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

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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.

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
Trileites (*Triletes*) *murrayi* (Harris, 1961) Marcinkiewicz, 1971 (as *Selaginellites* sp.; see Harris, 1961 for synonymy)	Black (1929)	Selaginellalean based on wall ultrastructure (Kempf, 1971a).
Echitriletes (*Triletes*) *polysceles* (Murray, 1939) Potonié, 1956 (as *Triletes polysceles* sp. nov.)	Murray (1939)	Genus lycopsid based on in situ reports (Balme, 1995) and selaginellalean or isoetalean based on wall ultrastructure (Batten, 2012).
Erlansonisporites (*Triletes*) *sparassis* (Murray, 1939) Potonié, 1956 (as *Triletes sparassis* sp. nov.)	Murray (1939)	Selaginellalean based on wall ultrastructure (Taylor and Taylor, 1988).
Horstisporites (*Triletes*) *harrisii* (Murray, 1939) Potonié, 1956 (as *Triletes harrisii* sp. nov.)	Murray (1939)	Selaginellalean based on wall ultrastructure (Kovach, 1994 interpretation of Bergad, 1978).
Minerisporites (*Triletes*) *richardsonii* (Murray, 1939) Potonié, 1956 emend. Harris, 1961 (as *Triletes richardsonii* 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).
Paxillitriletes (*Triletes*) *phyllicus* (Murray, 1939) Hall and Nicolson, 1973 (as *Triletes phyllicus* sp. nov.)	Murray (1939)	Genus isoetalean based on wall ultrastructure (Kovach and Dilcher, 1985; Baldoni and Taylor, 1987).
Trileites (*Triletes*) *murrayi* (Harris, 1961) Marcinkiewicz, 1971 (as *Triletes* sp. A; see Marcinkiewicz, 1971 for synonymy)	Murray (1939)	Selaginellalean based on wall ultrastructure (Kempf, 1971a).
Trileites sp. (in Batten and Kovach, 1990) (as *Trileites* sp. A)	Murray (1939)	Genus selaginellalean based on wall ultrastructure (Kempf, 1971a; Koppelhus and Batten, 1989).
Erlansonisporites (*Triletes*) *sparassis* (Murray, 1939) Potonié, 1956 (as *Triletes sparassis* Murray, 1939)	Kendall (1942)	Species selaginellalean based on wall ultrastructure (Taylor and Taylor, 1988)
Triletes cyttaria Kendall, 1942 (Harris, 1961 tentatively placed this in synonymy with *Horstisporites areolatus*)	Kendall (1942)	Genus selaginellalean based on wall ultrastructure (Kempf, 1971a; Koppelhus and Batten, 1989).
Erlansonisporites (*Triletes*) *sparassis* (Murray, 1939) Potonié, 1956 (as *Triletes sparassis* Murray, 1939)	Gilbert and Harris (1953)	Species selaginellalean based on wall ultrastructure (Taylor and Taylor, 1988)
Aneuletes patera Harris, 1961 (as *Aneuletes patera* gen. et sp. nov.)	Harris (1961)	Lycopsid selaginellalean based on wall ultrastructure (Batten, 2012)
Bacutriletes (*Triletes*) *corynactis* (Harris, 1961) Marcinkiewicz, 1971 (as *Triletes corynactis* 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)
Bacutriletes (*Triletes*) *onodios* (Harris, 1961) Hopkins and Sweet, 1976 (as *Triletes onodios* 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)
Echitriletes hispidus Marcinkiewicz, 1960 (as *Triletes russus* 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).
Erlansonisporites (*Triletes*) *sparassis* (Murray, 1939) Potonié, 1956 (as *Triletes sparassis* Murray, 1939)	Harris (1961)	Selaginellalean based on wall ultrastructure (Taylor and Taylor, 1988)
Horstisporites (*Triletes*) *areolatus* (Harris, 1935) Potonié, 1956 (as *Triletes areolatus* Harris, 1935)	Harris (1961)	Genus selaginellallean or isoetalen based on wall ultrastructure (Kempf, 1971a,b; Bergad, 1978; Taylor and Taylor, 1988; Morbelli, 1990).
Horstisporites (*Triletes*) *casses* (Harris, 1961) Marcinkiewicz, 1981 (as *Triletes casses* sp. nov.)	Harris (1961)	Genus selaginellallean or isoetalen based on wall ultrastructure (Kempf, 1971a,b; Bergad, 1978; Taylor and Taylor, 1988; Morbelli, 1990).
Horstisporites (*Triletes*) *harrisii* (Murray, 1939) Potonié, 1956 (as *Triletes harrisii* Murray, 1939)	Harris (1961)	Selaginellalean based on wall ultrastructure (Kovach, 1994 interpretation of Bergad, 1978).
Horstisporites (*Triletes*) *kendalliae* (Harris, 1961) Kempf, 1971b (as *Triletes kendalli* sp. nov.)	Harris (1961)	Species ?isoetalean based on wall ultrastructure (Kovach, 1994 interpretation of Kempf (1971a)
Minerisporites (*Triletes*) *richardsonii* (Murray, 1939) Potonié, 1956 emend. Harris, 1961 (as *Triletes richardsonii* 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).
Minerisporites volucris (Marcinkiewicz, 1960) (as *Triletes datura* 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).
Paxillitriletes (*Triletes*) *phyllicus* (Murray, 1939) Hall and Nicolson, 1973 (includes 'Giant form') (as *Triletes phyllicus* Murray, 1939)	Harris (1961)	Genus isoetalean based on wall ultrastructure (Kovach and Dilcher, 1985; Baldoni and Taylor, 1987).
Trileites candoris Marcinkiewicz, 1960 (as *Triletes turbanaeformis* sp. nov.; synonymised by Marcinkiewicz, 1981)	Harris (1961)	Genus selaginellalean based on wall ultrastructure (Kempf, 1971a; Koppelhus and Batten, 1989).
Trileites (*Triletes*) *murrayi* (Harris, 1961) Marcinkiewicz, 1971 (as *Triletes murrayi* 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.