Review of Palaeobotany and Palynology 156 (2009) 14–33

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Short communication

Wall ultrastructure in some dispersed megaspores and seed-megaspores from the Middle Devonian of northern Poland

E. Turnau [a], N. Zavialova [b,*], A. Prejbisz [c]

[a] Institute of Geological Sciences, Polish Academy of Sciences, Krakow Research Centre, Senacka 1, 31-002 Krakow, Poland
[b] Laboratory of Palaeobotany, Palaeontological Institute of the Russian Academy of Sciences, Moscow, Profsoyuznaya, 123, 117647, Russia
[c] Institute of Geological Sciences, Polish Academy of Sciences, Twarda 51/55, 00-818 Warsaw, Poland

ARTICLE INFO

Article history:
Received 4 January 2008
Received in revised form 24 May 2008
Accepted 24 July 2008
Available online 3 August 2008

Keywords:
seed-megaspore
Middle Devonian
wall ultrastructure

ABSTRACT

A detailed investigation using light microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM) has been undertaken on three dispersed megaspore taxa recovered from Givetian deposits of northern Poland. Morphology of *Contagisporites optivus* is the same as that of megaspores reported from sporangia of *Archaeopteris*, but the producers of the seed-megaspores *Granditetraspora zharkovae* and of *Biharisporites*? *capillatus* are unknown. The affinity of the former is of special interest as monomegaspory is one of the botanical innovations that characterizes the seed plants (though it also occurs in other heterosporous plants). Comparisons at ultrastructural level with megaspores and large spores of plant groups believed to have attained, in the Middle Devonian, some level of heterospory are discussed. It is suggested that the alveolate outer wall of the seed-megaspores studied, consisting of granular units, is similar to that of archaeopteridalean megaspores. Specimens of *G. zharkovae* bear also some morphological resemblance to anisodiametric tetrads from the Devonian and Carboniferous ovules of presumed or certain pteridosperms in being enclosed in resistant meshy membranes (mesh-sack). Wall thickness of aborted versus functional megaspores of *G. zharkovae*, and the lack of indication that the mature functional megaspore wall was stretched, point to a non-lycopsid origin of *G. zharkovae*. It is suggested that the anisodiametric tetrads discussed may have been produced by a plant related to archaeopteridaleans.

1. Introduction

This paper is the first contribution emanating from a larger project that aims to document spore wall ultrastructure among a variety of Middle Devonian dispersed megaspores from Western Pomerania in northern Poland (Fig. 1). The material studied has been derived from Eifelian and Givetian deposits from the Miastko 1 borehole. The first report concerning this megaspore assemblage was that by Fuglewicz and Prejbisz (1981) who described fifteen species, most of them new being new. Subsequently, Turnau and Karczewska (1987) discussed size distribution in some of these taxa. Recently, seed-megaspores were discovered in the Givetian strata of the same borehole by Turnau and Prejbisz (2006). They have been assigned to *Granditetraspora zharkovae* Arkhangelskaya and Turnau emend. Turnau and Prejbisz recorded previously from Russia (Arkhangelskaya and Turnau, 2003).

There is still relatively little known about the exospore ultrastructure of dispersed and in situ Devonian megaspores and seed-megaspores. Regarding Middle Devonian dispersed seed-megaspores, wall ultrastructure has been reported by Meyer-Melikian and Arkhangelskaya (2002) and Marshall and Hemsley (2003). Middle Devonian dispersed large spores (large isospores?) have been described at the fine structural level by Wellman (2001, 2002). Ultrastructural information is known for Late Devonian megaspores extracted from sporangia or from seed-like structures (Pettitt, 1966, Taylor and Brauer, 1983, Cichan et al., 1984, Telnova and Meyer-Melikian, 1993, 2002, Li et al., 1997). Ultrastructure of dispersed Late Devonian seed-megaspores has been documented by Hemsley (1990). Reports on wall ultrastructure of Late Devonian dispersed megaspores and large spores have been provided by Taylor et al. (1980) and Taylor and Schekler (1996).

