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Filamentous green algae from the Early Devonian Rhynie chert

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Abstract

A relatively neglected element of the biota of the Lower Devonian Rhynie chert Lagerstätte are filamentous green algae exceptionally preserved by silicification. Palynological processing of sediments associated with the cherts has yielded palynomorphs that we also interpret as the remains of filamentous green algae and one such taxon is described herein. Cells occur individually, in masses or joined end-to-end as an unbranched filament. The cells are characterised by end walls that form a ‘collar’ structure and inner bodies interpreted as reproductive structures. Because of a lack of preserved characters taxonomic precision is limited, although we suggest the fossils are most likely either zygnematalean or oedogonialean algae that inhabited ponds or lakes and were either attached to substrates and/or free-floating.

Keywords Pragian · Emsian · Green alga · Chlorophyta · Charophyceae

Introduction

Algae are an important and diverse component of modern terrestrial ecosystems (aquatic and subaerial) (Graham et al. 2016). Unfortunately, little is known concerning the geological history of terrestrial algae because they usually have low preservation potential (excepting those that secrete SiO₂, CaCO₃ or recalcitrant organic macromolecules at some stage of their life cycle). Consequently, algae have an incomplete and biased fossil record. However, it has long been suspected that terrestrial algae have a deep geological history and that they were one of the first life forms to invade the land. Indeed, the ancestors of the embryophytes (land plants) are

believed to derive from within the green algae. Reconstructions of pre-embryophyte terrestrial environments envisage freshwater bodies inhabited by aquatic algae, parts of the land surface covered by microbial mats with an algal component, and possibly also endolithic algae (Wellman and Strother 2015). When land plants (embryophytes) eventually appeared they would have interacted and competed with these pre-existing algae on the land surface they shared.

The famous Rhynie chert Lagerstätte provides our earliest insight into the complexity of early terrestrial ecosystems. It is part of a sequence of Early Devonian continental deposits that include a series of cherts formed as sinters deposited by hot-spring activity associated with a complex hydrothermal system (Rice et al. 1995, 2002). The cherts preserve terrestrial aquatic and subaerial (including soil) ecosystems. Preservation is exceptional in that: (i) the ecosystems are preserved intact and in their entirety, including components that are not normally preserved such as fungi (e.g. Krings et al. 2017a) and algae (e.g. Edwards and Lyon 1983); (ii) much of the biota was exceptionally preserved by the silicification process. For example, the fossil plants preserve exceptional cellular detail (Kidston and Lang 1917, 1920a, b, 1921a, b), including stages of the life cycle seldom fossilized, such as germinating spores (Lyon 1957), gametophytes (Remy and Remy 1980), sperm (Kerp et al. 2004) and cellular contents (Wellman et al. 2006). Thus, the Rhynie cherts provide a unique insight into early terrestrial ecosystems and their components, at a critical time in the

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early evolution of terrestrial ecosystems, i.e. when vascular plants were undergoing their first adaptive radiation.

Intriguingly, the Rhynie cherts preserve various terrestrial algal remains and provide our earliest insight into the role algae played in early terrestrial ecosystems. The aquatic charophyte *Palaeonitella cranii* (Kidston and Lang) Pia was first described by Kidston and Lang (1921b), with further morphological features subsequently elaborated upon by Edwards and Lyon (1983) and Kelman et al. (2004) and fungal/algal associations described by Taylor et al. (1992). Filamentous algae have been described by Edwards and Lyon (1983). These are *Mackiella rotundata* Edwards and Lyon (tentatively assigned to the Ulotrichales) and *Rhynchertia punctata* Edwards and Lyon (that they considered were probably Chlorophyta and particularly similar to members of the Cladophorales and Zygnematales). They also noted that a ‘filamentous alga incertae sedis’ (their fig. 26) is similar in general appearance to macrandous species of *Oedogonium*, but they considered that the lack of cap cells limited this comparison. Krings et al. (2017b) reported on a microscopic colony-forming alga *Hagenococcus aggregatus* Krings et al. Unicellular algal remains have been described by Kidston and Lang (1921b), Edwards and Lyon (1983), Dotzler et al. (2007) and Kustatscher et al. (2014a, b). Unfortunately, their affinities are generally uncertain, although Dotzler et al. (2007) and Kustatscher et al. (2014a, b) suggested an affiliation with prasinophycean algae.

Detailed palynological analysis has recently been undertaken on the Rhynie sequence (Wellman 2004, 2006, 2018). The rich palynomorph assemblages are dominated by land plant spores but also contain remains interpreted as algal. A taxon of particular interest, interpreted as a filamentous green alga, is the subject of this paper.

Geological setting, materials and methods

The Rhynie outlier in Aberdeenshire, Scotland consists of a small outcrop of Lower Devonian terrestrial-fluviatile-lacustrine ‘Lower Old Red Sandstone’ deposits (Rice et al. 1995, 2002) that include the Rhynie chert Lagerstätte. Biostratigraphical evidence indicates that these deposits are Pragian–? earliest Emsian in age (Wellman 2006) and radiometric dating has been provided by Mark et al. (2011) and Parry et al. (2011). Our understanding of the stratigraphic sequence of the Rhynie outlier is based predominantly on information from a series of boreholes sunk to investigate the deposits, including a deep borehole that penetrated 210 m of sedimentary sequence before encountering igneous basement (Trewin and Rice 1992; Trewin 1994, 1996; Rice et al. 1995, 2002). These boreholes have also provided fresh rock suitable for palynological analysis of the sequence (Wellman 2006).

Standard palynological techniques (HCl–HF–HCl bulk acid maceration) were used to isolate the organic contents of 118 samples of fine-grained sediments. These were collected from a number of the boreholes that contained suitable sediments. The sampling regime essentially represented the entire bored sequence, including clastic sediments from above and below the chert-bearing sequence, and interspersed with the cherts within the chert-bearing sequence. The stratigraphical sequence of the Rhynie outlier and coverage of the palynological sampling regime is outlined in Wellman (2006). The recovered palynomorph assemblages are dominated by spores, but also contain plant cuticles (embryophyte and nematophyte), tubular structures (including plant tracheids, nematophyte tubes and fungal hyphae), rare algal remains and arthropod cuticles.

The palynomorphs described here, interpreted as algae, are extremely well preserved and of relatively low thermal maturity. Detailed examination of the algal remains using light microscopy enabled morphological characterization of the taxa present and plotting of their distribution and relative abundances throughout the sequence. However, a formal taxonomic treatment of these fossils was not applied due to the limited information provided by the fossils and uncertainty regarding their exact affinities.

The algal remains described in this paper are abundant in a single sample [97/8 (14.5)] and rare in a further sample [97/9 (35.8)]. Both samples are from the Rhynie Cherts Unit of the Rhynie Block (see Wellman 2006). [97/8 (14.5)] is from a 15.1 m thick sequence of shales with thin sands that is present below a sequence of 6 cherts. The actual sample is 3.6 m below the lowermost chert. [97.9 (35.8)] is from a 1.7 m thick sequence of black shales that occurs directly below a chert-bearing sequence. The actual sample is 1.5 m below the lowermost chert. Both samples are from sediments interpreted as being deposited in small ponds or lakes.

All materials (rock, residue and slides) utilised in this study are housed in the Centre for Palynology of the University of Sheffield.

Description of the fossils

The specimens occur predominantly as single cells but less commonly in clusters or as pseudofilaments *sensu* Graham et al. (2016) (i.e. a linear array of cells that do not share common walls; rather, end walls of individual cells are attached). The cells occur in six basic morphotypes that intergrade (Morphotypes 1–6) (Fig. 1).

