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ORIGINAL PAPER

Dinosaur-plant interactions within a Middle Jurassic ecosystem—palynology of the Burniston Bay dinosaur footprint locality, Yorkshire, UK

Sam M. Slater[1,2] · **Charles H. Wellman**[2] · **Michael Romano**[3] · **Vivi Vajda**[1]

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Abstract Dinosaur footprints are abundant in the Middle Jurassic Ravenscar Group of North Yorkshire, UK. Footprints are particularly common within the Bathonian Long Nab Member of the Scalby Formation and more so within the so-called 'Burniston footprint bed' at Burniston Bay. The Yorkshire Jurassic is also famous for its exceptional plant macrofossil and spore-pollen assemblages. Here we investigate the spore-pollen record from the dinosaur footprint-bearing successions in order to reconstruct the vegetation and assess possible dinosaur-plant interactions. We also compare the spore-pollen assemblages with the macroflora of the Scalby Ness Plant Bed, which occurs within the same geological member as the Burniston succession. The spore-pollen assemblages are dominated by *Deltoidospora* spp., the majority of which were probably produced by *Coniopteris*. Lycophyte spores (including megaspores) are common in the Yorkshire Jurassic, but lycophyte parent plants are extremely poorly represented in the macroflora. Seed ferns, represented by *Alisporites* spp., are moderately abundant. Conifer pollen assemblages are dominated by *Araucariacites australis* (probably produced by *Brachyphyllum mamillare*), *Perinopollenites elatoides* and *Classopollis* spp., with additional bisaccate pollen taxa. Abundant *Ginkgo huttonii* in the macroflora suggests that much of the monosulcate pollen was produced by ginkgoes. The diverse vegetation of the Cleveland Basin presumably represented an attractive food source for herbivorous dinosaurs. The dinosaurs probably gathered at the flood plains for fresh-water and also used the non-vegetated plains and coastline as pathways. Although assigning specific makers to footprints is difficult, it is clear that a range of theropod, ornithopod and sauropod dinosaurs inhabited the area.

Keywords Jurassic · Palynology · Spores and pollen · Dinosaur footprints · Yorkshire · Ravenscar Group · Scalby Formation

Introduction

The Jurassic (201–145 million years ago) represents an important period in the history of terrestrial ecosystems as it saw several major evolutionary developments, including diversification of the dinosaurs, appearance of the first birds and expansion of bennettite and ginkgophyte floras (e.g. Upchurch and Barrett 2005; Anderson et al. 2007; Slater et al. 2018, this issue). The Jurassic deposits of Yorkshire, UK (Fig. 1a), are famous for their well-preserved fossil assemblages, and the Middle Jurassic portion of the succession (Fig. 1b) represents an exceptional example of an extensive sequence of non-marine deposits of this age. Plant macrofossils from this region are particularly well-preserved and have been studied extensively (e.g. Harris 1961, 1964, 1969, 1979; Harris et al. 1974; van Konijnenburg-van Cittert and Morgans 1999). The deposits also possess exquisite spore-pollen assemblages

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✉ Sam M. Slater
sam.slater@nrm.se

[1] Department of Palaeobiology, Swedish Museum of Natural History, 104 18 Stockholm, Sweden

[2] Department of Animal and Plant Sciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, UK

[3] 14 Green Lane, Dronfield, Sheffield S18 2LZ, UK

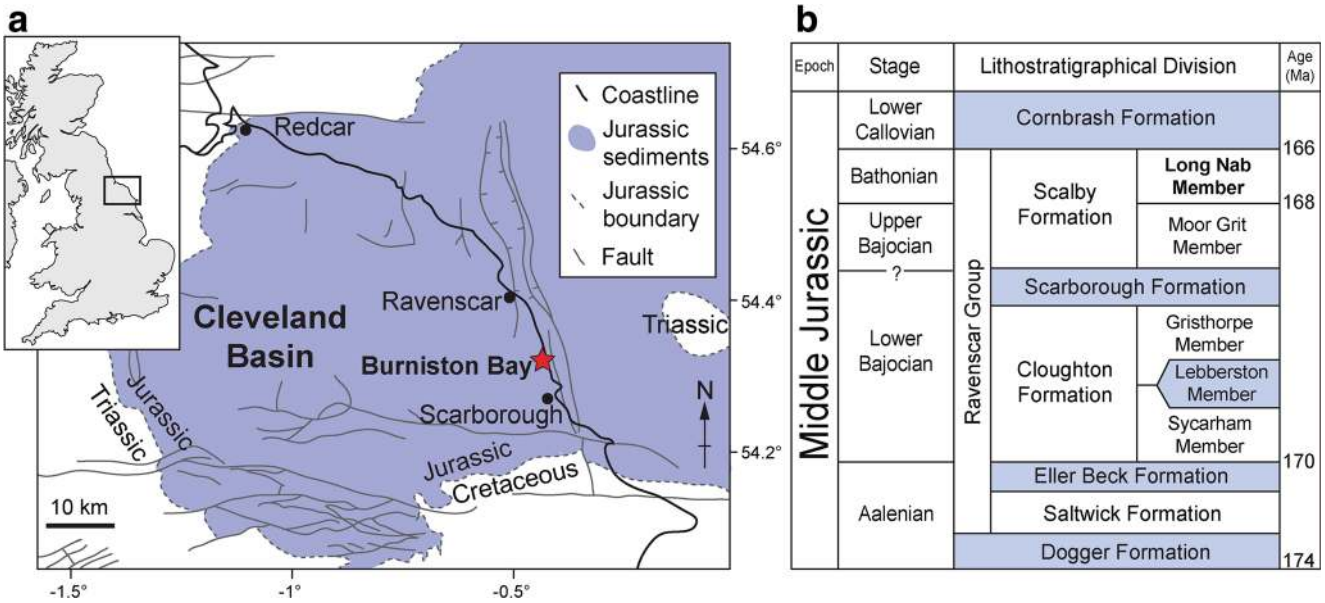


Fig. 1 Location (Burniston Bay) and stratigraphic position of the study section. **a** Geological map of the Cleveland Basin; modified from Milsom and Rawson (1989); Mjøs and Prestholm (1993); Palliani and Riding (2000); Rawson and Wright (2000). **b** Subdivision of the Middle Jurassic of Yorkshire. Shaded units represent marine successions. Modified from Rawson and Wright (2000)

(Couper 1958; Chaloner 1968; Chaloner and Muir 1968; Boulter and Windle 1993; Srivastava 2011; Slater and Wellman 2015, 2016a, b), and the abundant dinosaur footprints (Romano and Whyte 2003) make this an important region from which a relatively complete Middle Jurassic terrestrial ecosystem reconstruction can be made.

Dinosaur bones from the Jurassic of Yorkshire are extremely rare (e.g. Whyte et al. 2010; Manning et al. 2015), however, dinosaur trace fossils are highly abundant and have been well-documented since the early 1900s (e.g. Brodrick 1907; Hargreaves 1913, 1914). Based on the diversity and abundance of footprints, the Middle Jurassic of Yorkshire has been described as a 'megatracksite of global importance' (Romano and Whyte 2003). Although footprints are present throughout the Middle Jurassic of Yorkshire (selected traces shown in Fig. 3), dinosaur trace fossils are particularly common near the top of this succession from the deposits in and around Burniston Bay (Figs. 1 and 2). These sequences have yielded a wide range of track forms, including those of quadrupedal (sauropod, stegosaur) and bipedal (ornithopod, theropod) makers and possible swimming traces (Romano and Whyte 2003; Romano and Whyte 2015). The high diversity and abundance of footprints make the Burniston locality an ideal site to reconstruct the terrestrial ecosystem inhabited by the dinosaur fauna. Previous studies have shown that palynological analyses of specific beds hosting dinosaur remains or dinosaur tracks may provide a snapshot into the very ecosystems that the fauna inhabited during their lifetimes (Vajda et al. 2013a, b) and even, to some extent, the main food source of the local herbivores (Prasad et al. 2005; Vajda et al. 2016).

Most previous palynological investigations on the successions studied here have focussed on marine palynomorphs, e.g. dinoflagellate cysts (e.g. Fisher and Hancock 1985; Riding and Wright 1989). Here we examine the abundant and well-preserved dispersed spore and pollen assemblages, comparing the palynological signal between the 'Burniston footprint bed' (see below) and the adjacent beds, with the aim to reconstruct the terrestrial ecosystem in which the Yorkshire dinosaurs thrived, and ultimately investigate possible dinosaur-plant interactions.

Geological setting

The study area is located in the Cleveland Basin on the North Yorkshire coast, UK (Fig. 1a). The Mesozoic sequences of this region have been intensively studied since the early nineteenth century for their geological, sedimentological and palaeontological significance (e.g. Young and Bird 1822). The Middle Jurassic portion of the Yorkshire coast succession comprises the predominantly non-marine deposits of the Ravenscar Group (Fig. 1b). These represent mostly paralic, fluvial and lacustrine successions deposited at a time of regional uplift and associated sea-level fall (Knox 1973; Hemingway and Knox 1973; Livera and Leeder 1981; Alexander 1989, 1992; Powell 2010).

The section under investigation is located in Burniston Bay (National grid reference TA 02827/93016) and is stratigraphically situated within the Long Nab Member of the Scalby Formation, at the top of the Ravenscar Group (Fig. 2). The Scalby Formation is the youngest non-marine formation within the Ravenscar Group and is bounded below and above by the marine Scarborough and Cornbrash formations, respectively (Fig. 1b). The Scalby Formation represents fluvio-deltaic conditions (Leeder and Nami 1979; Fisher and

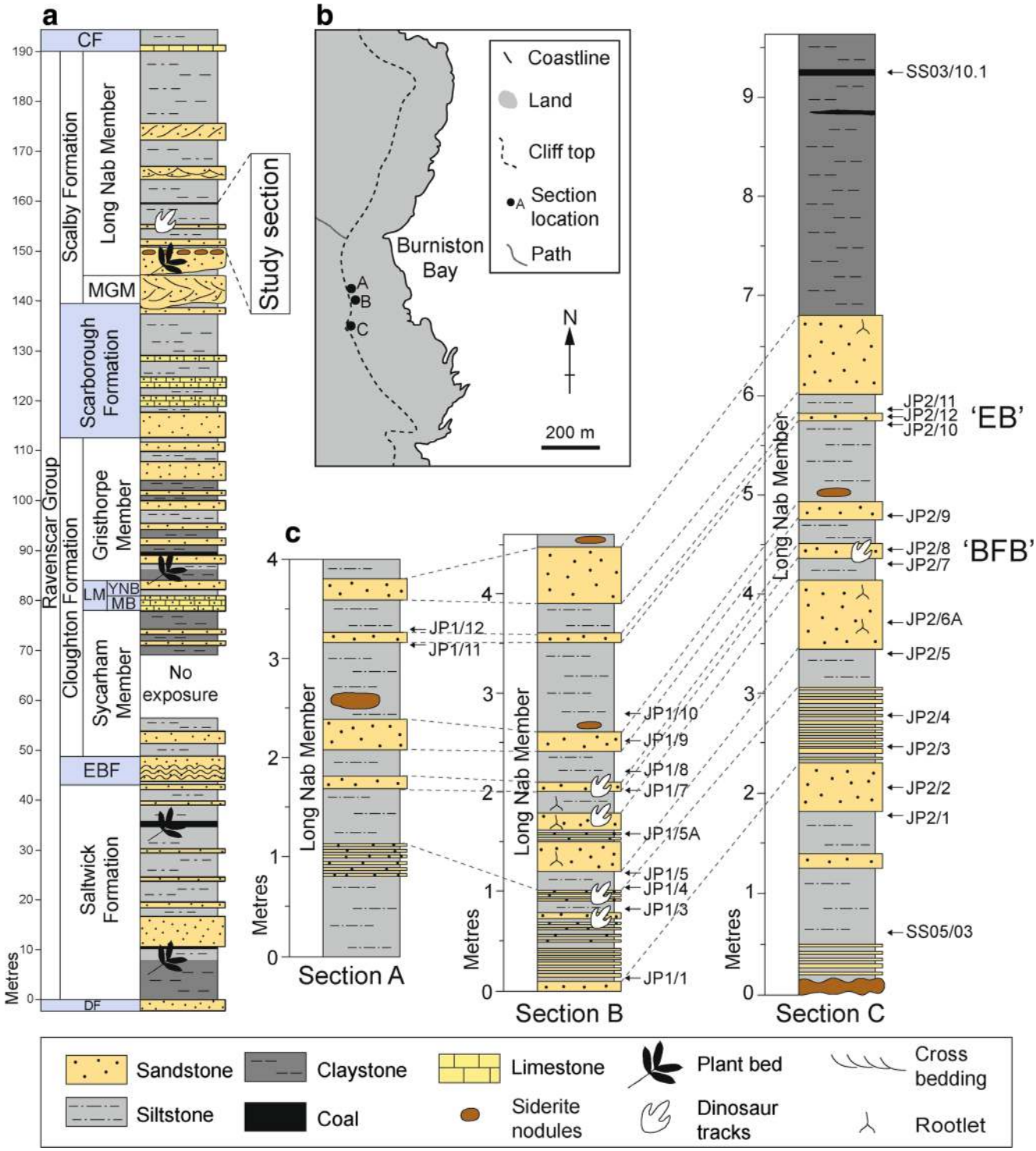


Fig. 2 Sedimentary logs and detailed location of the study section. **a** Composite sedimentary log of the Middle Jurassic of Yorkshire with the stratigraphic position of the study section. Shaded units represent marine successions. CF Cornbrash Formation, DF Dogger Formation, EBF Eller Beck Formation, LM Lebberston Member, MB Millepore Bed, MGM Moor Grit Member, YNB Yons Nab Beds. **b** Map showing locations of the studied sections. **c** Sedimentary logs of studied sections with sample horizons. 'BFB' 'Burniston footprint bed', 'EB' 'event bed'

