginellalean based on wall ultrastructure (Kovach, 1994 interpretation of Bergad, 1978).
<i>Minerisporites (Triletes) richardsonii</i> (Murray, 1939) Potonié, 1956 emend. Harris, 1961 (as <i>Triletes richardsonii</i> sp. nov.)	Murray (1939)	Genus lycopsid based on in situ reports (Balme, 1995) and isoetalean based on wall ultrastructure (Bergad, 1978; Archangelsky and Villar de Seoane, 1989).
<i>Paxillitriletes (Triletes) phyllicus</i> (Murray, 1939) Hall and Nicolson, 1973 (as <i>Triletes phyllicus</i> sp. nov.)	Murray (1939)	Genus isoetalean based on wall ultrastructure (Kovach and Dilcher, 1985; Baldoni and Taylor, 1987).
<i>Triletes (Triletes) murrayi</i> (Harris, 1961) Marcinkiewicz, 1971 (as <i>Triletes</i> sp. A; see Marcinkiewicz, 1971 for synonymy)	Murray (1939)	Selaginellalean based on wall ultrastructure (Kempf, 1971a).
<i>Triletes</i> sp. (in Batten and Kovach, 1990) (as <i>Triletes</i> sp. A)	Murray (1939)	Genus selaginellalean based on wall ultrastructure (Kempf, 1971a; Koppelhus and Batten, 1989).
<i>Erlansonisporites (Triletes) sparassis</i> (Murray, 1939) Potonié, 1956 (as <i>Triletes sparassis</i> Murray, 1939)	Kendall (1942)	Species selaginellalean based on wall ultrastructure (Taylor and Taylor, 1988)
<i>Triletes cyttaria</i> Kendall, 1942 (Harris, 1961 tentatively placed this in synonymy with <i>Horstisporites areolatus</i> )	Kendall (1942)	Genus selaginellalean based on wall ultrastructure (Kempf, 1971a; Koppelhus and Batten, 1989).
<i>Erlansonisporites (Triletes) sparassis</i> (Murray, 1939) Potonié, 1956 (as <i>Triletes sparassis</i> Murray, 1939)	Gilbert and Harris (1953)	Species selaginellalean based on wall ultrastructure (Taylor and Taylor, 1988)
<i>Aneuletes patera</i> Harris, 1961 (as <i>Aneuletes patera</i> gen. et sp. nov.)	Harris (1961)	Lycopsid selaginellalean based on wall ultrastructure (Batten, 2012)
<i>Bacutriletes (Triletes) corynactis</i> (Harris, 1961) Marcinkiewicz, 1971 (as <i>Triletes corynactis</i> sp. nov.)	Harris (1961)	Genus lycopsid based on in situ reports (Balme, 1995) and wall ultrastructure (Taylor and Taylor, 1988; Archangelsky and Villar de Seoane, 1991)
<i>Bacutriletes (Triletes) onodios</i> (Harris, 1961) Hopkins and Sweet, 1976 (as <i>Triletes onodios</i> sp. nov.)	Harris (1961)	Genus lycopsid based on in situ reports (Balme, 1995) and wall ultrastructure (Taylor and Taylor, 1988; Archangelsky and Villar de Seoane, 1991)
<i>Echitriletes hispidus</i> Marcinkiewicz, 1960 (as <i>Triletes russus</i> sp. nov. but synonymised by Marcinkiewicz, 1971)	Harris (1961)	Genus lycopsid based on in situ reports (Balme, 1995) and genus selaginellalean or isoetalean based on wall ultrastructure (Batten, 2012).
<i>Erlansonisporites (Triletes) sparassis</i> (Murray, 1939) Potonié, 1956 (as <i>Triletes sparassis</i> Murray, 1939)	Harris (1961)	Selaginellalean based on wall ultrastructure (Taylor and Taylor, 1988)
<i>Horstisporites (Triletes) areolatus</i> (Harris, 1935) Potonié, 1956 (as <i>Triletes areolatus</i> Harris, 1935)	Harris (1961)	Genus selaginellalean or isoetalean based on wall ultrastructure (Kempf, 1971a,b; Bergad, 1978; Taylor and Taylor, 1988; Morbelli, 1990).
<i>Horstisporites (Triletes) casses</i> (Harris, 1961) Marcinkiewicz, 1981 (as <i>Triletes casses</i> sp. nov.)	Harris (1961)	Genus selaginellalean or isoetalean based on wall ultrastructure (Kempf, 1971a,b; Bergad, 1978; Taylor and Taylor, 1988; Morbelli, 1990).
<i>Horstisporites (Triletes) harrisi</i> (Murray, 1939) Potonié, 1956 (as <i>Triletes harrisi</i> Murray, 1939)	Harris (1961)	Selaginellalean based on wall ultrastructure (Kovach, 1994 interpretation of Bergad, 1978).
<i>Horstisporites (Triletes) kendalliae</i> (Harris, 1961) Kempf, 1971b (as <i>Triletes kendalli</i> sp. nov.)	Harris (1961)	Species ?isoetalean based on wall ultrastructure (Kovach, 1994 interpretation of Kempf (1971a)
<i>Minerisporites (Triletes) richardsonii</i> (Murray, 1939) Potonié, 1956 emend. Harris, 1961 (as <i>Triletes richardsonii</i> Murray, 1939)	Harris (1961)	Genus lycopsid based on in situ reports (Balme, 1995) and isoetalean based on wall ultrastructure (Bergad, 1978; Archangelsky and Villar de Seoane, 1989).
<i>Minerisporites volucris</i> (Marcinkiewicz, 1960) (as <i>Triletes datura</i> sp. nov. but synonymised by Marcinkiewicz, 1971)	Harris (1961)	Genus lycopsid based on in situ reports (Balme, 1995) and isoetalean based on wall ultrastructure (Bergad, 1978; Archangelsky and Villar de Seoane, 1989).
<i>Paxillitriletes (Triletes) phyllicus</i> (Murray, 1939) Hall and Nicolson, 1973 (includes 'Giant form') (as <i>Triletes phyllicus</i> Murray, 1939)	Harris (1961)	Genus isoetalean based on wall ultrastructure (Kovach and Dilcher, 1985; Baldoni and Taylor, 1987).
<i>Triletes candoris</i> Marcinkiewicz, 1960 (as <i>Triletes turbanaeformis</i> sp. nov.; synonymised by Marcinkiewicz, 1981)	Harris (1961)	Genus selaginellalean based on wall ultrastructure (Kempf, 1971a; Koppelhus and Batten, 1989).
<i>Triletes (Triletes) murrayi</i> (Harris, 1961) Marcinkiewicz, 1971 (as <i>Triletes murrayi</i> sp. nov.)	Harris (1961)	Species selaginellalean based on wall ultrastructure (Kempf, 1971a).

