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Short Communication

Microalgae from the Lower Devonian Rhynie chert: a new *Cymatiosphaera*

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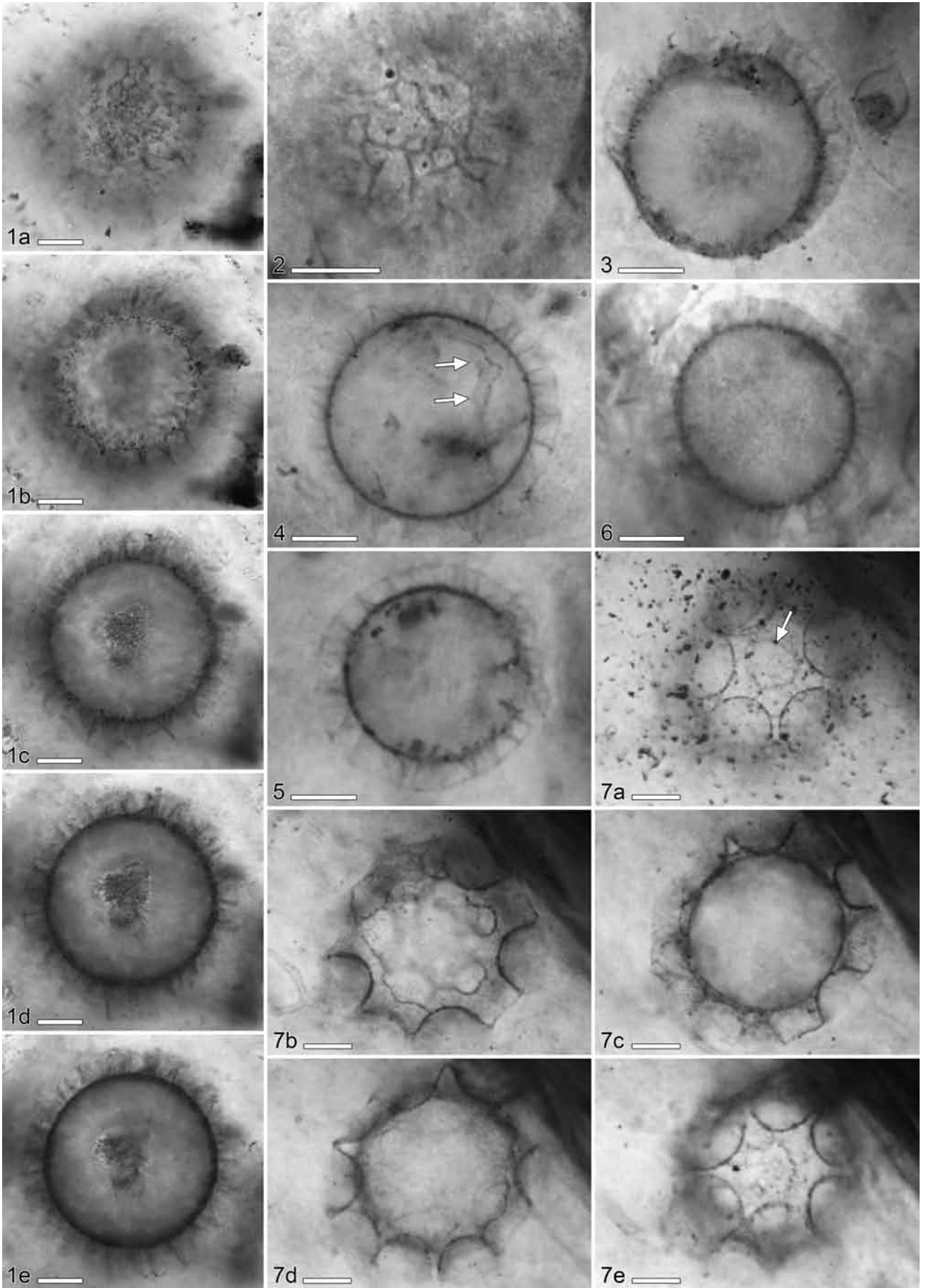
The life cycle of prasinophyte microalgae in the order Pyramimonadales (Pyramimonadophyceae, Chlorophyta) includes a unique non-motile stage termed the phycoma (Sym & Pienaar 1993; van den Hoek et al. 1995). In contrast to cysts and other resting stages, the alga remains metabolically active during the phycoma stage and undergoes reproduction (Leliaert et al. 2012). Phycomata are often morphologically distinctive, and thus widely used as diagnostic structures in species circumscription and identification (e.g., Eisenack et al. 1973; Parke et al. 1978; Throndsen 1997). Since the wall is composed of a resistant, sporopollenin-containing biopolymer, phycomata are frequently preserved in the fossil record and sometimes are used as a proxy record for certain paleoenvironmental conditions (e.g., Colbath & Grenfell 1995; Williams et al. 2000; Versteegh & Blokker 2004). The oldest microfossils interpreted as prasinophyte phycomata come from the Precambrian (e.g., Tynni 1978; Traverse 2007; Molyneux et al. 2013).