Hancock 1985; Riding and Wright 1989) and is sub-divided into the Moor Grit and Long Nab members. The Moor Grit Member comprises coarse channel sandstones, which are overlain by finer-grained sandstones, siltstones and mudstones of the Long Nab Member. The Long Nab Member at Burniston Bay represents localised channel sediments, and also includes an exceptionally preserved meander plain (Ielpi and Ghinassi 2014) that accumulated in a coastal

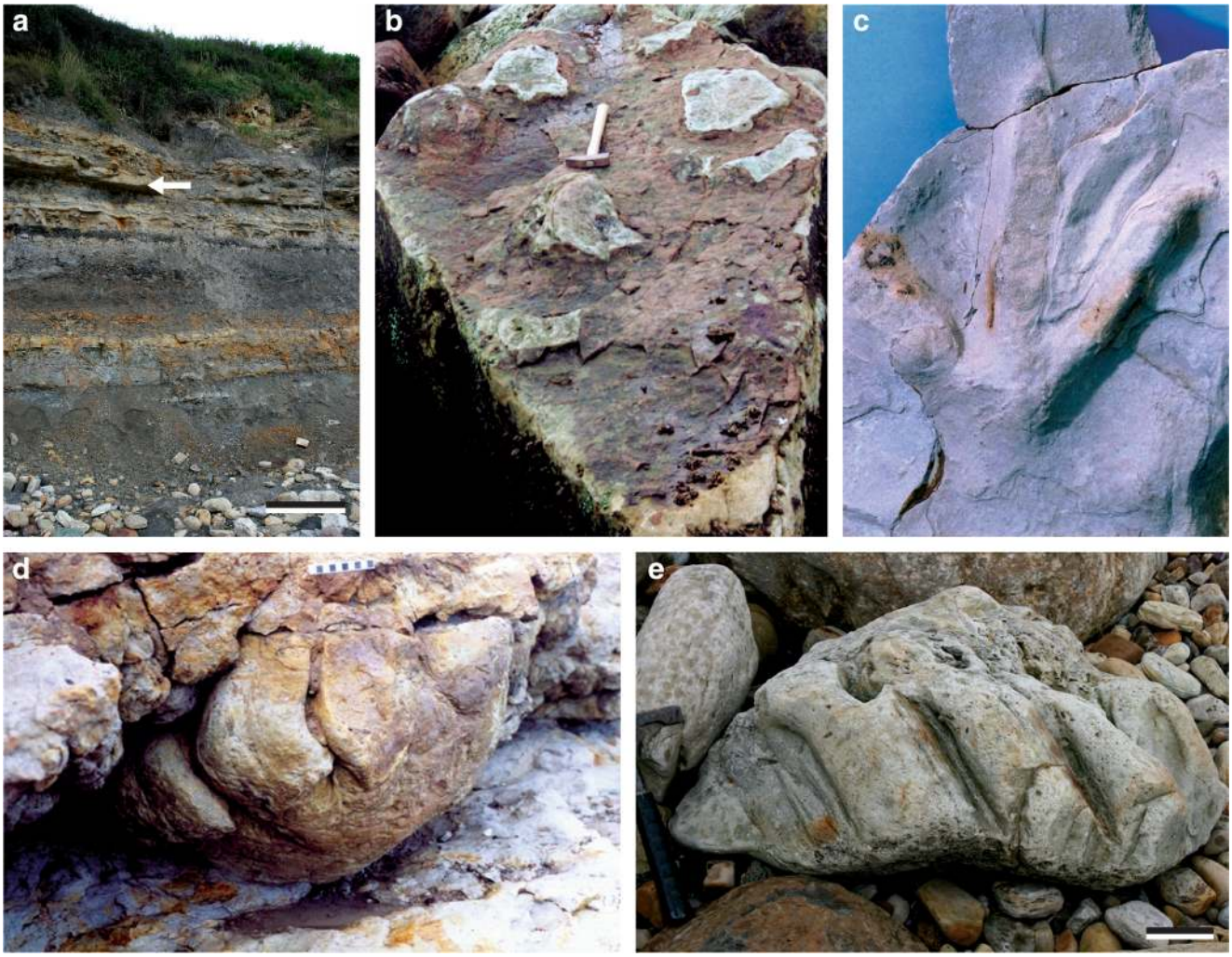


Fig. 3 The 'Burniston footprint bed' with examples of dinosaur tracks from the Jurassic of Yorkshire. **a** Sedimentary successions from Burniston Bay; arrow marks the 'Burniston footprint bed'. Scale bar = 50 cm. **b** *Deltapodus brodricki* trackway from the Saltwick Formation, Whitby, Yorkshire; note the hind foot (pes) and fore foot (manus) impressions (stegosaur maker) (Whyte and Romano 1993; Romano and Whyte 2015). Hammer is 37 cm long. **c** Imprint of a three toed-hind foot of a bipedal dinosaur; note the claw marks at the front of the digit impressions, the pads along the digits and the lack of a clearly defined heel, from the Scalby Formation, Scarborough (Romano and Whyte 2003). Print is 14 cm long. **d** Hind foot (pes) print of a sauropod dinosaur, showing the subvertical grooves made by the digits on entering, or leaving, the substrate, from the Scalby Formation, Scarborough. Note that the bulge at the base of the print does not represent the shape of the foot but is the result of preservation in the substrate (Romano and Whyte 2003). Scale bar = 10 cm. **e** Hind foot (pes) print of a sauropod dinosaur, showing the subvertical grooves made by the digits on entering, or leaving the substrate, from the Scalby Formation, Burniston Bay. Scale bar = 10 cm

plain setting (Nami and Leeder 1978; Hancock and Fisher 1981; Livera and Leeder 1981; Fisher and Hancock 1985).