non-marine/terrestrial part of the sequence. Regional uplift and associated sea-level fall led to the accumulation of fluviodeltaic sediments derived from uplifted land adjacent to the Cleveland Basin, although thin marine beds are present in the succession as a consequence of marine incursions from the south and east (Hemingway and Knox, 1973; Hemingway, 1974; Alexander, 1989, 1992; Rawson and Wright, 2000). The Ravenscar Group represents a rare example of Middle Jurassic non-marine deposits and is famous for its fossil plant remains (e.g. van Konijnenburg-van Cittert and Morgans, 1999) and dinosaur footprints (e.g. Romano and Whyte, 2003). The material studied in this paper is from the Bathonian Long Nab Member of the Scalby Formation. The deposits of this member are interpreted as localised channel sediments accumulating in a coastal plain setting (Nami and Leeder,

1978; Hancock and Fisher, 1981; Livera and Leeder, 1981; Fisher and Hancock, 1985).

Samples were collected in situ from a cliff section at Burniston Bay located 4 km north of Scarborough on the North Yorkshire coast (National Grid reference TA 02827/93016 as determined by a GPS). All of the megaspores were recovered from a single horizon known informally as the 'event bed' (Romano and Whyte, pers. comm.). This thin bed (40–145 mm) appears to be laterally persistent and can be traced for at least 165 m around Burniston Bay. It is interpreted as a confined crevasse splay, probably into a shallow water interdistributary bay environment (Mike Romano and Martin Whyte, pers. comm. 2012). The location and stratigraphic position of the megaspore-bearing sample are illustrated in Fig. 1.



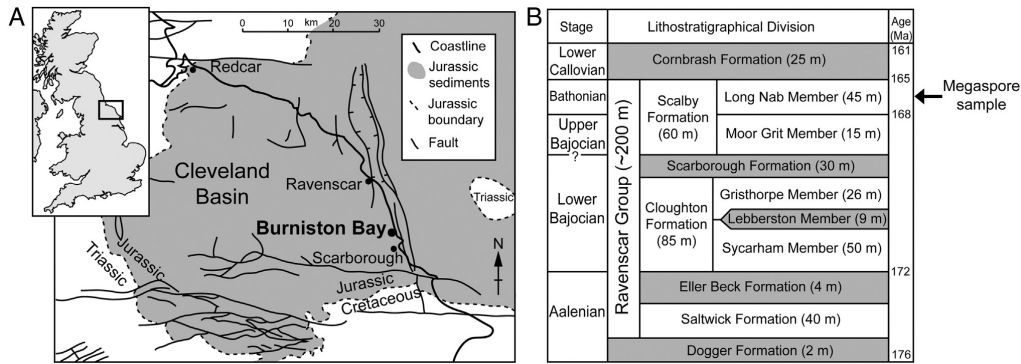


Fig. 1. Location and stratigraphic position of the megaspore-bearing sample. A, Locality and geological setting of Burniston Bay, northeast England; modified from Milsom and Rawson (1989); Mjos and Prestholm (1993); Palliani and Riding (2000); Cox and Sumner (2002); and Slater and Wellman (submitted for publication). B, Subdivision of the Middle Jurassic succession of the North Yorkshire coast with the marine units shaded; modified from Rawson and Wright (2000).

#### 4. Material and methods

The sample from Burniston Bay was subjected to digestion in 40% hydrochloric acid overnight to remove carbonates followed by three days in 40% hydrofluoric acid to remove silicates. The residue was then divided and a part of it was subjected to heavy liquid separation using zinc chloride. It was then sieved using a 20  $\mu\text{m}$  mesh and mounted on glass slides for LM examination using a Meiji Techno (MA151/35/50) light microscope. Ten specimens of the megaspore were identified under the LM. Photographs were captured using an Infinity 1-5C-180415 camera under  $\times 400$  magnification. The remainder of the residue was sieved using a 100  $\mu\text{m}$  mesh and megaspores individually picked out using a fine paint brush. Twelve were mounted on SEM stubs, gold coated using an Edwards Coater 5150B for 3 min, and examined under a Philips XL20 field emission SEM at 15 kV. Three were selected for TEM analysis. These were dehydrated in 100% ethanol for one week, impregnated with Spurr resin, and cut into ultrathin sections using a diamond knife. The sections were stained using uranyl acetate followed by Reynold's lead citrate and then studied and photographed under a FEI Tecnai Spirit TEM at 80 kV.

#### 5. Description

##### 5.1. Light microscope observation (Plate 1)

Ten megaspores were examined under a transmitted light microscope. Four are individual megaspores (Plate I, 2,4) and six occur as pairs (Plate I, 1,3). The megaspores consist of an originally spherical body with an equatorial diameter 300 (360) 450  $\mu\text{m}$  (10 specimens measured). They are partially compressed and most are broken. The megaspore pairs appear to be attached in equatorial or distal regions by entangling of their spines, although there is no obvious proximal surface/contact area discernible on any of the megaspores in LM. The sculpture is unusual in consisting of a highly irregular reticulum bearing spines (Plate I, 5,6). The muri are 1  $\mu\text{m}$  wide and 1.5  $\mu\text{m}$  high and the lumina are 10–20  $\mu\text{m}$  in maximum diameter. The arrangement of the muri and associated lumina varies considerably over the megaspore surface, much of which appears as an irregular network, but in places the muri and lumina are elongated. The spines have thickened bases (3.5–4.5  $\mu\text{m}$  wide) but are of fairly constant width (2–3  $\mu\text{m}$  wide) above; they are up to 40  $\mu\text{m}$  in length, although most appear to be broken, many having been snapped off immediately above the basal thickening (boss). Thus their apparently irregular distribution may be exaggerated because many are broken or missing. Under a LM the

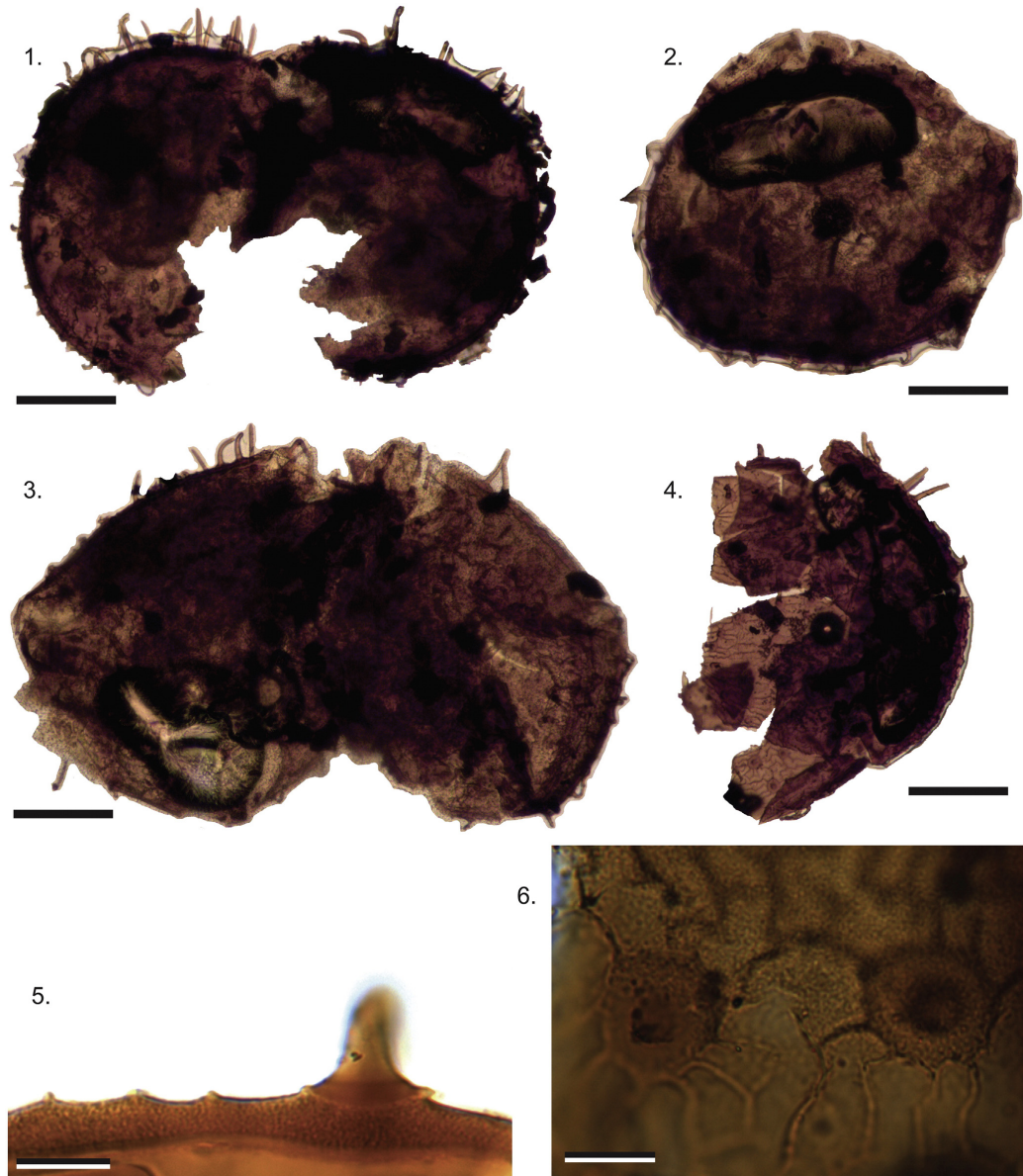
wall appears to be up to 10  $\mu\text{m}$  thick. It is predominantly spongy, but with a thin, outer, homogeneous layer that forms the muri, plateaus and spines (Plate I, 5).

##### 5.2. Scanning electron microscope observation (Plates II–III)

Twelve specimens were mounted for SEM analysis (eight individual megaspores and two pairs). In only one specimen is the nature of the presumed proximal face clearly discernible (Plate II, 2,4). It consists of a laevigate subrounded area, covering approximately one-third of the spore diameter. It appears to consist of a smooth inner layer exposed where an outer layer (bearing the reticulum and spines) that covers the remainder of the megaspore is missing. There is no obvious trilete mark on the proximal face (presumed contact area), but an irregular split possibly reflects the area of dehiscence. In other specimens that have been equatorially compressed at the margin of the contact area the outer layer appears to be somewhat extended (Plate III, 1,2,5). It is unclear if this feature is original or a consequence of compression. Details of the sculpture beyond the proximal contact areas are clearly apparent under the SEM. Elongation of the lumina in some specimens is apparent towards one of the poles, possibly towards the contact area (Plate III, 1,2,5,6). Most muri are clearly connected to others in a continuous network, but some end at spine pads and others simply terminate and are not connected to any sculptural features. The irregular nature of connections between muri forms patches of ornate sculpture where lumina are very irregular in shape (Plate II, 3). One or more spines are developed where a lumen is 'infilled' forming a plateau (Plates II, 3; III, 3). High magnification images of the spines (Plate III, 4) show that they have a roughened surface that includes occasional microspines 70 nm wide and 500 nm high. On the basis of our SEM observations we suggest that where the megaspores occur in pairs they are connected by entangled spines in equatorial or distal regions (Plates II, 7; III, 7) and not at a proximal contact area (Plates II, 7; III, 1). In broken specimens the wall layering (Plate II, 5–6) appears to consist of a thin homogeneous inner layer, a thick spongy middle layer, and a thin homogeneous outer layer that forms the sculpture (measurements given below).