Fossil phycomata are typically encountered in palynological preparations (Playford 2003; but see Vigran et al. 2008); the vast majority of forms are known from marine sediments (Tyson 1995; Throndsen 1997). There are also several reports of prasinophyte phycomata from freshwater paleoenvironments (e.g., Tappan 1980; Clausing 1993; McFadden et al. 1998), but the record is exceedingly meagre, and thus of the evolutionary history of these algae and their significance in the functioning of freshwater ecosystems through time remain largely unknown. The oldest fossil evidence of freshwater prasinophytes are phycomata corresponding to *Cy-*

matiosphaera O. Wetzel, 1933 emend. Deflandre, 1954 from the Lower Devonian Rhynie chert (Dotzler et al. 2007).

The Rhynie chert Lagerstätte is one of the most important sources of new information on the diversity of life in an Early Devonian non-marine ecosystem because of the exquisitely preserved fossils of vascular plants, animals, and various groups of microorganisms (e.g., Kerp & Hass 2004). The Rhynie chert occurs within a sequence of sedimentary and volcanic rocks located northwest of the village of Rhynie in Aberdeenshire, Scotland. The Lagerstätte consists of several fossiliferous beds containing lacustrine shales and cherts that have been dated as 407 (Mark et al. 2011) and 411.5 Ma (Parry et al. 2011) old, respectively, and are interpreted as a series of ephemeral freshwater pools and lakes within a hot spring environment (Rice et al. 2002; Rice & Ashcroft 2004). Preserved in the chert are both aquatic (freshwater) facies from the pools/lakes and subaerial soil/litter horizons with in situ plants that occupied the edges of the bodies of water.

A thin sections of the Rhynie chert that is housed in the collection of the Bayerische Staatssammlung für Paläontologie und Geologie at Munich, Germany (accession number SNSB-BSPG 2013 V 13), contains a total of 7 specimens of a microfossil that closely resembles the *Cymatiosphaera* fossils described previously from the Rhynie chert (Dotzler et al. 2007). The new specimens can be distinguished, however, by the pattern of the surface ornamentation. The specimens occur singly within a loosely organized to somewhat compacted accumulation of sediment particles, fungal hyphae, spores, and



plant debris; two of the specimens occur inside degraded land plant fragments. Specimens (Pl. 1, Figs 1–6) consist of a spherical vesicle ranging from 30 to 40 μm in diameter that is ornamented with laevigate muri. The muri are (3–)4(–5) μm high, positioned perpendicularly to the vesicle surface, and have distinct outer margins that are oriented parallel to the vesicle surface (Pl. 1, Figs 1d–e, 4–6). The ornament is organized in a series of polygonal (usually pentagonal to heptagonal) fields (campi or lacunae), which are variable in size and shape (Pl. 1, Figs 1a, 2). Muri in cross section, as well as the intersections (corners) of the polygons, appear as narrow columns or elongate triangles in lateral view (Pl. 1, Figs 1d, 4–5). The lacunae floors are laevigate (Pl. 1, Fig. 2). One of the specimens shows what appears to be a slit-like rupture in the vesicle (arrows in Pl. 1, Fig. 4).

The specimens described in this paper are morphologically similar to the *Cymatiosphaera* fossils described by Dotzler et al. (2007). The most important feature in common is the presence of a surface ornament composed of muri that divide the vesicle surface into polygonal fields, but without displaying a system of equatorial differentiation of fields. A surface ornamentation of this type (i.e. a constant tabulation pattern sensu Reaugh 1978) is a typical feature of the fossil genus *Cymatiosphaera* (Deflandre 1954). As a result, we interpret the structures described here as a second species of *Cymatiosphaera* from the Rhynie chert. Dotzler et al. (2007) pointed out that virtually all forms described within the genus *Cymatiosphaera* are based on specimens discovered in palynological samples. This makes it difficult to evaluate whether the Rhynie chert specimens represent a new taxon or belong to a form that has already been described based on palynological preparations. To address this issue, we will retain the new form in open nomenclature as *Cymatiosphaera* sp. 2.

The new specimens differ from the form described previously with regard to the surface reticulum (Tab. 1). The fossils described by Dotzler et al. (2007), henceforth called *Cymatiosphaera* sp. 1 (Pl. 1, Fig. 7a–e), are characterized by prominent muri that divide the vesicle surface into a relatively small number of orderly arranged polygonal fields, whereas the number of fields in *C.* sp. 2 is appreciably larger. Moreover, the fields in *C.* sp. 2 are smaller than in *C.* sp. 1 and more variable in size and shape. In addition, the muri in *C.* sp. 2 are less prominent (i.e. 3–5 μm high vs. 4–6 μm high in *C.* sp. 1). Pores have not been detected in *C.* sp. 2, while circular openings occur in some of the lacunae in *C.* sp. 1 (e.g., arrow

in Pl. 1, Fig. 7a). On the other hand, one of the specimens of *C.* sp. 2 shows a slit-like rupture or opening (arrows in Pl. 1, Fig. 4) that might represent an excystment structure (dehiscence line; see Tappan 1980). Interestingly, Dotzler et al. (2007) note a striking variability with regard to vesicle diameter (24–48 μm) among the >100 specimens of *C.* sp. 1 included in their study. This variability is a typical feature of prasinophyte phycmata, and is the result of continued growth and reproduction of the metabolically active alga within the phycoma (e.g., Tappan 1980). A similar size range has not been observed in *C.* sp. 2. However, the sample set available of the new form is <10, and thus not statistically viable.

The discovery of *Cymatiosphaera* sp. 2 represents only the second record of a prasinophyte phycoma from the Rhynie chert. The fossil genus *Cymatiosphaera* ranges from the Cambrian to the Neogene and occurs throughout the world (e.g., Tappan 1980). Extant algae producing phycmata that correspond to *Cymatiosphaera* are included in the genus *Pterosperma* Pochet, 1893 (e.g., Parke et al. 1978). The published record of *Cymatiosphaera* from the Devonian is substantial, but the records exclusively are from marine sediments (e.g., Nautiyal 1976; Reaugh 1978; Wicander & Wright 1983; Hammann et al. 1998; Amenábar et al. 2006; Mullins & Servais 2008 and references therein; Rubinstein et al. 2008). Other than the specimens reported from the Rhynie chert, the oldest record from freshwater is Pennsylvanian–Early Permian in age (Clausing 1993).

It is interesting to note that the prasinophyte phycmata described from the Rhynie chert all occur within accumulations of plant debris intermixed with sediment and other microorganisms; none have been documented in thin sections containing well preserved (in situ) land plants. This is somewhat puzzling since those portions of the chert containing the land plants have been studied much more intensively. The layers containing the phycmata most likely represent litter layers from around the margin or bottom of the small ponds within the Rhynie paleoecosystem. It is probable that empty phycmata were washed into the litter accumulations and subsequently became trapped between or within the plant debris and sediment particles. Alternatively, the occurrence of the phycmata within the litter layers might also reflect some biological requirement of the algae. For example, it has been demonstrated that certain prasinophyte blooms are related to sudden increases in nutrient availability (Meng et al. in press). Since the litter layers in the Rhynie paleoecosystem were probably rich in nutrients the possibility

Plate 1: *Cymatiosphaera* from the Lower Devonian Rhynie chert. (1–6) *Cymatiosphaera* sp. 2 (this paper); slide SNSB-BSPG 2013 V 13. (1a–e) Optical sections through specimen. (2) Surface view, showing irregular surface reticulum. (3) Specimen in median optical section, showing muri in lateral view. (4) Specimen in (optical) section view; arrows indicate slit-like excystment(?) structure. (5, 6) Specimen in (optical) section view, showing muri in section view. (7a–e) *Cymatiosphaera* sp. 1 (Dotzler et al. 2007), several optical sections of specimen; note more prominent muri, fewer and larger fields, and circular orifices in some of the lacunae (e.g., arrow in Fig. 7a); slide SNSB-BSPG 1965 I 292. All scale bars = 10 μm .

Table 1: Morphological features of *Cymatiosphaera* sp. 1 (from Dotzler et al. 2007) and *Cymatiosphaera* sp. 2 (this paper)

	<i>Cymatiosphaera</i> sp. 1	<i>Cymatiosphaera</i> sp. 2
Vesicle shape	Spherical	Spherical
Vesicle diameter	24–48 µm	30–40 µm
Surface ornamentation	reticulum of polygonal fields; all fields similar in size and shape	reticulum of polygonal fields; fields variable in size and shape
Muri	4–6 µm high, with distinct outer margins, laevigate	(3–)4(–5) µm high, with distinct outer margins, laevigate
Lacunae	penta- to heptagonal, regular, 15–20 µm in diameter, laevigate	penta- to heptagonal, irregular, 2–6(–10) µm in diameter, laevigate
Openings	circular or oval opening may be present in center of lacunae	slit-like rupture in one specimen

exists that the presence of phycmata in these layers was somehow associated with nutrient availability. Moreover, Channing & Wujek (2010) suggested that accumulations of decaying plants may have served as buffers from the transient extreme water conditions in hot spring environments.

Prasinophytes are an interesting group of organisms because they have the potential to shed light on the nature of the last common ancestor of all green plants, as well as on the origin of the advanced chlorophytes (Turmel et al. 2009). The phycmata described in this paper suggest that the diversity of prasinophytes in freshwater may have been extensive by the Early Devonian, and that these organisms may have played important roles in the functioning of early non-marine ecosystems, perhaps as primary producers in food webs.

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