

Microfossils with suggested affinities to the Pyramimonadales (Pyramimonadophyceae, Chlorophyta) from the Lower Devonian Rhynie chert

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ABSTRACT. An assemblage of unusual microfossils occurs within an accumulation of plant debris, hyphae, and various types of propagules in the Early Devonian Rhynie chert. Specimens consist of a vesicle with one or more prominent wings (alae) arising from the surface; one wing forms a rim around the equator of the vesicle. The microfossils are interpreted as phycomata of a prasinophycean green alga based on morphological similarities to *Pterospermella*, a microfossil similar to phycoma stages of the extant *Pterosperma* (Pyramimonadales). This report represents the third record of phycomata in the Rhynie chert, suggesting that this Early Devonian ecosystem served as habitat to a variety of prasinophyte algae. Moreover, the new microfossils add to the inventory of fossil freshwater representatives of this predominantly marine group of algae.

KEYWORDS: green algae, non-motile stage, phycoma, *Pterosperma*, *Pterospermella*, prasinophytes

INTRODUCTION

The Early Devonian Rhynie chert is one of a few geological sites where preservation of fossils is so extraordinary that even certain organisms not typically reported in the fossil record, as well as various types of interactions between organisms, are faithfully preserved (e.g. Kerp & Hass 2004). Among the life forms documented in the Rhynie chert are various land plants and animals, as well as microorganisms including fungi (Taylor et al. 2004), peronosporomycetes (Krings et al. 2012, 2013), a lichen-like symbiosis (Taylor et al. 1997), green algae (Edwards & Lyon 1983, Dotzler et al. 2007), cyanobacteria (Croft & George 1959, Krings et al. 2007, 2009), and bacteria (Kidston & Lang 1921).

To date, documented evidence of microscopic algae from the Rhynie chert is comparatively rare; only two forms have been formally described (Edwards & Lyon 1983). This is somewhat perplexing since the Rhynie paleoecosystem must have provided ample habitats for these organisms, and also represented a depositional environment conducive to the preservation of even the most delicate forms. The scarcity of reports of microscopic algae from the Rhynie chert appears, at least in part, to be due to the fact that important diagnostic characters (e.g. organelles, flagellar organization, pigmentation) are not normally preserved (Dotzler et al. 2007). As a result, fossils representing the motile stages of microscopic algae

are difficult to identify and interpret (Sym & Pienaar 1993); moreover, they may be easily confused with cyanobacterial cells or certain types of fungal propagules. On the other hand, many microscopic algae are known to produce morphologically distinct non-motile (resting) stages (e.g. phycmata, cysts), which are often highly characteristic and abundant in the fossil record. These are typically encountered in palynological samples, especially from marine sediments (Colbath & Grenfell 1995, Tyson 1995). Two forms that are consistent in morphology with the dispersed fossil genus *Cymatiosphaera* Wetzel ex Deflandre, which is commonly considered to represent the phycmata of prasinophyte algae (Colbath & Grenfell 1995), have been described from the Rhynie chert (Dotzler et al. 2007, Kustatscher et al. 2014). These fossils represent the oldest evidence of prasinophytes in a freshwater paleoecosystem to date. Other than the specimens reported from the Rhynie chert, the earliest records of prasinophyte phycmata from freshwater paleoecosystems come from the Pennsylvanian-Lower Permian (Doubinger 1967, Clausing 1993).

This paper describes an assemblage of Rhynie chert microfossils that closely resemble *Pterospermella* A. Eisenack, a taxon used for fossil structures that are morphologically indistinguishable from the phycmata produced by members in the extant prasinophyte genus *Pterosperma* Pouchet (Pyramimonadales). This discovery adds to the diversity of fossil freshwater representatives of the predominantly marine prasinophytes. Moreover, the new microfossils indicate that the Early Devonian Rhynie ecosystem served as habitat to several different prasinophytes.

GEOLOGICAL SETTING, MATERIAL, AND METHODS

The Rhynie chert locality is situated northwest of the village of Rhynie, Aberdeenshire, Scotland. The so-called Rhynie Block in the northern part of the Rhynie Outlier consists of an extensive sequence of sedimentary and volcanic rocks. The fossil-bearing cherts occur in the Windyfield Shales Member, i.e. within the lower part of the Dryden Flags Formation (Parry et al. 2011). This Lagerstätte is made up of fossiliferous beds containing lacustrine shales and cherts that have been interpreted as a series of ephemeral freshwater pools which existed within a hot-spring environment (Rice et al. 2002, Rice & Ashcroft 2004). Preserved within the cherts are sinter surfaces, aquatic (freshwater) facies

from the pools, and subaerial soil/litter horizons with in situ plants that are thought to have grown along the margins of the pools. Preservation of the biota is interpreted as being a result of temporary flooding of the site by waters rich in silica, or by groundwater high in silica percolating up to the surface (Powell et al. 2000). The cherts have been dated as Pragian-?earliest Emsian based on spore assemblages (Wellman 2006, Wellman et al. 2006). High-precision age constraints on the Rhynie Lagerstätte indicate absolute ages of 407.1 ± 2.2 Ma (Mark et al. 2011) and 411.5 ± 1.3 Ma (Parry et al. 2011).