Most common is Morphotype 1 (Fig. 1a) that occurs as cells that are broadly rectangular in outline, although some merge into a square shape, that measure 27 (49) 90 μm by 17 (25) 33 μm (100 specimens measured). Clearly, they have been flattened (compressed) during sediment compaction,

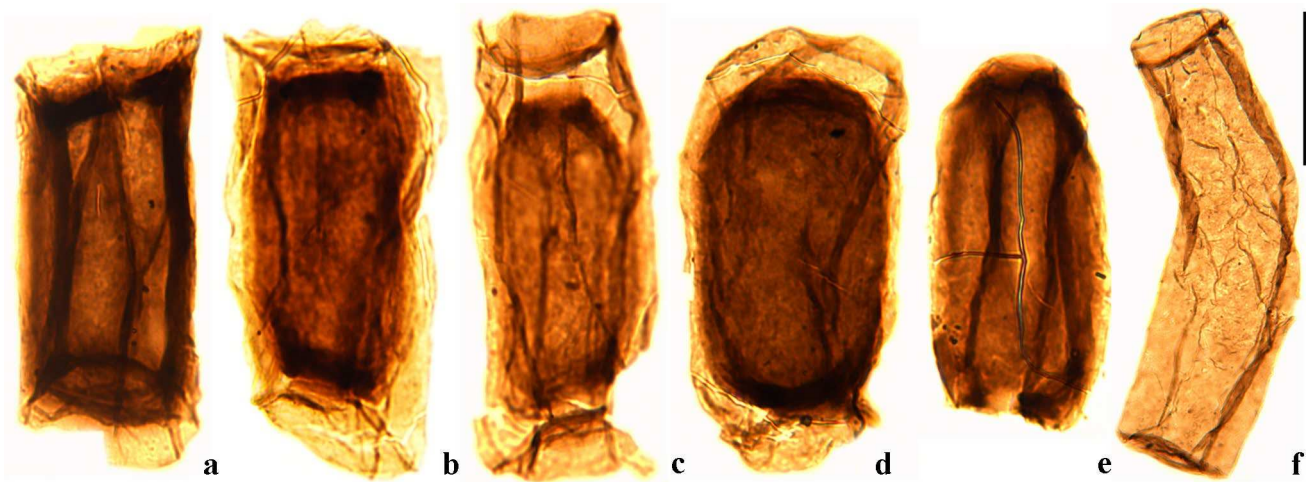
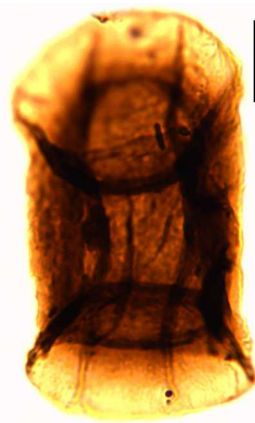


Fig. 1 Light microscope images of individual specimens of the six different morphotypes reported. **a** Morphotype 1. Sample [97/8, slide 14.5/6, E.F. no. V36]. **b** Morphotype 2. Sample [97/8, slide 14.5/6, E.F. no. M48/3]. **c** Morphotype 3. Sample [97/8, slide 14.5/6, E.F. no.

F27/2]. **d** Morphotype 4. Sample [97/8, slide 14.5/6, E.F. no. U32]. **e** Morphotype 5. Sample [97/8, slide 14.5/6, E.F. no. H46]. **f** Morphotype 6. Sample [97/8, slide 1, E.F. no. F41]. Scale bar is 20 μm (except for **f**, where it is 13 μm)

Fig. 2 Light microscope image of an individual specimen illustrating the nature of the circular flanges at the ends of a specimen of Morphotype 1. Sample [97/8, slide 14.5/6, E.F. no. W37/3]. Scale bar is 10 μm



and it seems likely that they were originally cylindrical. The cell walls are bilayered with a thin, faintly yellow, translucent outer layer that is $<0.5 \mu\text{m}$ in thickness and a thicker, brownish, translucent inner layer that is $1\text{--}2 \mu\text{m}$ in thickness. The cell surface usually has a number of linear striations and these are interpreted as representing compressional folding of the thin outer layer rather than primary ornamentation. At each end of the cell the thin outer layer is extended by $1\text{--}7 \mu\text{m}$ forming a circular ‘collar’ (Fig. 2). Morphotypes 2–4 (Fig. 1b–d) have the thin outer layer separated from the thick inner layer that forms an inner body. In Morphotype 2 (Fig. 1b) both the outer layer and inner body remain rectangular-square in shape. In Morphotype 3 (Fig. 1c) the outer layer is rectangular-square in shape but the inner body is elliptical. In Morphotype 4 (Fig. 1d) both the outer layer and inner body are elliptical. Morphotype 5 (Fig. 1e) consists of the inner body, elliptical in shape, which has lost

the outer layer. Morphotype 6 (Fig. 1f) consists of the outer layer, which presumably has shed the inner body.

The cells occur either individually or more rarely in clusters or pseudofilaments (Fig. 3). Occasionally the cells occur in clusters of randomly orientated individuals including all of the Morphotypes 1–5 (Fig. 3h). Occasionally the cells occur as pseudofilaments (particularly in sample [97/8 (14.5)/2]) and are joined at the collars described above (Fig. 3g). The number of individuals forming a pseudofilament is 2–5 (2:85%, 3:12%, 4:2% and 5:1% based on a count of 100). The longest filament observed comprised 5 individuals. The individual cells are firmly attached, usually in the narrowest dimension, but occasional in the widest dimension. Close inspection did not reveal any holes in the wall of the unicells or holes connecting adjacent joined cells in the pseudofilaments. The cells comprising the pseudofilaments are predominantly of Morphotype 1, but occasionally include Morphotypes 2–4. Cells in a pseudofilament may be of different lengths but are uniform in width.

Biological affinities

Based on a survey of extant organisms, the morphology of the described fossils suggests affinities with filamentous green algae. A relationship with filamentous cyanobacteria is ruled out due to the fossils’ large size, ability to form internal? reproductive structures, and the fact that they appear to preserved actual cell walls, whereas cyanobacteria are generally preserved as cell units (i.e. extracellular protein secretion (EPS) envelopes faithfully preserving the shapes of the actual cells). Previously described filamentous

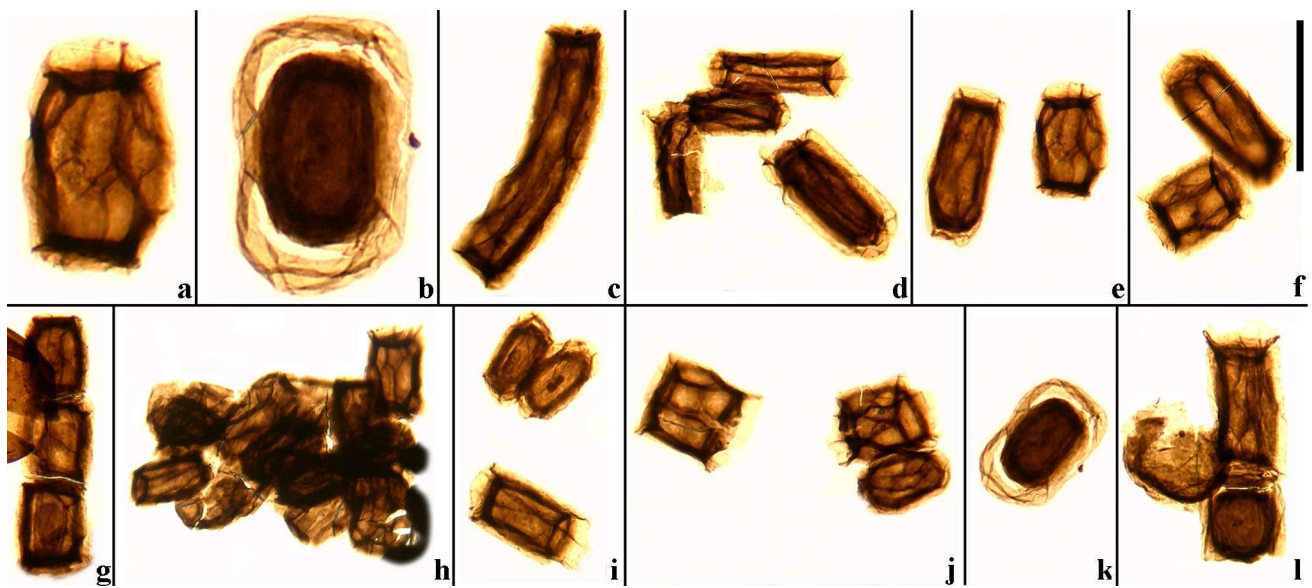


Fig. 3 Light microscope images of a variety of specimens illustrating different type of occurrence. **a** Magnified image of an individual specimen of Morphotype 1. Sample [97/8, slide 14.5/5, E.F. no. C46/3]. **b** Magnified image of an individual specimen of Morphotype 4. Sample [97/8, slide 14.5/5, E.F. no. C33]. **c** Elongate specimen of Morphotype 1. Sample [97/8, slide 14.5/5, E.F. no. D30/1]. **d** Cluster of specimens including Morphotypes 1 and 3. Sample [97/8, slide 14.5/5, E.F. no. E44/4]. **e** Two specimens of Morphotype 1 illustrating differences in shape and dimensions. Enlarged image of specimen to left in **a**. Sample [97/8, slide 14.5/5, E.F. no. C46/3]. **f** Two specimens of Morphotypes 1 and 3 illustrating differences in morphology, shape and dimensions. Sample [97/8, slide 14.5/5, E.F. no. E44/2]. **g** Pseudofilament of three individuals of Morphotype 1. Sample [97/8,

slide 14.5/5, E.F. no. D43]. **h** Cluster of individuals predominantly of Morphotype 1. Sample [97/8, slide 14.5/5, E.F. no. H33]. **(i)**, Cluster of specimens including Morphotype 2 (lower) and two ?attached specimens of Morphotype 4 (upper). Sample [97/8, slide 14.5/5, E.F. no. D43]. **j** Two ?pseudofilaments including two specimens of Morphotype 1 that appear to be attached side on (left) and two attached specimens belonging to Morphotypes 2 and 4. Sample [97/8, slide 14.5/5, E.F. no. E48]. **(k)**, Individual specimen of Morphotype 4 [see enlarged image in **(b)**]. Sample [97/8, slide 14.5/5, E.F. no. C33]. **l** Two attached specimens of Morphotype 2 and 3 (with a specimen of Morphotype 4 to the left). Sample [97/8, slide 14.5/5, E.F. no. C43/4]. *Scale bar* (vertical bar in top right) is 60 μm for **a–b**, 37.5 μm for **c, d, e, f, g, i, j, k, l**

cyanobacteria from the Rhynie chert are always much smaller (Kidston and Lang 1921b; Croft and George 1959; Krings et al. 2007; Krings 2019). However, more refined taxonomic identification among the living filamentous green algae is extremely difficult due to the lack of characters preserved in these palynomorphs, where mainly the cell wall is preserved. Essentially we must rely on: (i) cell size and shape (and in particular the nature of the end wall ‘collar’); (ii) cell habit (to occur individually or line up as pseudofilaments or occasionally form masses); (iii) the fact that the cell wall is composed of recalcitrant material that survives as a palynomorph (both the outer wall and inner wall—internal body).

The living algae most similar to the described fossils belong with the zygnematalean or oedogonialean algae based primarily on the nature of the ‘collars’. In the Oedogoniales rings are always present. Zygnematales may display replicate end walls (but not always). Collar-like structures in other filamentous green algae appear rather different, such as those of *Microspora* and *Tribonema* where the H-shaped end walls are much longer.

The fossil alga appears to form internal bodies that are presumably reproductive structures. Both the filament wall and internal body wall survive in the standard palynological record (they are not exceptionally preserved in chert). This suggests they are composed of a recalcitrant organic macromolecule. Zygnemataleans produce resistant-walled zygotes with the walls composed of a sporopollenin-like material (DeVries et al. 1983). They also produce thick walled resting cysts on occasions. Oedogonialean zoospores initially lack a wall, but develop a thick one after fertilisation. Oedogonialeans also produce oogonia. Acetolysis experiments provide evidence as to the presence of decay-resistant walls in extant algae (e.g. Graham et al. 2013). Such experiments show that at least some oedogonialeans, like the palynomorphs described here, break apart into single cells or few-celled filaments, and that the distinctive cell wall rings survive acetolysis, and that wall remains may result from the presence of crystalline celluloses.

Previously, the earliest generally accepted fossil evidence for Zygnemataceae was the fossil filaments observed in thin sections of cherts preserved in limestones from

marine Middle Devonian (Eifelian) deposits of the Onondaga Formation of New York state, USA (Baschnagel 1966). They were interpreted as freshwater algae transported into a marine environment. *Paleodidymoprium didymium* is interpreted as belonging to the Class Zygnemaphyceae, Order Zygnematales, Family Zygnemataceae (e.g. Edwards et al. 1993). These specimens are similar to the Rhynie ones in that they comprise filaments. However, they are smaller with the cells measuring 25–30 µm long by 12–15 µm wide. Zygotes similar to those produced by certain extant zygnematalean algae have been widely reported in the palynological record from the Carboniferous onwards (see Hoshaw and McCourt 1990; Grenfell 1995; van Geel and Grenfell 1996). Older Devonian forms were reported by Wood and Miller (1997).

There is a very limited fossil record reported for the Oedogoniales. Baschnagel (1966) described *Palaeoedogonium micrum* Baschnagel in his assemblage of algae from the Mid Devonian of North America (see above). Bian and Liu (1999) reported Oedogoniales from Late Ordovician marine deposits of Jiangxi Province, China. The potential oedogonialean alga described from the Rhynie chert by Edwards and Lyon (1983) is smaller than the material described herein.

Comparisons with the filamentous algae previously described from the Rhynie chert by Edwards and Lyon (1983) are difficult because of taphonomic differences. The petrified chert material is uncompressed and contains contracted remnants of cell contents, in contrast to the specimens described herein that are compressed and preserved as palynomorphs (essentially coalified compressions of recalcitrant cell walls with no cell contents preserved). *Mackiella rotundata* Edwards and Lyon, *Rhynchertia punctata* Edwards and Lyon and the various specimens described as ‘filamentous alga incertae sedis’ all have filamentous form and are broadly similar in size and fall within the size range of the material described herein. Critically, however, they consist of a single, thin wall (except, perhaps, *R. punctata* where some cells appear to possess an internal body) and lack the distinctive collar.

Palaeoenvironmental implications

Species of zygnematalean and oedogonialean have rarely been reported from hot springs, which tend to be dominated by cyanobacteria and unicellular red and green algae (Phoenix et al. 2006; Rajapaksha et al. 2014; Varshney et al. 2015; Schuler et al. 2017). Instead, extant members of these two groups are widespread in freshwater environments such as

streams, ponds, or lakes (Hall and McCourt 2015; John and Rindi 2015), where they live freely suspended in water or attached to plants or other substrates. This is entirely consistent with the interpretation of the sediments from which the fossil remains are recovered as pond/lake sediments. Furthermore, both zygnemataleans and oedogonialeans are known for their ability to form dense and luxurious growths or blooms. The presence of vast numbers of algal remains in one of the samples is suggestive of a bloom.

Conclusions

Fossil remains recovered from palynological preparation of pond/lake sediments from the Rhynie outlier are interpreted as filamentous green algae (most likely zygnematalean or oedogonialean). These algae are interpreted as inhabiting freshwater pond/lakes, where they were attached to plants or other substrates and occasionally bloomed. A more detailed evaluation and taxonomic placement of this element of the algal flora will be achieved if these fossils, preserved as palynomorphs, were to be located preserved by petrification in the actual Rhynie chert.

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