An erosive boundary is present between the Scarborough and Scalby formations (Eschard et al. 1991); based on sedimentological and palynological evidence, several authors have concluded different interpretations for the time-gap represented. One hypothesis suggests a large time gap spanning the lower and middle part of the Bathonian (Leeder and Nami 1979; Hogg 1993), whilst other authors (e.g. Fisher and Hancock 1985; Riding and Wright 1989) consider the time gap to be less extensive (reviewed in Riding and Wright 1989).

Seventeen dinosaur print morphotypes were recognised from this part of the sequence by Romano and Whyte (2003); subsequently, an additional morphotype was described from the northern part of Burniston Bay (Whyte et al. 2006). This latter example was from a bed considered to be the lateral equivalent of the 'Burniston footprint bed'. The readily accessible exposures of the 'Burniston footprint bed' (Fig. 3a), in the middle of Burniston Bay, is undoubtedly a factor in the high density and diversity of dinosaur prints recorded from this part of the Ravenscar Group. However, since Hargreaves (1913, 1914) first recorded this unit, there has been no detailed study of the

sedimentology or occurrence of dinosaur prints within the 'footprint bed'. Dinosaur prints occur most commonly at the base of the lowest sandstone of this unit, but are also present towards the top of this 60 cm thick sandstone package in the middle of Burniston Bay. Further south, the package changes in character, with a higher proportion of mudrock, but dinosaur prints (normally only recognisable in section) still occur within the unit.

Material and methods

Twenty-five rock samples were collected from three cliff sections (A–C) from Burniston Bay (Figs. 2 and 3). Samples represent c. 1–5 cm in vertical section from distinct beds. Samples JP1/7 (Fig. 2c, section B) and JP2/8 (Fig. 2c, section C) were collected from the 'Burniston footprint bed'. Dry rock samples (20 g per sample) were dissolved in 40% HCl for at least 24 h, followed by 2 weeks in 40% HF. After sieving, centrifuging residues in zinc chloride was undertaken to remove heavy minerals. Sample processing details are provided in Supplementary Table 1. Residues were then sieved again to remove the heavy liquid, and final residues were spread across cover slips and gently heated to remove excess water. Cover slips were mounted onto slides using epoxy resin. Counts of a minimum of 200 spores and pollen were conducted in systematic traverses across the slides, after which the remainder of each slide was examined to identify taxa that were present in samples but not in counts. To reconstruct vegetation, we follow previous studies (e.g. Balme 1995) in linking spores and pollen to botanical groups.

Excess residues of slides that yielded megaspores were sieved at 100 μm, and specimens were picked using a fine paint brush and mounted onto SEM stubs. Specimens were gold coated using an Edwards Coater 5250B for 3 min and examined under a Philips XL20 field emission SEM at 15 kV. All materials (rock samples and slides) are housed in the collections of the Centre for Palynology at the University of Sheffield, UK.

Results

The Burniston Bay succession

Well-preserved spore and pollen assemblages (Figs. 4 and 5) of relatively high diversity in association with plant cuticle fragments (Fig. 4j) were recovered throughout the Burniston section. A total of 70 (45 spore and 25 pollen) taxa were identified. The commonly used Chao2 species richness estimator (with bias correction) (e.g. Gotelli and Colwell 2001) gave a species estimate of 72.4 (standard deviation of 3.05) for the whole dataset, indicating that the assemblages were well-sampled. Raw spore and pollen count data is provided in Supplementary Table 2. Abundance changes of selected spores and pollen and botanical groups are provided in Fig. 6.

Fern spores comprise ~ 58% of the total assemblage (ranging between 24 and 91%) and are consistently dominated by *Deltoidospora* spp. (47%) with low abundances of *Dictyophyllidites harrisii* (4.5%). Lycophyte spores are low in abundance (4%) and bryophyte spores are rare (0.1%). Seed ferns represented by *Alisporites* spp. are moderately abundant (10%). The seed fern Caytoniales is represented by the small bisaccate pollen *Vitreisporites pallidus*, and the presence of Caytoniales in the Yorkshire Jurassic ecosystem is corroborated by the occurrence of macrofossils from the world-famous plant beds scattered throughout the Ravenscar Group (e.g. Hasty Bank and Gristhorpe plant beds; see van Konijnenburg-van Cittert and Morgans 1999). Conifer pollen comprises ~ 26% of the total assemblage and is dominated by *Araucariacites australis* (8.3%), *Perinopollenites elatoides* (6.6%) and *Classopollis* spp. (3.8%), with additional bisaccate pollen taxa (5.4%). Monosulcate pollen (*Chasmatosporites* spp. [0.5%] and *Cycadopites* spp. [1.1%]) comprises a small portion of the assemblage. Abundances through the section are relatively consistent between samples, suggesting that the vegetation was reasonably stable through the studied interval; this is not particularly surprising considering the section is rather short and probably represents a relatively restricted time interval. Cuticle fragments recovered here are typically more abundant and larger than in samples from the Aalenian and Bajocian of the Yorkshire Jurassic (Slater and Wellman 2016a). This potentially indicates shorter/lower energy transportation distances in the Bathonian part of the succession as delicate cuticle would likely be damaged or destroyed during long-distance/high-energy transportation; alternatively, larger leaf fragments may have been transported and subsequently degraded to cuticle post-burial.

Megaspores were recovered from several samples; *Paxillitriletes phyllicus* (Fig. 5a, b) was recorded throughout the section within samples JP2/6A, JP2/5, JP2/4, JP2/3 and JP2/2, and *Reticuspinosporites whytei* (Fig. 5c) was recorded from a single sample, JP2/12, collected from a bed known informally as the 'event bed' (Fig. 2c, section C). This is a 40–145 mm thick bed that can be traced laterally for at least 165 m in Burniston Bay and probably represents a confined crevasse splay into a shallow water interdistributary bay setting (Romano and Whyte, pers. comm.).