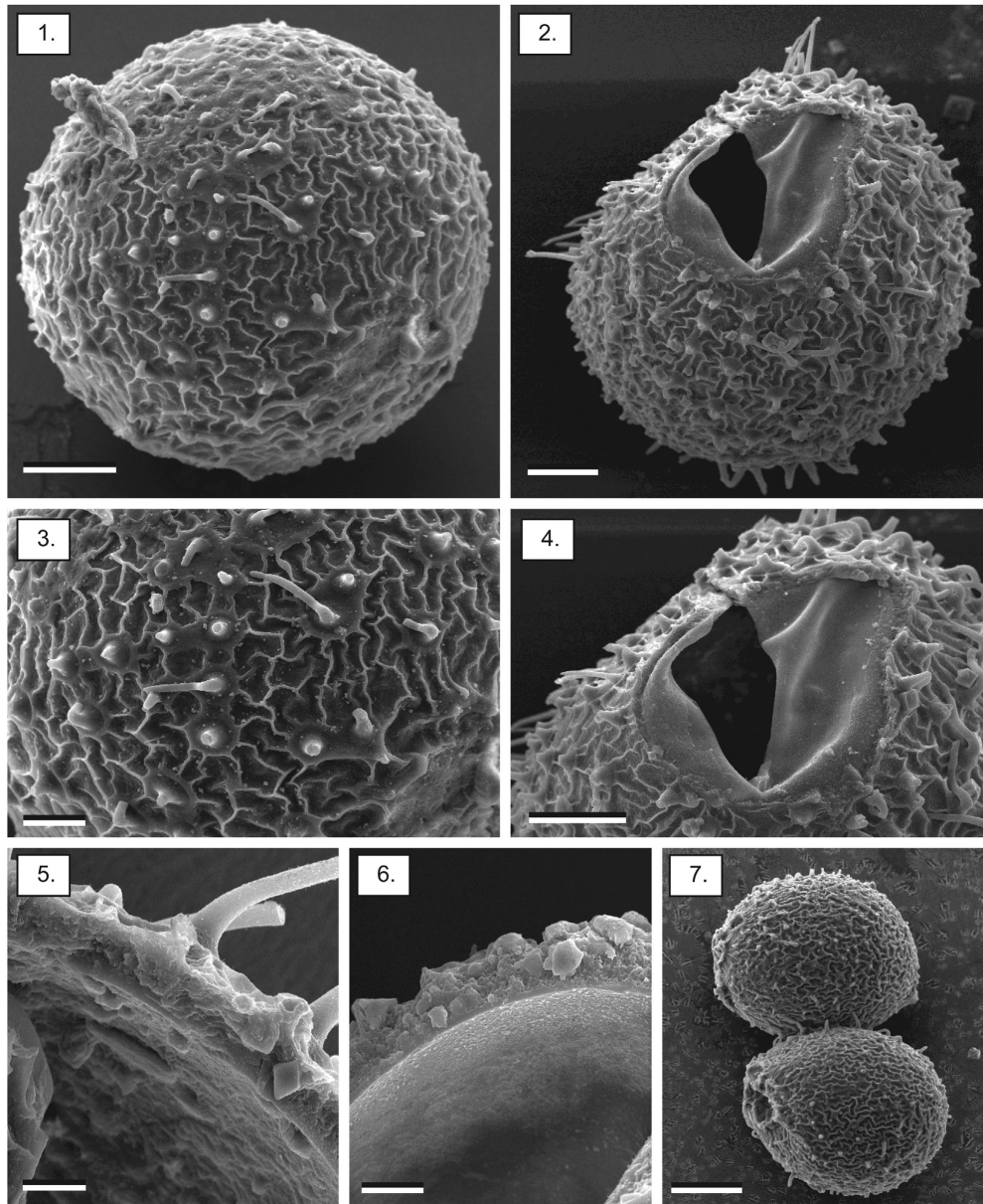
##### 5.3. Transmission electron microscope observation (Plates IV–V; Fig. 2)

Three specimens were sectioned and examined under a TEM. This clearly revealed the four-layered nature of the megaspore wall: an innermost, separated lamina; an inner homogeneous layer; a thick central spongy layer; and an outermost homogeneous layer that forms the sculpture (Fig. 2).



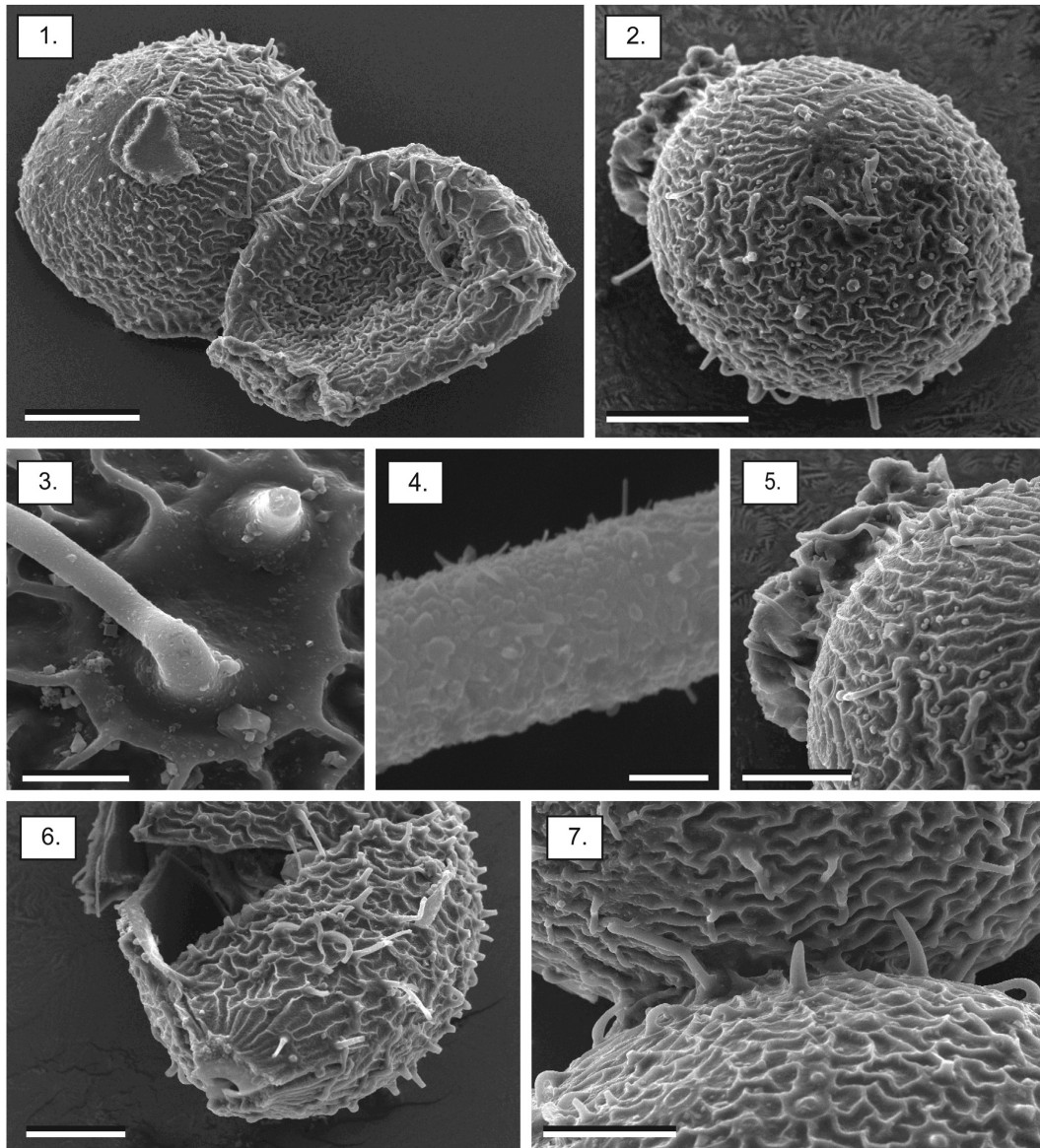
**Plate I.** LM images of *Reticusporites whytei* gen. et sp. nov.

