sciendo DOI: 10.2478/fbgp-2024-0001

RHIZOPHYDITES BICORNIS NOV. SP. (FOSSIL CHYTRIDIOMYCOTA) FROM THE RHYNIE CHERT, SCOTLAND

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Abstract: *Fungal spores from the Lower Devonian Rhynie chert are frequently colonized by other fungi; however, only a few of these colonizers have been described.* Rhizophydites bicornis *nov. sp., which occurs on certain thin-walled fungal spores, is monocentric and characterized by inoperculate zoosporangia that are broadly citriform or spindle-shaped, ovoid, inversely triangular, or irregular, up to 25 µm high and 40 µm wide, and usually lie with their long axis perpendicular to the point of insertion on the host. They typically have two lateral opposite discharge papillae. In some cases, secondary zoosporangia have developed from the walls of old sporangia. