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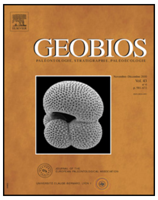

Original article

Deciphering interfungal relationships in the 410-million-yr-old Rhynie chert: Sporocarp formation in glomeromycotan spores☆

Michael Krings[a,b,*], Thomas N. Taylor[b], Hans Kerp[c], Christopher Walker[d,e]

[a] Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität, and Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 Munich, Germany
[b] Department of Ecology and Evolutionary Biology, and Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence, KS 66045-7534, USA
[c] Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Westfälische Wilhelms-Universität Münster, Heisenbergstraße 2, 48149 Münster, Germany
[d] Royal Botanic Garden Edinburgh, 21A Inverleith Row, Edinburgh EH3 5LR, UK
[e] School of Earth Sciences and Environment, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

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ABSTRACT

Fungi today enter into relationships with other fungi in many ways. Although this was likely also the case in the geologic past, detailed descriptions of interfungal associations and interactions based on fossils remain scarce. Sporocarps bounded by a peridium-like envelope occur singly within the lumen of large glomeromycotan spores (*Palaeomyces gordonii* var. *major*) from the Lower Devonian Rhynie chert. The envelope consists of multi-branched, interlacing hyphae. At the tips of hyphae extending from the envelope into the lumen are produced spheroidal to urn-shaped spores. Similar sporocarps are found in several present-day species in the Glomeraceae. Clusters of spores, superficially resembling sporocarps, may also form within dead spores from any member of the Glomeromycota, including non-sporocarpic groups such as *Ambispora*, *Acaulospora*, and the Gigasporaceae, probably because they provide a shielded or otherwise advantageous environment for sporulation. The sporocarps in *P. gordonii* var. *major* from the Rhynie chert provide important information for reconstructing the numerous levels of fungal associations and interactions that existed in early continental ecosystems.

1. Introduction

One of the major contributions to our understanding of early terrestrial ecosystems was a series of papers on structurally preserved land plants and microorganisms from the Lower Devonian Rhynie chert in Aberdeenshire, Scotland (Kidston and Lang, 1917, 1920a, b, 1921a, b). Since the initial descriptions there have been numerous contributions that have provided additional details about the land plants, and others that have greatly expanded our knowledge of the organisms (e.g., animals, fungi, algae, cyanobacteria) that co-occur with the land plants in the Rhynie chert. Still other studies have focused on associations and interactions that existed between different organisms in the Rhynie paleoecosystem. One of the most frequently encountered associations in the Rhynie chert is the colonization of fungal spores by various types of other fungi (Taylor et al., 2003). Kidston and Lang (1921b) illustrate several examples of such intrusive fungi in the form of reproductive units of various sizes that occur in the lumen of the host spores. Other fungal spores in the Rhynie chert contain tenuous mycelia with terminal reproductive units (Krings et al., 2009, 2010). Still other Rhynie chert fungi developed on the surface or between individual layers of the wall of fungal spores (Taylor et al., 1992; Hass et al., 1994; Krings and Taylor, 2014). Nevertheless, only a few of these intricate interfungal relationships have been described and evaluated in detail.

In this paper, we revisit one of the interfungal relationships from the Rhynie chert initially reported by Kidston and Lang (1921b). We based our study on new specimens that are better preserved than the material used in the original description, and thus permit a more complete assessment and photographic documentation of details. The association consists of large glomeromycotan spores containing sporocarps or clusters of spores and mycelium formed by another fungus. The sporocarps are bounded by a peridium-like hyphal envelope and produce spores on hyphae extending from the envelope into the lumen.

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* Corresponding author. Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität, and Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 Munich, Germany.

E-mail address: m.krings@lrz.uni-muenchen.de (M. Krings).

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This interfungal relationship expands our knowledge of the numerous levels of fungal associations and interactions that existed in the Rhynie ecosystem ~410 Ma ago, and thus represents an important component necessary to understand the roles that microbial life played in early continental ecosystems.

2. Geological setting

The Rhynie chert locality is situated northwest of the village of Rhynie in Aberdeenshire, Scotland. The fossil-bearing layers occur in the Windyfield Shales Member, within the lower part of the Dryden Flags Formation (Parry et al., 2011). The Lagerstätte is made up of fossiliferous beds containing lacustrine shales and cherts that have been interpreted as a series of ephemeral freshwater pools within a hot spring environment (Rice et al., 2002; Rice and Ashcroft, 2003). Preserved in the cherts are both aquatic (freshwater) facies from the pools and subaerial soil/litter horizons with *in situ* plants from the margins of the pools. Preservation of the biota is interpreted as being the result of temporary flooding of silica-rich water, or by groundwater high in silica percolating to the surface (Powell et al., 2000).

The Rhynie chert has been regarded as Early (but not earliest) Pragian to earliest Emsian in age based on spore assemblages (Wellman, 2006; Wellman et al., 2006). A more recent high-precision U-Pb age estimate indicates an absolute age of 411.5 ± 1.3 Ma (Parry et al., 2011), while another age constraint using ^{40}Ar/^{39}Ar yields a mean age (recalculated to be U-Pb comparable) of the fossilized biota of 407.1 ± 2.2 Ma (Mark et al., 2011). According to the latest International Chronostratigraphic Chart (www.stratigraphy.org), an absolute age of 411.5 ± 1.3 Ma would correspond to the Lochkovian-Pragian boundary (410.8 ± 2.8 Ma), while the age suggested by Mark et al. (2011) would correspond to the Pragian-Emsian boundary (407.6 ± 2.6 Ma).