1. Megaspore 'pair' (both megaspores broken). Slide JP2/12(2); England-finder G46. Scale bar = 100  $\mu$ m.
2. Single entire megaspore. This semi-compressed specimen contains a large air bubble toward the centre top. Slide JP2/12(3); England-finder X42. Scale bar = 100  $\mu$ m.
3. Megaspore 'pair' (both megaspores fairly complete). This semi-compressed specimen contains a large air bubble toward the bottom of the megaspore on the left. Slide JP2/12(1); England-finder T46/1. Scale bar = 100  $\mu$ m.
4. Single broken megaspore. Note the reticulate ornament that is clearly discernible on the left-hand side where only a single wall is present (i.e. one is not looking through both walls of the megaspore compressed together). Slide JP2/12(3); England-finder M32. Scale bar = 100  $\mu$ m.
5. High magnification image of the specimen illustrated in Plate I, 4. This shows the margin of the megaspore illustrating the wall with spongy structure, a single spine, and a series of three muri to the left of the spine. Note that the spine, its basal thickening, and the 'infilled lumen' are solid rather than spongy. Scale bar = 10  $\mu$ m.
6. High magnification image of the wall surface of a single megaspore. This illustrates the surface ornamentation with a reticulum and two spines. Note that the spines have a basal thickening that extends from an 'infilled lumen'. The bottom left sector is focussed on the megaspore surface and appears smooth as it is focused on the laevigate surface whereas the top right sector is focused within the megaspore wall and shows its spongy nature. Slide JP2/12(1); England-finder G28/2. Scale bar = 10  $\mu$ m.



**Plate II.** SEM images of *Reticuspinosporites whytei* gen. et sp. nov.

1. Distal view of entire megaspore. Note the erratic distribution of the reticulum, plateaus and spines. Note also the high number of broken spines represented only by their basal boss. Specimen CW096A1. Scale bar = 50  $\mu$ m.
2. Proximal view of entire megaspore. Note the laevigate contact area surrounded by the reticulate/spinose surface elsewhere. The split in the contact area is interpreted as a possible line of dehiscence. Specimen (CW096C02). Scale bar = 50  $\mu$ m.
3. High magnification image of part of the distal surface of the specimen illustrated in Plate II, 1. Specimen (CW096A1). Scale bar = 25  $\mu$ m.
4. High magnification image of the contact area on the specimen illustrated in Plate II, 2. Specimen (CW096C02). The contact area appears to be characterised by the absence of the reticulate layer. Scale bar = 50  $\mu$ m.
- 5, 6. Distal megaspore wall exposed because of fortuitous fractures of specimens CW096B3 and CW097B1 respectively. Note the inner homogenous layer, the middle spongy layer, and the outer homogeneous layer that covers the megaspore surface including the muri and spines. Scale bars = 10  $\mu$ m.
7. Megaspore 'pair'. Note how they are joined in equatorial regions with the proximal poles apparently to the left. Specimen (CW096D1). Scale bar = 100  $\mu$ m.



**Plate III.** SEM images of *Reticuspinosporites whytei* gen. et sp. nov.

1. Megaspore 'pair'. Note the irregular distribution of the reticulum over the specimens. We interpret the megaspores as being in lateral compression with the proximal surfaces facing towards the bottom left with the ridges representing the junction of the outer sculptured layer with the contact area. Specimen (CW097D1). Scale bar = 100  $\mu$ m.
2. Individual megaspore. We interpret the specimen as being in lateral compression with the proximal face oriented towards the top left with the ridge representing part of the junction of the outer sculptured layer with the contact area. Specimen (CW096C1). Scale bar = 100  $\mu$ m.
3. High magnification image of two spines. Note the 'infilled' lumen that forms a plateau and the basal thickenings of two emerging spines one of which is broken. Specimen (CW096A2). Scale bar = 10  $\mu$ m.
4. High magnification image of the spine. Note the irregular granulate surface and microspines. Specimen (CW096B4). Scale bar = 1  $\mu$ m.
5. High magnification image of the edge of the contact area from the specimen illustrated in Plate III, 2. Specimen (CW096C2). Scale bar = 50  $\mu$ m.
6. Isolated, broken, megaspore. We interpret the structure facing towards the bottom left as the proximal surface with a contact face consisting of a laevigate inner layer surrounded by the reticulate outer layer that covers the remainder of the spore. Specimen (CW096B1). Scale bar = 50  $\mu$ m.
7. High magnification image of the linkage between the megaspore pair illustrated in Plate II, 7 (CW096D2) showing entwined spines connecting individual spores. Note the contact between the spines of the two individual spores. Scale bar = 50  $\mu$ m.

The innermost lamina is approximately 150 nm in thickness (Plate IV, 1–2; Plate V, 2–3). It is always separated from the remainder of the wall and is often highly folded.

The inner homogeneous layer is approximately 2  $\mu\text{m}$  in thickness (Plate IV, 1–2; Plate V, 2–4). It is generally less electron dense than the central spongy layer. However, toward the contact with the central spongy layer it becomes more electron dense (Plate V, 2–4). There is possibly a single lamella between this layer and the adjacent central spongy layer (Fig. 2) but this is barely perceptible (Pl. V, 2).

The central spongy layer constitutes the thickest section of the spore wall (ca. 7  $\mu\text{m}$ ) (Plate IV, 1–2). There is a solid, continuous base in contact with the inner homogeneous layer below (Plate V, 2–4). This rapidly transforms into a spongy structure consisting of globular to laminated units (Plate IV, 3–4).

The outer homogeneous layer is approximately 0.5  $\mu\text{m}$  in thickness (Plate IV, 1–4; Plate V, 1). This layer forms the outer surface of the megaspore, including all of the ornament. It is extended up to 1.5  $\mu\text{m}$  forming the muri that constitute the reticulum (Plate IV, 2). It is also extended where lumina are 'infilled', forming plateaus, which extend into spines (Plate IV, 2; Plate V, 1).

#### 6. Systematic palaeontology

All materials (rock, residue, slides, SEM stubs, TEM blocks and sections) are housed in the collections of the Centre for Palynology of the University of Sheffield.

Genus *Reticusporites* gen. nov.

Type species: *R. whytei* gen. et sp. nov.

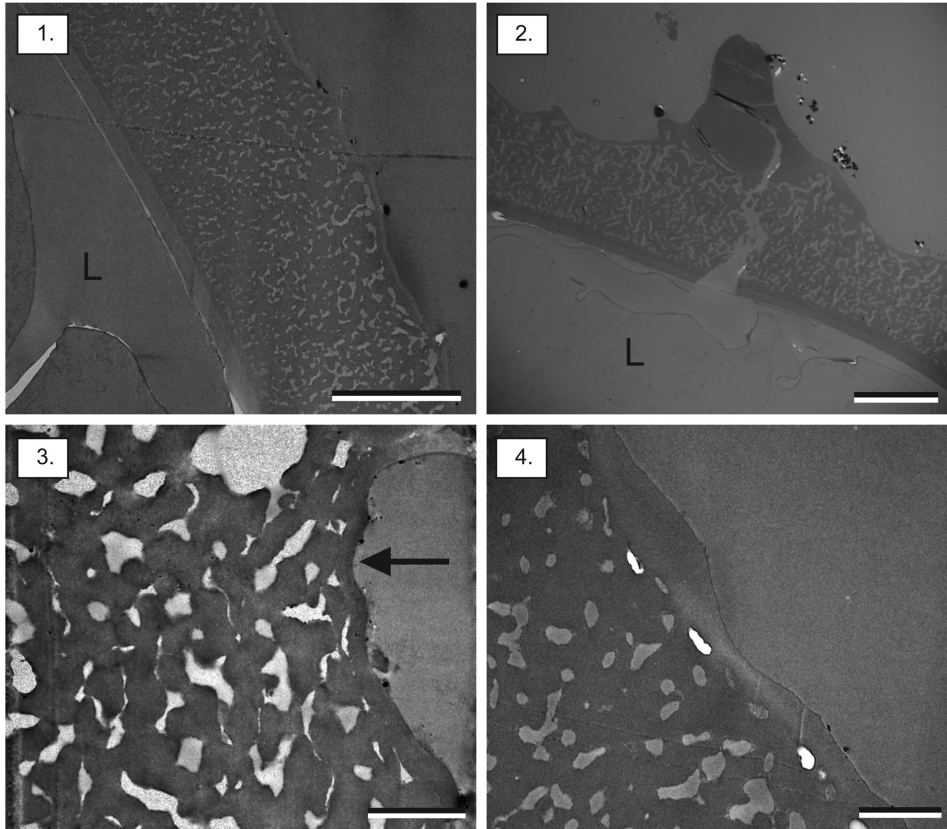
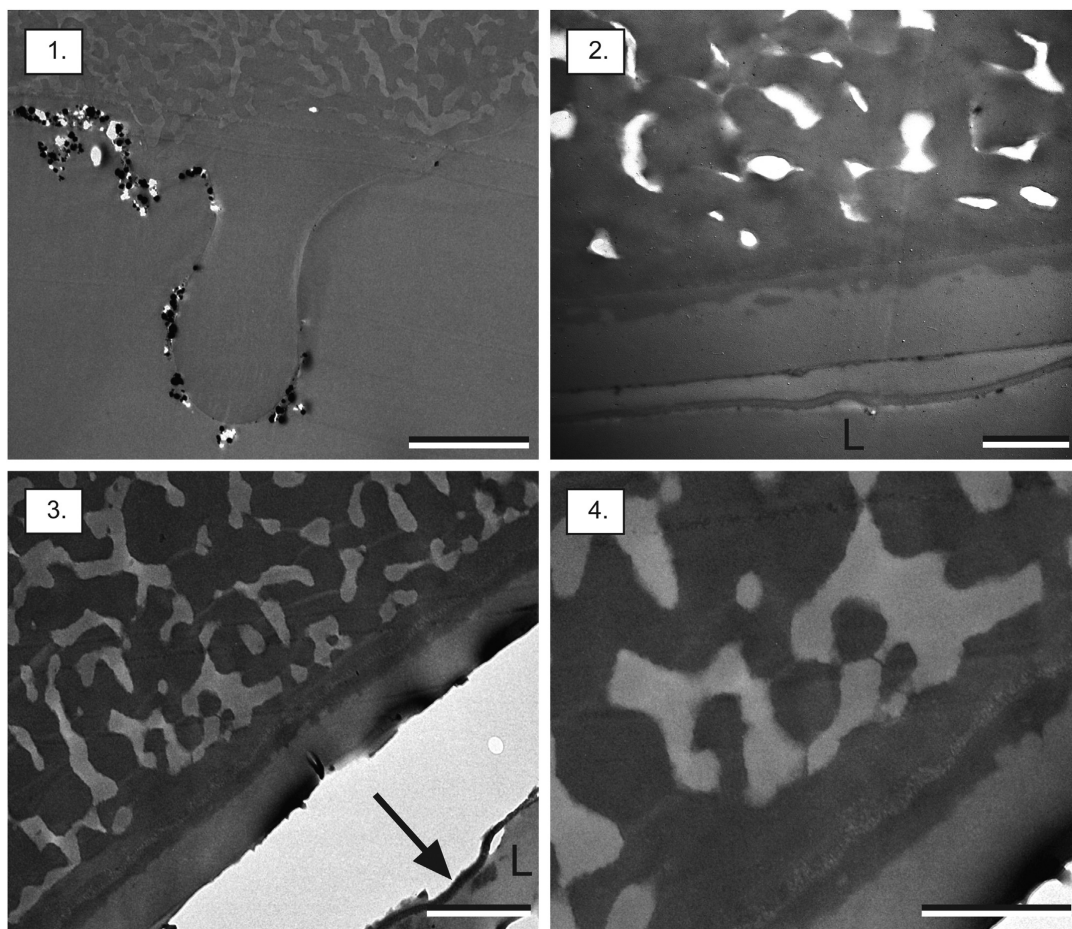