The 'Burniston footprint bed'

Samples from the 'Burniston footprint bed' (JP2/8 and JP1/7; Fig. 7) are dominated by fern spores (75% [average of samples JP2/8 and JP1/7]), the vast majority of which are *Deltoidospora* spp. (61.2% of the total composition), with

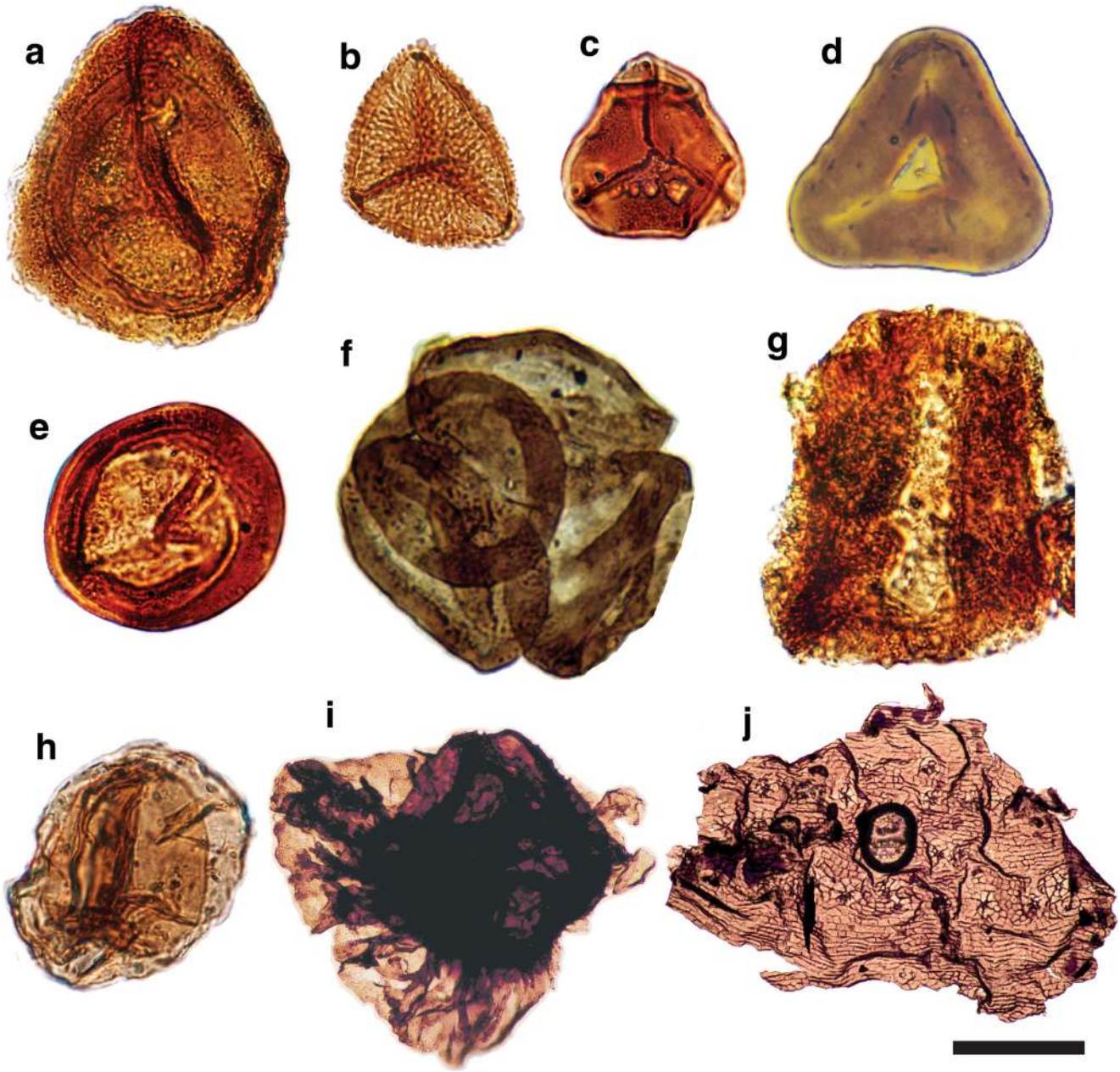


Fig. 4 Light microscope images of selected spores and pollen. **a** *Densoisporites velatus*, slide JP1/5i (England finder C40/2). **b** *Sestrosporites pseudoalveolatus*, slide JP2/6Aii (England finder F49/2). **c** *Cibotiumspora jurienensis*, slide JP1/5i (England finder Q50/2). **d** *Deltoidospora minor*, slide JP1/7i (England finder G37/4). **e** *Classopollis* spp., slide JP2/3i (England finder U43/1). **f** *Classopollis* spp. tetrad, slide JP2/11ii (England finder B41/C). **g** *Quadraeculina anellaeformis*, slide JP1/3i (England finder F39/4). **h** *Perinopollenites elatoides*, slide JP2/3ii (England finder W39/1). **i** *Paxillitriletes phyllicus*, slide JP2/3ii (England finder G24/3). **j** Cuticle fragment, sample JP1/10iv (England finder Q39/2). Scale bar = 20 μm for **a**–**h** and 100 μm for **i** and **j**

low abundances of lycophyte spores (2.8%). Conifer pollen comprises 13% of the total composition of the 'Burniston footprint bed' and is dominated by *Araucariacites australis* (4% of the total composition). Interestingly, *Cerebropollenites mesozoicus* peaks in abundance in sample JP2/8 where it comprises 6.2% of the sample. The probable seed fern pollen *Alisporites* spp. records high abundances, comprising 6 and 9.5% of the assemblage in samples JP1/7 and JP2/8, respectively. Abundances of *Perinopollenites elatoides* (1.4% [average for samples JP2/8 and JP1/7]), *Classopollis* spp. (0.5%), *Spheripollenites* spp. (0.5%) and *Callialasporites* spp. (0.2%) are low. Monosulcate pollen producers, represented by *Cycadopites* spp. and *Chasmatosporites* spp., comprise a small component (1.4%) of the assemblage.