Considering the paucity of ultrastructural information on Devonian megaspore walls, we think that its documentation is of considerable value. This paper concerns three species: *Biharisporites? capillatus* Fuglewicz and Prejbisz (1981), *Contagisporites optivus* (Chibrikova) Owens (1971), and *Granditetraspora zharkovae* Arkhangelskaya and Turnau emend. Turnau and Prejbisz (2006). The latter represents seed-megaspores. Our objective is to compare at fine structural level the megaspores *Contagisporites* that were repeatedly reported from archaeopteridalean fructifications (see Allen, 1980), and *B.? capillatus* of similar wall ultrastructure, with the seed-megaspores *G. zharkovae*, one of the earliest known reproductive structures of its type. We hope that our data may provide evidence for affinity of this species. This would be of relevance to our understanding of seed evolution. Our study of the exospore of aborted and functional

* Corresponding author.
E-mail address: zavial@mail.ru (N. Zavialova).

0034-6667/$ – see front matter
doi:10.1016/j.revpalbo.2008.07.009

megaspores of a single tetrad may elucidate some problems of exospore formation.

2. Material and methods

2.1. Locality and geology

The palynological material has been recovered from samples of cored mudstone from the borehole Miastko 1 drilled in northern Poland (Fig. 1). The Middle Devonian continental and marine deposits of that area are dated on spores and also partly on marine fauna. The biostratigraphy and lithostratigraphy of these deposits are explained in Turnau (1996) and Turnau and Prejbisz (2006). The Devonian strata from the Miastko 1 borehole have been assigned, on spore data, to the upper Eifelian and lower to middle Givetian (Turnau, 1996). The stratigraphy of these strata and the position of the relevant samples are shown in Fig. 2.

2.2. Preservation

The studied material is carbonized due to deep burial so that the miospores accompanying the megaspores are dark brown in colour. The independent rank data are available only for the Upper Devonian of Western Pomerania (Narkiewicz et al., 1998). According to these authors, the Miastko 1 borehole is situated in the area where the vitrinite reflectance (R_0) indices are 0.90. It is conceivable that the homogenous ultrastructure of the inner layer in all megaspores studied by us is due to carbonization.

Compression of the exospores is reflected by the reduction of lumen to a narrow slit or by its complete obliteration. It is hard to tell how much, if at all, the compression affected the wall ultrastructure. Mostly, the alveolae are not aligned to the plane of compression.

2.3. Preparation and techniques

A sample of mudstone was palynologically processed by standard techniques involving treatment with HCl and HF (Wood et al., 1996). The organic matter was recovered by heavy liquid flotation. The residues were washed and dried, and megaspores were picked with a fine brush. Specimens for LM study were oxidized using fuming HNO_3 (but no ammonia). Unoxidized specimens were mounted on standard SEM stubs with carbon discs, coated with platinum, and examined at 20 kV using a JEOL JSM-840A SEM.

After SEM, specimens were removed from stubs and embedded in epoxy resin mixture (Meyer-Melikian and Telnova, 1991). Since the studied specimens were large for TEM processing, larger specimens were cut into two to three pieces before embedding to achieve proper embedding and cutting. Some of the specimens were treated with butyl acetate for about half an hour to remove remnants of the carbon discs that stuck to the lower surfaces of spores hampering proper embedding. The specimens were polymerized during two days at 60 °C, orientated, and cut using an LKB 3 ultramicrotome with a diamond knife. The sections were viewed with a Hitachi H-600 TEM unstained. Most ultramicrographs were made with an Olympus CO-770 digital camera, some blow-ups under greater magnification were photographed on films, and subsequently transformed to digital form via an Epson Perfection V700 Photo Scanner. Composite images were sewed using the Photoshop 7.0 program. The individual ultramicrographs and composite images in their original size are stored at Laboratory of Paleobotany of PIN RAS (Moscow) as tif-files on DVD disks and negative films (in the present publication, they were reduced to fit the plate size); the sections are stored at the same laboratory.