Plate IV. TEM images of *Reticusporites whytei* gen. et sp. nov. L = lumen.

1. Section through entire spore wall. All four wall layers are discernible: the innermost, separated lamina; the inner homogeneous layer; the central spongy layer; the outermost homogeneous layer. Scale bar = 10  $\mu\text{m}$ .
2. Section through entire spore wall in the region of a spine. All four wall layers are discernible. Note that the outermost homogeneous layer is extended to form the muri and the 'infilled' plateau and spine (including boss). Scale bar = 5  $\mu\text{m}$ .
3. Section showing part of the central spongy layer and outer homogeneous layer (arrow). Scale bar = 2  $\mu\text{m}$ .
4. Section showing part of the central spongy layer and outer homogeneous layer. Scale bar = 2  $\mu\text{m}$ .



**Plate V.** TEM images of *Reticusporites whytei* gen. et sp. nov. L = lumen.

1. Section through outer part of spore wall in the region of a spine. Only part of the central spongy layer and outermost homogeneous layer are shown. Note that the outermost homogeneous layer is extended to form the muri and the 'in-filled' plateau and spine (including boss) homogeneous layer. Scale bar = 5  $\mu$ m.
2. Section through inner part of spore wall showing part of the central spongy layer, the inner homogeneous layer and the innermost separated lamina. Note: (i) the continuous contact between the central spongy layer and inner homogeneous layer; (ii) the irregular darkening of the inner homogeneous layer as it approaches the central spongy layer. Scale bar = 2  $\mu$ m.
3. Section through inner part of spore wall showing part of the central spongy layer, the inner homogeneous layer and the innermost separated lamina. Note: (i) the continuous contact between the central spongy layer and inner homogeneous layer; (ii) the irregular darkening of the inner homogeneous layer as it approaches the central spongy layer; (iii) the split in the embedding medium/section immediately inside the innermost, separated lamina. Scale bar = 2.5  $\mu$ m.
4. Close up of part of (3) highlighting the continuous basal part of the central spongy layer, its continuous contact with the inner homogeneous layer and the irregular darkening of the inner homogeneous layer as it approaches the central spongy layer. Scale bar = 1  $\mu$ m.

**Generic diagnosis:** Megaspore originally spherical. Presumed contact area sub-circular and delineated by the absence of an outer sculptured wall layer revealing an inner laevigate wall layer. No obvious trilete mark. Outer sculptured layer covers the remainder of the megaspore and bears a highly distinctive sculpture consisting of a reticulum with solid areas surmounted by spines.

**Comparisons and remarks:** The presumed contact area is delineated by the absence of an outer sculptured wall layer revealing an inner laevigate wall layer. In this region the outer sculptured layer is either not developed (most likely) or has been removed, i.e. operculate (less likely).

*Echitriteles* Potonié, 1956 is apiculate (with capilli to spinae) but lacks a reticulum and is trilete. *Erlansonisporites* Potonié, 1956 is reticulate but lacks the solid areas with surmounting spines and also bears a trilete mark, although this is sometimes difficult to distinguish from the muri of the reticulum.

**Derivation of name:** After the distinctive reticulate-spinose ornament.

*R. whytei* gen. et sp. nov.

(Plates I–V)

**Holotype:** Specimen CW096C (Plate II, 2.4.) examined under a SEM.

**Type locality:** Cliff section at Burniston Bay, northeast Yorkshire, UK; Long Nab Member, Scalby Formation, Ravenscar Group (Bathonian).

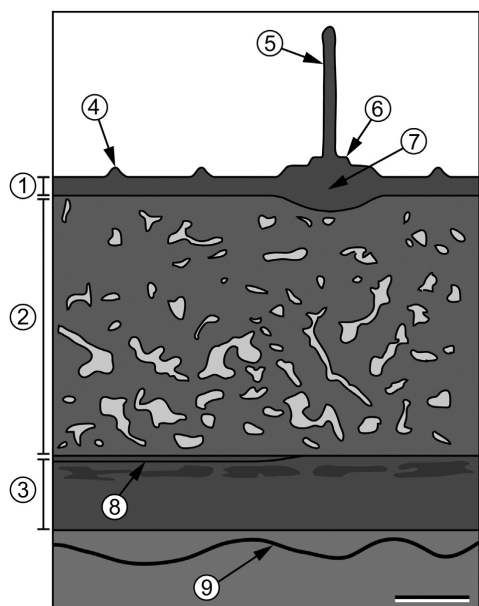


Fig. 2. Diagrammatic representation of the wall layering in *Reticulospinosporites whytei* gen. et sp. nov. 1, outermost homogeneous layer; 2, central spongy layer; 3, inner homogeneous layer (more electron dense toward exterior); 4, muri; 5, spine; 6, basal spine boss; 7, 'infilled' plateau; 8, possible lamella between inner homogeneous layer and central spongy layer; and 9, innermost separated lamina. Scale bar = 2  $\mu$ m.

**Specific diagnosis:** Comparatively small megaspore with inferred contact area approximately one-third of the diameter of the megaspore in width. Reticulum composed of narrow, low muri encompassing irregular lumina some of which are 'infilled' to form plateaus from which spines emerge. Commonly occur in pairs joined by interlinked equatorial or distal spines.

**Description:** Megaspore 300–450  $\mu$ m in diameter with an originally spherical body. Contact area sub-circular and occupies approximately one-third of the spore diameter, delineated by the absence of an outer sculptured layer that is either not developed or has been removed (?operculate) revealing an inner laevigate layer. Reticulum composed of muri 1  $\mu$ m wide and 1.5  $\mu$ m high forming highly irregular lumina 10–20  $\mu$ m in maximum diameter. Some of the lumina are 'infilled' to form plateaus from which spines up to 40  $\mu$ m high emerge. Exospore consists of four distinct layers; an innermost, separated lamina; an inner homogeneous layer; a central spongy layer consisting of globular units; and an outer homogeneous layer that forms the ornament.

**Derivation of name:** Named in honour of Martin Whyte in recognition of his enormous contribution to understanding the Jurassic geology of Yorkshire, and in particular his work on dinosaur footprints. Together with Mike Romano he kindly introduced us to this locality.

## 7. Discussion

### 7.1. Biological affinities

Assessing botanical affinities of dispersed Mesozoic megaspores relies on evidence from rare cases where in situ megaspores are present in parent plants of known affinity, analysis of morphological and ultrastructural characters of these and other fossil dispersed megaspores, and comparisons with extant heterosporous plants (water ferns and the lycopsids *Selaginella* and *Isoetes*). Previous research has

demonstrated that megaspore morphology alone is not a reliable indicator of botanical affinity but it is greatly enhanced when wall ultrastructure is also taken into account (e.g. Kovach, 1994; Taylor, 1994; Batten, 2012).

The wall ultrastructure of *R. whytei* is rather unusual and does not compare directly with that in previously described extant and fossil megaspores. In terms of the megaspores of extant plants it is most similar to that in extant *Selaginella*, particularly with respect to the central spongy layer. Wall structure of extant *Isoetes* megaspores is composed of a loosely structured exospore of sporopollenin plates that are orientated parallel to the spore surface (e.g. Pettitt, 1971; Tryon and Lugardon, 1990; Taylor, 1992, 1993; Batten, 2012). Conversely, the wall in extant *Selaginella* megaspores can consist, at least in part, of a well-ordered, compact, grid-like framework or a loosely structured labyrinthine structure (Kovach, 1994; Batten, 2012). The wall ultrastructure in *R. whytei* is most like that in the latter. The central spongy layer is also similar to that in various Mesozoic megaspores assigned to lycopsids of selaginellalean affinity (e.g. Kovach, 1994; Taylor, 1994; Batten, 2012). However, there are also similarities with spongy layers in walls of certain rhizomorphic lycopsids (e.g. Wellman et al., 2009).

Consequently we tentatively suggest lycopsid affinities based largely on similarities with the spongy layer. However, we note the rather unusual morphology and wall ultrastructure of *R. whytei* and hence our designation is tentative.

### 7.2. Implications regarding the palaeoecology of the Middle Jurassic flora of Yorkshire

*R. whytei* is the eighteenth distinct megaspore species (placed in eight genera) described from the Middle Jurassic of Yorkshire and the East Midlands (Table 1). Most, if not all, of these probably derive from lycopsids. However, lycopsid megafossils are notable in being almost absent from the Yorkshire Jurassic. Harris (1961) summarised work on *Selaginellites* (*Lycopodites*) *falcatus* (Lindley and Hutton, 1833) Schweitzer et al., 1997 (see also Hill et al., 1985), but other than this taxon there are no further convincing reports of lycopsids. A similar disparity between the number of lycopsid megaspore morphotypes recovered and scarcity of megafossil remains is typical of many other Mesozoic successions (e.g. the Wealden Early Cretaceous succession of southern England; see Batten, 2011). Even allowing for possible lack of recognition of delicate plant remains (Skog and Hill, 1992) the relative abundance of lycopsid megaspores clearly indicates a preservational bias. Indeed investigations of dispersed spores/pollen from the Middle Jurassic of Yorkshire indicate that lycopsids are of low abundance but relatively diverse and a very persistent feature of dispersed spore assemblages from throughout the sequence (Slater and Wellman, submitted for publication). Nevertheless, despite the fact that both the dispersed megaspore and miospore records suggest that lycopsids were more diverse and abundant than is evident from the plant megafossil evidence they were probably a relatively minor component of Middle Jurassic vegetation of Yorkshire and elsewhere: most were herbaceous forms related to extant selaginellales (heterosporous), lycopodiales (homosporous) and the aquatic isoetaleans (heterosporous) (Skog and Hill, 1992).

### 7.3. Why in pairs?

The fact that several of the megaspores occur in pairs is highly interesting. Clearly the pairs are robust because they have not separated during palynological processing. However, it is noteworthy that the megaspores we discovered were only found as singles or in pairs, and not in larger aggregations of three or more. It seems likely that the megaspore tetrads disassociated during or soon after development, because the dyads are not attached at their contact areas. Thus we suggest that they were not attached via a common wall that formed during spore development. Rather that they are simply attached by

intertwining of spines in equatorial and/or distal regions due to juxtapositioning either prior to or after release from the sporangium. This linking may have been facilitated by the spines having irregular granulate surfaces bearing microspines (Plate III, 4). However, in this respect the fact that they occur only as singles or in pairs is intriguing. We note that Looy et al. (2005, p. 875) reported on intact spore tetrads from the end-Permian in which "individual spores are juxtaposed or connected to each other by interlocking of the paraexospores at either the intraradial contact areas or equatorial regions".

We suggest that dispersal in pairs (and possibly also larger clumps) may be an adaptation facilitating dispersal of the megaspores. We note that in some of the megaspores of water ferns clumping aids dispersal by water. In this respect it is interesting that our Middle Jurassic megaspores have thus far only been recovered from a bed that is interpreted to reflect a large catastrophic flooding event. Perhaps the parent plants inhabited environments, such as floodplains or river banks, which were prone to flooding.

## 8. Conclusions

Heterosporous lycopsids were reasonably diverse and widely distributed in the Middle Jurassic sedimentary succession of Yorkshire, but are under-represented in the megafloora. We have erected a new genus and species of probable lycopsid megaspore from this succession based primarily on its novel structure and wall ornament. Analysis of wall ultrastructure suggests that it is most likely of lycopsid, possibly selaginellalean, affinity. Intriguingly the megaspores often occur dispersed in pairs. This may have been an adaptation to dispersal by water, which in turn suggests that the parent plant inhabited flood-prone environments.

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