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Morphology and wall ultrastructure of the megaspore *Lagenicula* (*Triletes*) *mixta* (Winslow 1962) comb. nov. from the Carboniferous (Early Mississippian: mid Tournaisian) of Ohio, USA

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ABSTRACT

Megaspores assigned to *Lagenicula* (*Triletes*) *mixta* (Winslow, M., 1962. Plant Spores and Other Microfossils from Upper Devonian and Lower Mississippian Rocks of Ohio. Geol. Surv., Prof. Paper 364, 1–93.) comb. nov., from the Carboniferous (Early Mississippian: mid Tournaisian) of northeastern Ohio, USA, have been analysed using light microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM). These studies provide new information on morphology, gross structure and wall ultrastructure. This taxon has a confused taxonomic history, and the new morphological information allows recognition as a distinct species that can be placed with the genus *Lagenicula* as a new combination. Morphological/ultrastructural studies confirm the lycopsid affinities of this megaspore and it is suggested that it probably derived from an arborescent lycopsid that belonged with the Lepidocarpaceae. Thus it is an early example of a megaspore derived from an arborescent lycopsid of the type that went on to dominate the Euramerican Coal Measure forests. The Ohio Tournaisian megaspore assemblage is surprisingly diverse revealing an interesting insight into vegetation ecology at this poorly understood time in plant history.

1. Introduction

This paper is a continuation of the description of an unusually diverse and well preserved megaspore assemblage of mid Tournaisian (Early Mississippian: earliest Carboniferous) age from northeastern Ohio, USA (Arioli et al., 2007). The megaspore assemblage is of particular interest because dispersed megaspores from the early part of the Carboniferous (Tournaisian) are relatively poorly understood due to a paucity of described assemblages. Intriguingly, this gap in knowledge masks an important change in megaspore assemblages, with marked differences in morphological composition and diversity between those from the Upper Devonian and later Carboniferous (Viséan-Stephanian) (e.g. Glasspool and Scott, 2005; Arioli et al., 2007). Upper Devonian megaspore assemblages are dominated by relatively small forms, many of which are characterised by grapnel-tipped processes (e.g. Allen and Robson, 1981; Candilier et al., 1982; Higgs and Scott, 1982). Later Carboniferous (Viséan-Stephanian) megaspore assemblages lack grapnel-tipped forms and are dominated by larger megaspores that are characteristic of the plants that dominated the Euramerican Coal Measure forests. Interestingly the mid Tournaisian assemblage from Ohio appears to comprise a mixture of forms more typical of the Upper Devonian and forms more typical of the later Carboniferous. A full taxonomic description of the assemblage is currently being prepared by Spinner and Wellman (in prep.). This report focuses on a conspicuous and common element of the assemblage: *Lagenicula* (*Triletes*) *mixta* (Winslow 1962) comb. nov.

L. mixta is an early example of a lageniculate megaspore (i.e. those with a well developed apical prominence/gula) so typical of the later Carboniferous. This taxon has a rather confused taxonomic history. It was originally described as a variety by Winslow (1962): *Triletes catenulatus* var. *mixtus* Winslow (1962). Later Dybova-Jachowicz et al. (1979) placed it in synonomy with *Sublagenicula* (*Triletes*) *variabilis* (Winslow) Dybova-Jachowicz et al. (1979) (see also Dybova-Jachowicz et al., 1987). Here we regard it as a species in its own right but place it in a new combination with the genus *Lagenicula*. In order to present a detailed description of its morphology, gross structure and wall ultrastructure we have conducted a thorough investigation using LM, SEM and TEM. The aim is to use this new information to compare this species of *Lagenicula* with earlier and later megaspores in order to determine its biological affinities and evolutionary relationships and,

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hopefully in the process, shed some light on: (i) the nature of the Tournaisian vegetation; (ii) the origins of the plants that went on to dominate the Euramerican Coal Measure forests.

2. Material and methods

2.1. Locality and geology

Studied material consists of six samples collected from the upper part of the Cuyahoga Formation (Wooster Member) and overlying lower part of the Logan Formation (Byer Member) from two localities in Wayne County, northeastern Ohio, USA (Fig. 1). The location of the site and the description of the samples are outlined by Clayton et al. (1998). These deposits are interpreted as accumulating in terrestrial to nearshore marine environments associated with an interdistributary setting of a deltaic environment. Dispersed miospore assemblages from all six samples belong with the *Spelaeotriletes pretiosus–Raistrickia clavata* (PC) Miospore Biozone of Western Europe, indicating an early Mississippian age (which corresponds to the mid Tournaisian in Western Europe). The geology of the site is summarised by Coleman and Clayton (1987) and Clayton et al. (1998).