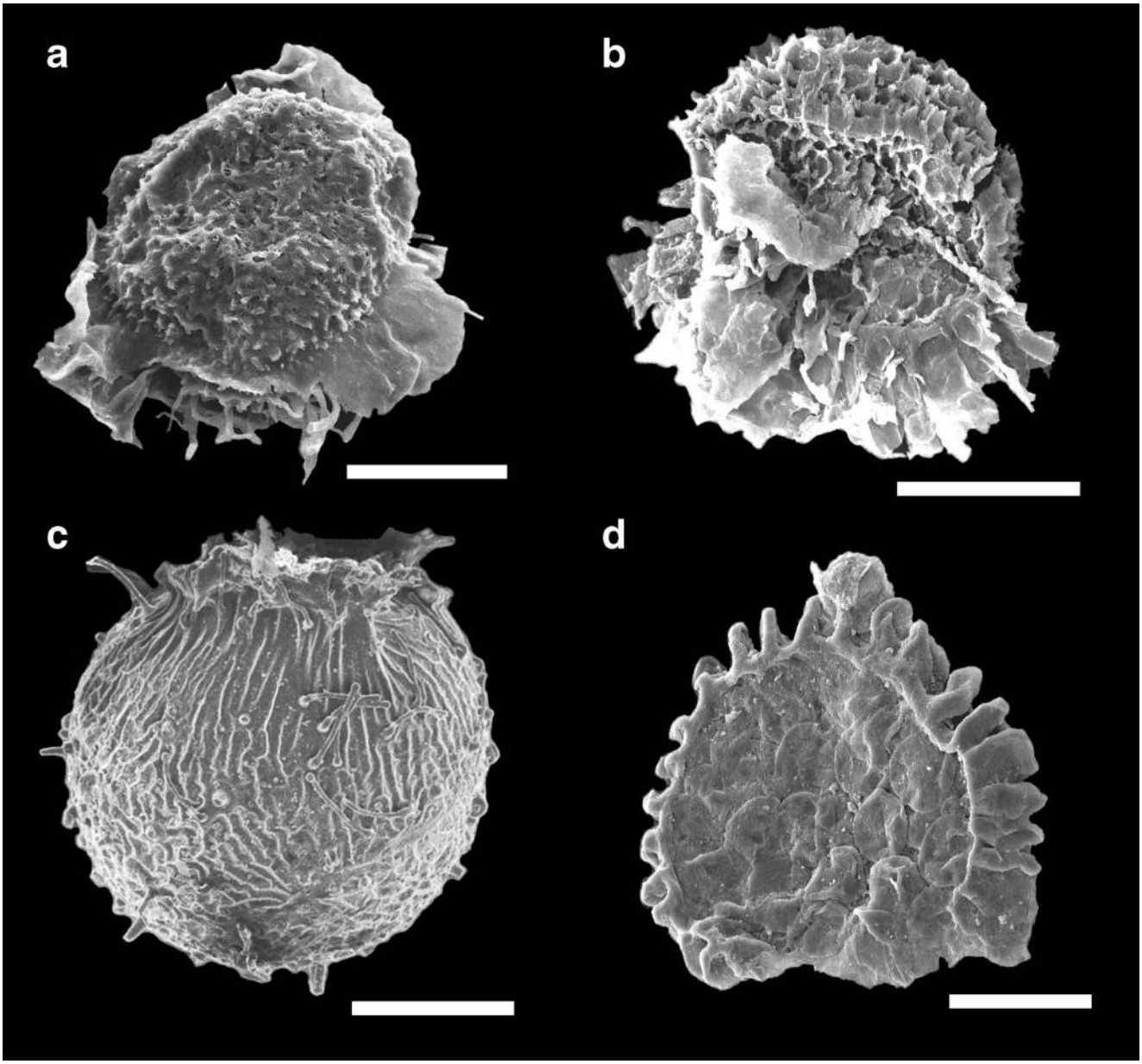


Fig. 5 Scanning electron microscope images of selected megaspores and a fern sporangium. **a**, **b** *Paxillitriletes phyllicus*: **a** sample JP2/3, **b** sample JP2/4. **c** *Reticuspinosporites whytei*, sample JP2/12. **d** Fern sporangium, sample JP2/2 (Slater and Wellman 2016a). All scale bars = 100 μm

Discussion and conclusions

Floral reconstruction

Reconstructions of the Yorkshire Jurassic flora are primarily based on the extensively studied plant macrofossil beds (see van Konijnenburg-van Cittert and Morgans 1999), which indicate a heterogeneous flora of abundant sphenopsids, ferns, seed ferns, Caytoniales, cycadophytes, ginkgophytes, Czekanowskiales, bennettites and conifers (e.g. Spicer and Hill 1979). The Scalby Ness Plant Bed, which occurs within the same member as the Burniston succession (the Long Nab Member), has yielded ~ 50 plant taxa, but particularly abundant are the leaves of *Ginkgo huttonii* (*Ginkgo huttonii* pollen is comparable to the dispersed taxa, *Cycadopites minimus*; Van Konijnenburg-van Cittert 1971; van Konijnenburg-van Cittert and Morgans 1999). Other common components include *Coniopteris bella* (fern); *Otozamites graphicus* (Bennettitales); *Czekanowskia blackii* (Czekanowskiales) and the conifers *Brachyphyllum mamillare*, *Cyparissidium blackii* and *Pityocladus scarburgensis* (van Konijnenburg-van Cittert and Morgans 1999). In the palynoflora, the monosulcate pollen probably represents mostly the ginkgophytes and bennettites,

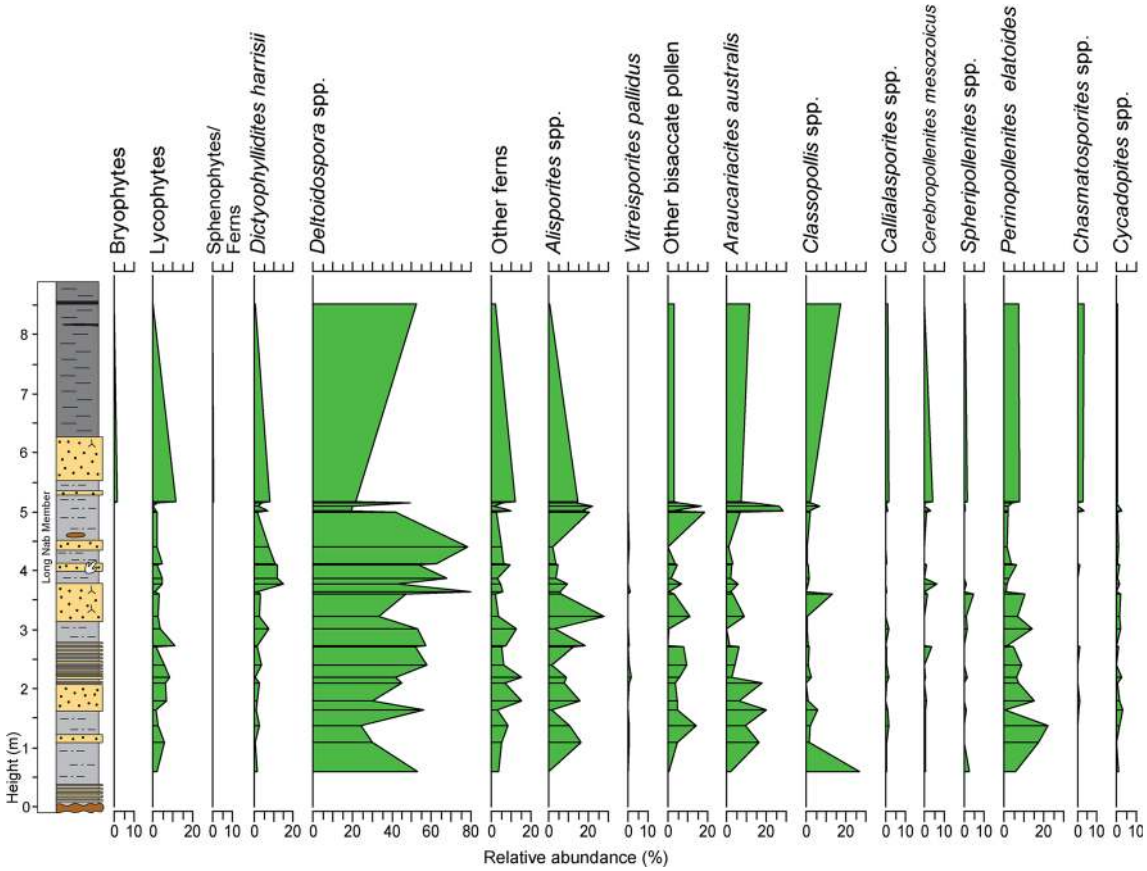


Fig. 6 Relative abundance (percentage) chart of botanical groups and selected spore-pollen taxa from all samples

and *Araucariacites australis* was probably produced by *Brachyphyllum mamillare* (van Konijnenburg-van Cittert 1971).

It is typically difficult to assign specific producers to *Deltoidospora* spp. as this genus has broad botanical affinities (e.g. Balme 1995). However, the occurrence of the ferns *Coniopteris bella* and *Coniopteris hymenophylloides* (both of which produce spores comparable to *Cyathidites*/*Deltoidospora* spp. [van Konijnenburg-van Cittert 1989; Balme 1995]) in the Scalby Ness plant bed (van Konijnenburg-van Cittert and Morgans 1999) tentatively suggests that the majority of *Deltoidospora* spp. recorded here were produced by *Coniopteris* parent plants.

The spore-pollen data preserves a more complete record of bryophytes and lycophytes—despite extensive collection of plant macrofossils from the Yorkshire Jurassic, no moss-like plants have been recorded from the plant beds (van Konijnenburg-van Cittert and Morgans 1999); liverworts and lycophytes have been described, but are rare (Harris 1961; Thomas 2017). Bryophyte and lycophyte spores are,

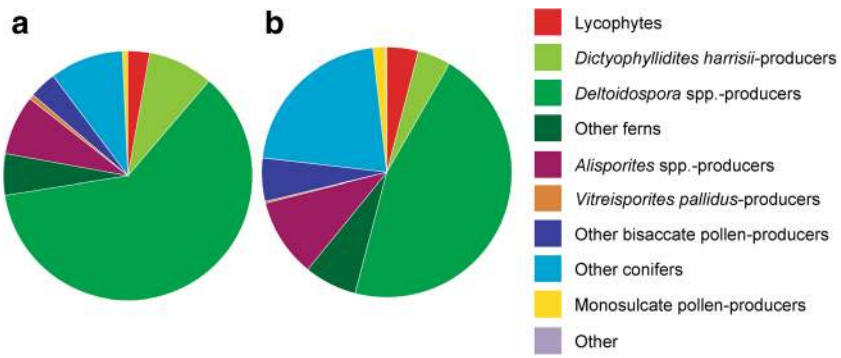


Fig. 7 Pie charts comparing the spore-pollen assemblages of the 'Burniston footprint bed' with all other samples studied here. **a** Relative abundances (average percentages) of botanical groups and selected spores/pollen from samples from the 'Burniston footprint bed' (JP2/8 and JP1/7). **b** Relative abundances (average percentages) of botanical groups and selected spores/pollen from all other samples