3. Taxonomic discussion

3.1. *Biharisporites* Potonié, 1956

The dispersed genus *Biharisporites* includes cavate spores ornamented distally and proximo-equatorially with minute coni. These diagnostic characters are trivial, so it is not surprising that various dispersed species, described from the Devonian to Cretaceous, have been included in this genus. There could be no doubt about various affinities of these species (according to Balme, 1995, the type species of *Biharisporites* – *B. spinosus* (Singh) Potonié from the Permian of India has almost certainly lycopsid affinity). The Devonian megaspores included in *Biharisporites* are either ornamented by minute coni (like *B. ellesmerensis* Chaloner, 1959) or they bear long spinose processes (like *B.*? *capillatus* or *B. arcticus* Chi and Hills, 1976). The species characterized by an ornament of long spines like *B.*? *capillatus* and *B. arcticus* fit better in the wider concept of the genus by Bhardwaj and Tiwari (see Jansonius and Hills, 1976), though the creators of these taxa, i.e. Chi and Hills, 1976, and Fuglewicz and Prejbisz (1981) indicated that they used the concept of Potonié. The Devonian megaspores showing minute conate sculpture are comparable to archaeopteridalean in situ megaspores, and should be excluded from the Permian genus under discussion. *Biharisporites* (Singh) Potonié is also not suitable for *B.*? *capillatus*, and we consider as too wide the concept of the genus by Bhardwaj and Tiwari. But creation, at present, of a new genus would be premature. The wall ultrastructure of our species is not as clearly non-lycopsid unlike that of the two other species studied. More ultrastructural studies of the exospore of similar Devonian species is needed to produce a meaningful diagnosis. Therefore, in this paper, we have limited expression of our reservations to inclusion of the question mark after the generic name.

3.2. *Granditetraspora* Arkhangelskaya and Turnau emend. Turnau and Prejbisz, 2006

The external morphology of the genus *Granditetraspora* is very similar to that of *Spermasporites* (Hemsley, 1993), both taxa are sparsely ornamented and the mesh-sack enclosing the tetrads of *Granditetraspora* may be compared to the membrane clinging to the external surface of the *Spermasporites* tetrads. However, both taxa differ significantly in exospore ultrastructure. In spite of this, we will not emend the generic diagnosis of *Granditetraspora* in this paper. This is because the exospore ultrastructure of the type species of this genus has been described only very briefly in a conference abstract (Meyer-Melikian and Arkhangelskaya, 2002) and no illustration was given. We feel that at this time of rapid progress in the knowledge of fine

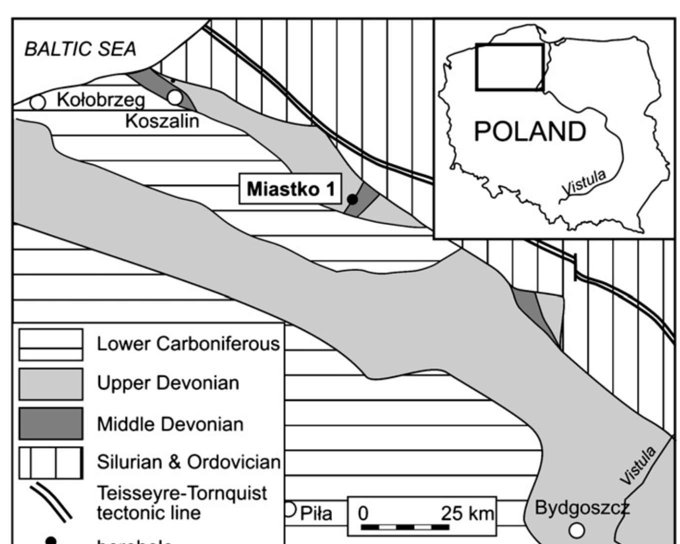

Fig. 1. Location of the Miastko 1 borehole on a geological map of Western Pomerania showing the subsurface extent of sub-Permian deposits (adopted from Matyja et al., 2000).