3. Material and methods

The fossils considered in this study (Figs. 1–3) were found in thin sections of Rhynie chert that were prepared from four different blocks according to standard procedures outlined in Hass and Rowe (1999). Slides are deposited in the Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) at Munich, Germany, under accession numbers SNSB-BSPG 1964 XX 95, SNSB-BSPG 1965 I 319, SNSB-BSPG 2013 V 27 and 77, and SNSB-BSPG 2013 XV 37, 156, and 157. For elucidation and comparison, several images of extant glomeromycotan fungi from the holdings of one of us (C.W.), now deposited at the Herbarium of the Royal Botanic Garden Edinburgh (Herb E), have been provided in Figs. 4 and 5.

4. Description

4.1. Host spores

The spores that contain the sporocarps occur singly within the cortex of (largely) degraded land plant axes (Figs. 1(1, 7), 2(1), 3(1)), probably of *Horneophyton lignieri* (Kidston et W.H. Lang) Barghoorn et Darrah and *Rhynia gwynne-vaughanii* Kidston et W.H. Lang; one specimen occurs in a partially degraded land plant sporangium (Fig. 2(4)). The host spores are spheroidal, 430–560 μm in diameter, and appear to have been relatively thick-walled *in vivo*. However, all host spores have undergone some level of physical and/or biological degradation. The spore wall is highly degraded and disassociated, or even completely missing (Fig. 2(4)); it is mostly replaced with a distinctive layer (HSW in Figs. 1(4), 2(2, 3)) that appears white in thin sections in transmitted light, and may be unstructured or display a faint reticulation (Fig. 2(2, 3)). On the other hand, the outer spore wall component of certain extant Glomeromycota can expand considerably in acidic mounting media such as PVLG (Polyvinyl alcohol-lactic acid-glycerol) and, as a result, becomes very difficult to see (Fig. 4). It is therefore also possible that the condition of the fossil host spores is a preservation artifact resulting from the expansion of the wall or a wall component during fossilization. In some host spores, there is evidence of a prominent funnel-shaped neck region and subtending hypha (Fig. 1(7, 8)); a septum separating the neck from the subtending hypha proper is recognizable in one of the specimens (arrow in Fig. 1(8)).

4.2. Sporocarps

The glomeromycotan host spores contain a single, spherical sporocarp that fills the entire spore lumen (Figs. 1(1, 7), 2(1), 3(1)) and may even extend into the neck region (Fig. 1(7, 8)); evidence of how the fungus that formed the sporocarps entered the host spore is not recognizable. Sporocarps of this type have not been found in other types of glomeromycotan spores or elsewhere in the Rhynie chert. Sporocarps are 360–490 μm in diameter. Specimens usually contain large numbers of small spores that do not appear to be organized in any particular order. One specimen contains only a few spores (Fig. 2(4)). The number of spores produced in a sporocarp probably was as large as several hundred, although the exact number can only be estimated since these spores are only viewed in a single section. Spores may be more or less evenly distributed within the sporocarp (Fig. 1(1, 7)), or they are sparse to absent in the sporocarp centre (Figs. 2(1), 3(1)); they may be tightly packed (Fig. 1(7)) or relatively loosely organized (Fig. 1(1)).

All sporocarps are bounded by what appears to be a hyphal peridium that perfectly lines the inner side of what formerly was the host spore wall (HE in Fig. 1(3, 4)). It is possible, however, that this structure results from the expanding glebal mycelium becoming constrained by the host spore wall, rather than representing an evidently differentiated hyphal peridium with further differentiated glebal hyphae. We therefore use the terms "peridium-like hyphal envelope", or simply "(hyphal) envelope", rather than "peridium" for this structure. The shape and construction of the envelope is best recognizable in the specimen illustrated in Fig. 2(4), which basically represents an empty envelope, with the majority of spores released from the sporocarp and little left of the host spore and its subtending hypha. Perhaps the most interesting aspect of this specimen is that it demonstrates how the envelope continues into the neck region of the host spore (arrow in Fig. 2(4)). The second specimen showing this condition (Fig. 1(7, 8)) also demonstrates that spores even are formed in the envelope extension into the host spore neck.

The envelope is 8–15 μm thick and composed of several layers of tightly interlacing and interlocking hyphae that repeatedly branch at wide angles (50–90°), resulting in a characteristic, coralloid pattern (Figs. 2(5–9), 3(9,10)). Envelope hyphae are (2-)2.5–5.5(-8) μm wide, more or less tubular or with numerous shallow, irregular constrictions (Fig. 2(7, 8)); they possess what appear to be irregularly distributed septa (arrows in Fig. 3(9, 10)). Branch hyphae may extend around the circumference of the structure, and thus add to the envelope, or extend inwardly to give rise to spores (Figs. 1(10) [arrows], 3(2–4)). Branches that produce the spores are on average slightly narrower (~3–5 μm wide) than the envelope hyphae, unbranched or branched, and in some specimens fill the sporocarp lumen with a gleba-like meshwork (Fig. 1(3, 4)). In other specimens, however, a confluent gleba-like meshwork is not recognizable (Fig. 3(1)).