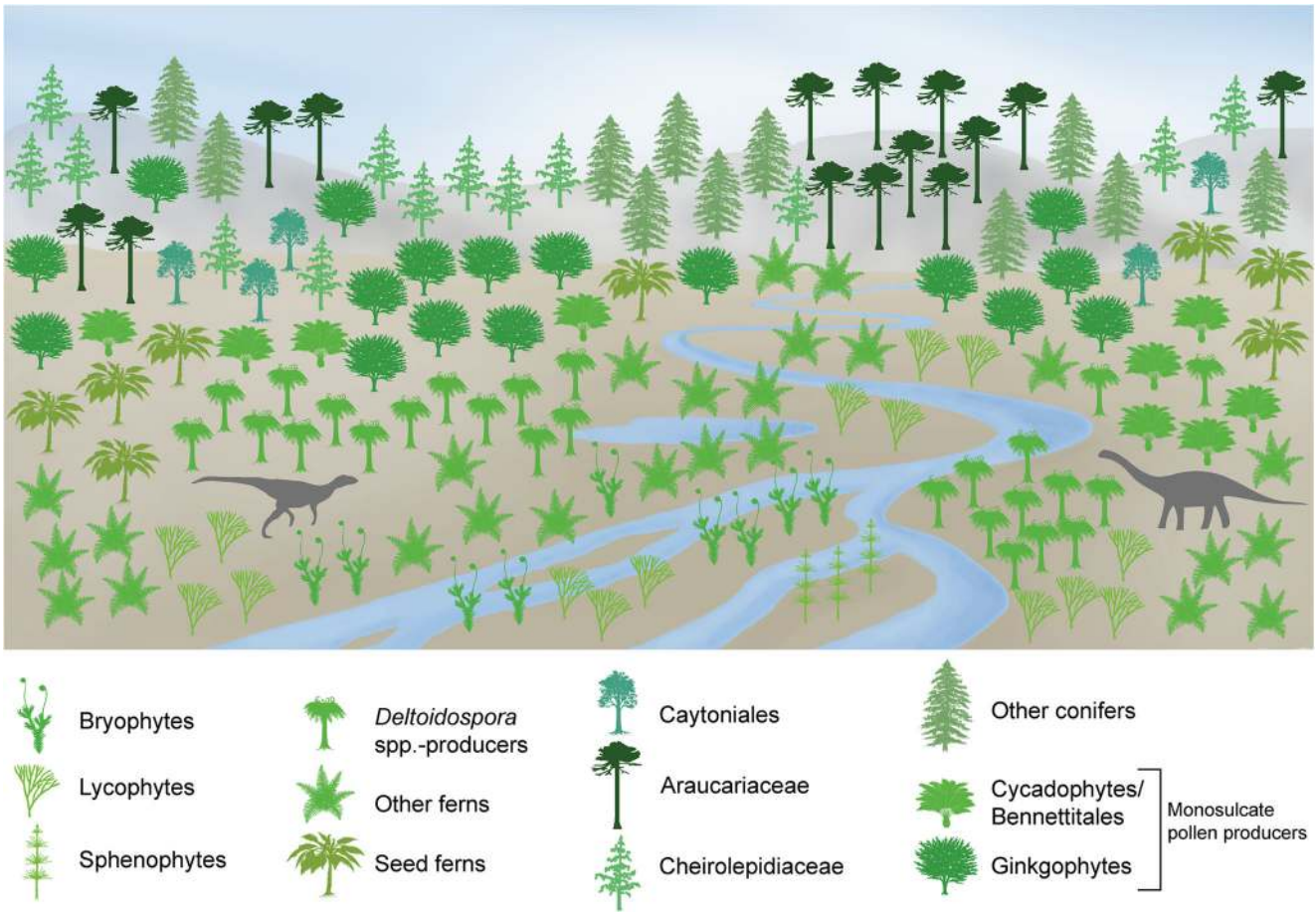


Fig. 8 Environmental reconstruction. Plant groups and distributions are based on spore-pollen assemblages

however, relatively diverse and are recovered throughout the Ravenscar Group (Slater and Wellman 2016a). Megaspores are also relatively common (e.g. Morris and Batten 2016) and most, if not all of the megaspores described from the Yorkshire Middle Jurassic originate from lycopsids. Their relatively high diversity (summarised in Slater et al. 2015) in association with lycophyte microspores indicate that lycophytes were more abundant and diverse than the macrofossil record would suggest. An explanation for the poor representation of lycophytes in the macroflora, also recognised from broadly coeval deposits elsewhere (e.g. Neri et al. 2018, this issue), is that the parent plants were possibly small herbaceous forms, some of which may have been epiphytic, and thus preservation potential would presumably be extremely low. Furthermore, a lack of recognition of delicate lycophyte remains in the Yorkshire Jurassic has contributed to their low representation in the macrofossil record (Skog and Hill 1992; Slater and Wellman 2015).

The spore-pollen assemblages of Burniston Bay differ from the older Aalenian and Bajocian parts of the Yorkshire Jurassic in containing higher abundances of lycophyte spores, fern spores and *Alisporites* spp., and lower abundances of monosulcate and conifer pollen, especially *Classopollis* spp., produced by Cheirolepidiaceae (Balme 1995), and *Perinopollenites elatoides*, produced by Cupressaceae (Balme 1995; Slater and Wellman 2016a). The Burniston assemblages compare well with the 'fern prairies' described by Boulter and Windle (1993) based on spore-pollen data from Bathonian deposits of Oxfordshire, Northamptonshire and Yorkshire. The palynology of the Burniston succession is also similar to Middle Jurassic spore-pollen assemblages from the UK North Sea (Slater et al. 2017), Scandinavia (Tralau 1967, 1968; Tralau and Artursson 1972; Gry 1969; Guy-Ohlson 1971, 1978, 1986, 1989; Mehlqvist et al. 2009; Vajda 2001; Vajda and Wigforss-Lange 2009) and Ukraine (Shevchuk et al. 2018, this issue), revealing extensive, relatively homogenous vegetation extending across Europe at this time.

Dinosaur palaeoecology

The dinosaurs of the Yorkshire Jurassic, many of them herbivores, probably gathered at the flood plains of the Cleveland Basin to gain access to fresh-water and also used the non-vegetated plains and coastline (cf. Diedrich 2011) as pathways. The diverse vegetation and low-lying land of the Cleveland Basin (Fig. 8) presumably represented an attractive

and easily accessible food source for the dinosaurs. Whilst at present it has generally not proved possible to assign specific makers to the footprints, it is clear that a range of theropod (large and small), ornithopod (large and small gracile) and sauropod dinosaurs inhabited the area during the Middle Jurassic; in particular, a top theropod predator may tentatively be assigned to *Megalosaurus* (Whyte et al. 2006).

The topic of dinosaur herbivory has received much attention in recent years (e.g. Sander et al. 2010; Gee 2011; Sander et al. 2011; Clauss et al. 2013; Barrett 2014). Direct evidence of diets (e.g. 'stomach' contents) is rare in the fossil record; however, assessing diets through the study of coprolites has revealed valuable information concerning the habitat in which the animals lived (Scott et al. 2003; Vajda et al. 2016). High phosphate content (originating from undigested skeletal matter) and the presence of bone fragments in coprolites characterise carnivores, and these tend to fossilise to a greater extent (Chin 2002). Interestingly, enhanced preservation of palynomorphs within coprolites compared to host-rocks has been noted and attributed to rapid burial and encasement in calcium phosphate preventing degradation of sporopollenin (Vajda et al. 2016). Caution should, however, be taken when referring pollen and cuticle contents of coprolites to diets as particles tend to attach to faecal matter when moist (Andrews and Fernández-Jalvo 1998), and further, fungi often develop on faeces, which can falsely suggest a fungal diet (Sander et al. 2010).

Several examples of coprolites have been recorded from the Yorkshire Jurassic. Hill (1976) described a cluster of c. 250 coprolite pellets from the Saltwick Formation, each measuring 8–18 mm in diameter, which are considered to be dinosaurian in origin (Chin 1997, 2007; Weishampel et al. 2004). Cuticles were recovered from the coprolites comprising > 99% *Ptilophyllum pectinoides* (Bennettitales). Harris (1946, 1951, 1956, 1964) and Harris et al. (1974) recorded smaller clusters of smaller pellets from the Jurassic of Yorkshire which were predominantly composed of *Caytonia*, *Solenites*, *Androstrobus* and thin bennettitalean cuticles; however, these were probably not produced by dinosaurs (Whyte et al. 2010).

Based on experiments to evaluate metabolizable energy content of various gymnosperms and spore-producing plants, Hummel et al. (2008) demonstrated that *Equisetum*, *Araucaria*, *Ginkgo* and *Angiopteris* represented viable food sources for sauropods. These plant genera are frequently recovered from dinosaur-bearing deposits (e.g. Hinz et al. 2010), and *Equisetum* is abundant in the lower parts of the Ravenscar Group (Spicer and Hill 1979), where dinosaur footprints also occur (Romano and Whyte 2003). In the Burniston succession, abundances of *Araucariacites australis* are high within conifer pollen assemblages, and the dominance of *Ginkgo* in the Scalby Ness Plant Bed points towards a possible Araucariaceae and *Ginkgo* food source. Speculation of dinosaurian diets based on vegetation reconstructions in dinosaur-inhabited regions is, however, tentative, and potential future direct lines of evidence from the Yorkshire Jurassic will assist to test such hypotheses.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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