2.2. Preparation and techniques

Samples were macerated using standard HCl-HF-HCl palynological techniques. The residues were sieved using a 120-μm mesh. The megaspores are very well preserved with little, if any, corrosion and with delicate spines preserved intact. Because of their low thermal maturity (megaspores are translucent and yellow-brown in colour) oxidation was not required. Megaspores were picked directly from the organic residue using a fine paintbrush. All of the megaspores were first mounted on glass slides using glycerine for LM observation and photography. Selected specimens were later recovered from the slides and prepared for either SEM or TEM analysis.

For SEM analysis megaspores were mounted on SEM stubs using double-sided sticky carbon tabs and gold coated using a sputter-coater. They were observed using a Philips 501B SEM at 30 kV (University of Sheffield). For TEM analysis megaspores were placed on blocks of freshly prepared agar and sealed into the blocks by covering them in molten agar which solidifies on cooling. Then the megaspores were dehydrated in ethanol and embedded in Spurr resin. The sections made using a microtome armed with a diamond knife and were stained with uranyl acetate followed by Reynold's lead citrate. They were examined using a Philips CM10 TEM at 80 kV (University of Sheffield). Note that all the megaspores selected for TEM analysis were preserved in lateral compression and cut perpendicular to the plane of compression, so that apparent dimensions approximate true thicknesses.

Twenty four specimens of *L. mixta* were identified and mounted for examination using LM. Three of these specimens were recovered from LM slides and mounted for SEM analysis (SEM stub CW140a–c). Another three specimens were recovered from LM slides and embedded in individual blocks for TEM analysis (TEM blocks CW086 to CW088).

3. Systematic palaeontology

3.1. Terminology

Terminology utilized in descriptions is from Grebe (1971) with the exception of the use of the terms gula and apical prominence (*sensu* Spinner 1969, 1983) and catenulate (*sensu* Winslow 1962) (see below).

3.2. Repository of material

All material (sample, residue, slides, stubs, blocks and sections) is stored in the Centre for Palynology of the University of Sheffield.

3.3. Taxonomy

Anteturma SPORITES Potonié, 1893

Turma TRILETES (Reinsch 1881) Potonié and Kremp, 1954

Subturma LAGENOTRILETES Potonié and Kremp, 1954 emend. Bhardwaj, 1957

Infraturma GULATI Bhardwaj, 1957

Genus LAGENICULA (Bennie and Kidston, 1886) Potonié and Kremp, 1954 emend. Spinner 1969

Type species. Lagenicula horrida Zerndt 1934

Lagenicula (*Triletes*) *mixta* (Winslow 1962) comb. nov.

Triletes catenulatus var. *mixtus* Winslow 1962, p.33, plate 7, 4

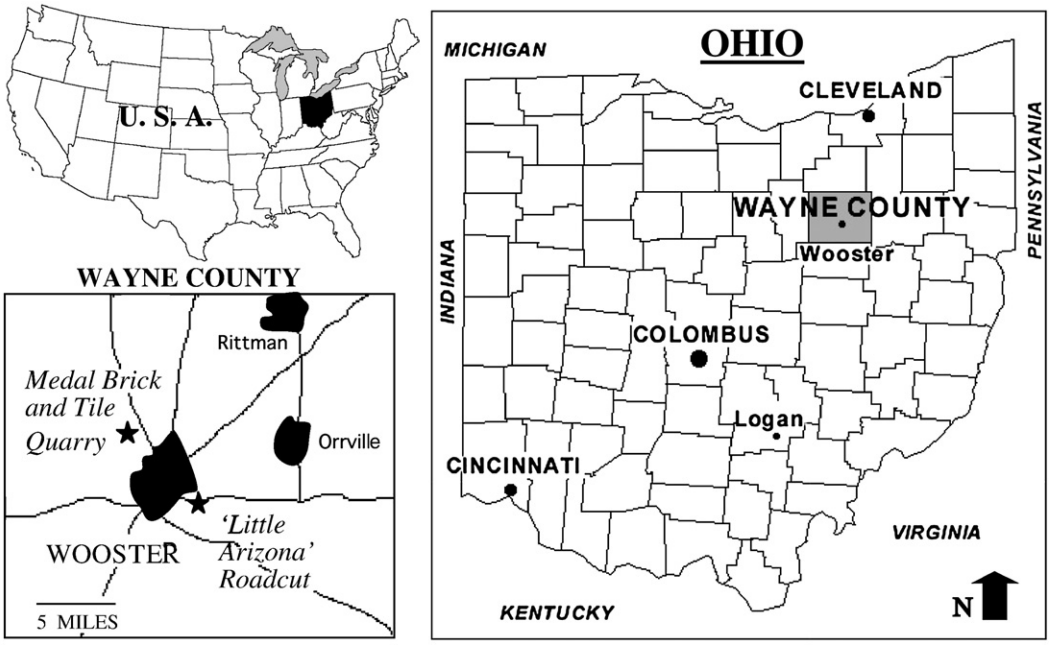

Fig. 1. Location of sections.