The assemblage of microfossils was identified in a thin section prepared by cementing a thin wafer of the chert to a glass slide and then using silicon carbide to grind the rock chip until sufficiently thin to transmit light. The slide is deposited in the Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) at Munich, Germany, under accession number SNSB-BSPG 1965 I 385. The slide was examined using normal transmitted light microscopy equipment; digital images were captured with a Leica DFC-480 camera.

DESCRIPTION

The assemblage of microfossils includes ca 50 specimens (Pl. 1, figs 1, 2), which are present within a loose accumulation of land plant debris, fungal hyphae, and various types of small propagules, most of which probably represent fungal (resting) spores.

The microfossils consist of a smooth-walled, lens-shaped (i.e. dorsiventrally compressed) to more or less globose vesicle between (25–)30 and 35(–38) μm in diameter (Pl. 1, figs 3–12). The vesicle wall varies in thickness, from <0.5 μm in small (Pl. 1, figs 9, 10) to ~ 1.2 μm in the largest specimens (Pl. 1, figs 3–8); in a few specimens, the wall appears to be two-layered (Pl. 1, figs 4, 6). One or more prominent laevigate, straight or slightly undulating wings (alae) extend perpendicularly from the vesicle surface. One wing that is consistently present in all specimens extends around the equator and divides the vesicle into two nearly equal hemispheres. The equatorial wing extends out from the vesicle ca 8–10 μm and gives the vesicle a cingulate appearance. Additional wings present in some specimens may extend across the surface (Pl. 1, fig. 5) or to the poles (Pl. 1, fig. 7), or divide the surface into triangular, quadrangular, or polygonal areas (Pl. 1, figs 11, 12); there does not appear to be a regular pattern to this ornamentation among the specimens. In ca 20% of the specimens a circular or oval orifice, between 5 and 7 μm in

diameter, occurs in one of hemispheres (arrows in Pl. 1, figs 10, 11). The orifice is consistently located slightly off center (i.e. not in polar position). Moreover, in one specimen a prominent tube-like protrusion (~8.5 μm wide; arrow in Pl. 1, fig. 13) of the vesicle terminates in what appears to be a thin-walled spheroid structure ca 30 μm in diameter.

At least two of the specimens are colonized by epibiotic chytrid zoosporangia (e.g. arrows in Pl. 1, fig. 15) resembling *Illmanomyces corniger* M. Krings et T.N. Taylor (see Krings & Taylor 2014). Co-occurring with the microfossils are several other spheroid propagules. One type (Pl. 1, fig. 14) is up to 40 μm in diameter and characterized by a massive, multi-layered wall and irregularly wrinkled or rugose outer surface.

DISCUSSION

Evidence of algae in the Rhynie chert has been very slow to accumulate. The record currently includes the charophyte *Palaeonitella cranii* (Kidst. & W.H. Lang) J. Pia (e.g. Kelman et al. 2004) and several planktonic unicellular and filamentous algae. Two filamentous algae have been formally described as *Mackiella rotunda* and *Rhynchertia punctata*, and tentatively attributed to the Ulotrichales (Edwards & Lyon 1983). Moreover, two prasinophyte phycomata have been described in open nomenclature as *Cymatiosphaera* sp. 1 and 2 (Dotzler et al. 2007, Kustatscher et al. 2014).

We interpret the microfossils described in this paper as representing a third type of prasinophyte phycoma based on morphological similarities seen in other fossil phycomata that have been described from palynological samples and assigned to the fossil genus *Pterospermella* (e.g. Prebble et al. 2006: fig. 5i). The most important diagnostic feature of *Pterospermella* is one to several prominent perpendicular wings (alae) that extend from the vesicle surface, one of which forms a rim around the equator that divides the vesicle into two hemispheres (Al-Ameri 1986). The additional (secondary) wings, if present, are irregularly distributed; they may divide the surface into areas, but do not form a regular pattern (Parke et al. 1978, Teyssèdre 2006). The microfossils from the Rhynie chert are characterized by a single prominent wing dividing the central

lens-shaped body into two hemispheres (Pl. 1, figs 3–8). Moreover, additional wings may be present (e.g. Pl. 1, figs 7, 11), but there is no consistent pattern recognizable among the specimens. As a result, we attribute the Rhynie chert microfossils to *Pterospermella*. Dotzler et al. (2007) indicated that virtually all Paleozoic prasinophyte phycomata known to date are described from macerated samples and not thin sections. This makes it especially difficult, if not impossible, to determine whether the Rhynie chert phycomata represent a new species or have already been described based on palynological preparations. We therefore follow Dotzler et al. (2007) and include the Rhynie chert phycomata in open nomenclature as *Pterospermella* sp.

An alternative interpretation associates the Rhynie chert microfossils with the problematic and ill-defined chlorellalean green algae genus *Trochiscia* Kütz. (Oocystaceae, subfamily Lagerheimioideae; see Komárek & Fott 1983) based on the occurrence in a freshwater paleoenvironment. Members in *Trochiscia* as currently understood are mostly solitary, spherical to subspherical unicellular organisms (8–50 μm in diameter) that are characterized by thick cell walls variously ornamented with spines, ridges, reticulations, or rounded projections (e.g. Silva 1996, Keshri & Ghosh 2012, Guiry 2014); many forms (may) represent resting stages or zygotes of other algae (e.g. Hoham et al. 1978, Tsarenko & John 2002, Štenclová 2013, Guiry 2014). Although median optical sections of certain *Trochiscia* species may be suggestive of a morphology similar to that seen in the Rhynie chert microfossils, none of the species currently recognized in *Trochiscia* possess an equatorial wing/ala dividing the cell into hemispheres. Forms that are characterized by an equatorial wing, and that have historically been assigned to *Trochiscia* [e.g. forms in *Trochiscia* sectio *Pterosperma* (Pouchet) Lemmerm.; see Lemmermann 1908] have been transferred to *Pterosperma* (Parke et al. 1978: p. 242).

Vesicle diameter in the *Pterospermella* phycomata from the Rhynie chert is variable, ranging from 25 to 38 μm . This size differential corresponds with the general intrapopulational differences in phycoma diameter that have been observed for many extant and fossil prasinophycean algae, including the *Cymatiosphaera* specimens described previously from

the Rhynie chert by Dotzler et al. (2007). The variability in vesicle diameter is a direct result of continued growth and reproduction of the alga within the phycoma (e.g. Tappan 1980, Knoll et al. 1991, Teyssèdre 2006).

Dehiscence in prasinophyte phycomata usually occurs via an elongate rupture along a preformed line of weakness within the outer wall layer (excystment structure; see Tappan 1980). Several of the Rhynie chert microfossils described in this paper possess a single circular opening or orifice (arrows in Pl. 1, figs 10, 12), which may represent an excystment structure. Adding some support to this hypothesis is the specimen illustrated in Pl. 1, fig. 13, which shows a phycoma and a portion of a second globose structure physically connected via what appears to be a tubular element. One interpretation is that this microfossil illustrates a portion of the inner membranous phycoma wall and contained cell material extending through an opening in the outer phycoma wall (for comparison, refer to Tappan 1980: No. 7 in fig. 10.7).

Parke et al. (1978: pl. I, figs E, F, H) figure several extant *Pterosperma* phycomata in which lateral membranous expansions form a reticulate pattern on the vesicle surface. This pattern is somewhat reminiscent of the surface ornamentation in *Cymatiosphaera*, which is composed of muri partitioning the vesicle surface into polygonal fields (e.g. Mädler 1963, Teyssèdre 2006). This has led to some confusion regarding the affinities of certain forms to *Pterospermella* or *Cymatiosphaera*. Some authors have also included *Cymatiosphaera* in the 'Pterospermella group' or family Pterospermaeae, thus indicating a close affinity between the taxa (e.g. Wicander & Wright 1983, Lebedeva 2010). However, the two fossil genera are in fact quite distinct morphologically: Vesicles of *Cymatiosphaera* are usually globose and the surface of the phycomata divided into polygonal fields by prominent muri that are perpendicular to the surface, but without displaying a system of equatorial differentiation of fields (Deflandre 1954, Mullins 2001). Conversely, the *Pterospermella* vesicle is mostly lens-shaped (rarely globose) and the surface ornamentation is principally formed by a single prominent equatorial wing. Moreover, the surface patterns formed by the additional wings (if present) are not congruent on the two hemispheres and not consistent among the specimens.

The fossil genus *Pterospermella*, as well as its modern equivalent *Pterosperma*, have to date been reported exclusively from marine environments (e.g. Parke et al. 1978, Wicander & Wright 1983, Hannah et al. 2000, Prebble et al. 2006, Götz et al. 2009, Lebedeva 2010). However, a distribution in nearshore conditions (e.g. Tahoun & Mohamed 2014) with preferably a freshwater swamp/non-brackish environment (Apaalse & Atta-Peters 2013), low-salinity environments with stratified water masses (Prebble et al. 2006), or brackish water (Feng et al. 2009) has been suggested for some forms. Moreover, an increase in abundance toward glaciers and meltwater plumes has also been recorded (Prebble et al. 2006). Nevertheless, we are not aware of any report from a strictly freshwater paleoenvironment. Thus, the phycomata from the Rhynie chert appear to represent the earliest evidence of *Pterospermella* within a freshwater paleoecosystem. We can rule out that the microfossils were transported into the Rhynie paleoecosystem from a marine or brackish habitat by either water or wind. No direct connection existed between the Rhynie ecosystem and any marine environment, thus excluding water as a potential vector. Moreover, the specimens are exquisitely preserved, lacking any preservational damage (e.g. shrinkage, wrinkling, destruction of the delicate wings) often seen in specimens dispersed long distances. This suggests that the Rhynie chert phycomata became preserved in situ. Finally, ca 50 phycomata are preserved in close proximity to each other within a single assemblage. This adds credibility to the hypothesis that they did not enter the depositional environment by wind or any other abiotic system. Rather, we believe that during the Early Devonian certain prasinophyte green algae producing *Pterospermella* phycomata thrived in strictly freshwater ecosystems. On the other hand, Channing & Edwards (2009) speculate that the Rhynie chert might have formed in an environment governed by elevated salinity levels, based on comparisons to modern hot-spring ecosystems. This interesting hypothesis has remained controversial as there is currently no direct evidence of elevated salinity within the Rhynie paleoecosystem.

Two of the *Pterospermella* phycomata from the Rhynie chert are colonized by fungi (e.g. arrows in Pl. 1, fig. 15). Conversely, fungal infection has not been observed in any of the *Cymatiosphaera* specimens described

previously from the Rhynie chert (Dotzler et al. 2007, Kustatscher et al. 2014). Dotzler et al. (2007) suggested that the scarcity of fungal infection in the fossil specimens is the result of the short duration of the phycoma stage, which renders these structures unsuitable as hosts for parasites.

CONCLUSIONS

New organisms are continuously being discovered in the Lower Devonian Rhynie chert, especially from chert blocks that preserve segments of the ecosystem which have largely remained unstudied. For example, the litter horizons that are comprised of fragmented and degraded, often compacted plant material and sediment layers have received little attention because they do not contain well preserved and easily recognized plant remains. However, we would argue that it is exactly these segments of the ecosystem that hold a rich source of new evidence of life forms, further demonstrating that the Rhynie ecosystem was inhabited by a still larger diversity of organisms than currently envisioned. The discovery of a third type of organic-walled algal non-motile stage in the chert suggests that microscopic algae were important constituents of this ecosystem. We anticipate that, as the Rhynie chert continues to be explored, additional types of organisms will be discovered, the life history biology of many organisms expanded, and the community biodiversity of this terrestrial ecosystem more completely recorded. These activities will not only expand our understanding of the morphology and biology of the Rhynie chert organisms, but will also continue to increase our knowledge base of the evolution and biological dynamics of a non-marine ecosystem that existed some 410 Ma ago.

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PLATE

Plate 1

Pterospermella sp. from the Lower Devonian Rhynie chert (all images from slide SNSB-BSPG 1965 I 385)

1. Assemblage of phycomata, land plant debris, fungal hyphae, and various types of other propagules; scale bar = 50 μm
2. Intrapopulational differences in phycoma diameter (detail of Pl. 1, fig. 1); scale bar = 50 μm
- 3–8. Phycomata showing prominent equatorial and secondary wings (arrows); scale bars = 10 μm
9. Small phycoma with thin-walled vesicle; scale bar = 20 μm
10. Phycoma showing circular orifice (arrow); scale bar = 20 μm
- 11, 12. Phycomata with secondary wings dividing vesicle surface into polygonal areas; arrow in Pl. 1, fig. 12 indicates orifice; scale bars = 10 μm
13. Specimen showing tube-like protrusion (arrows) of vesicle that terminates in thin-walled spheroid; scale bar = 20 μm
14. Thick-walled propagule (probably a fungal or algal resting stage) co-occurring with the phycomata; scale bar = 10 μm
15. Phycoma colonized by epibiotic chytrid (arrows); scale bar = 10 μm

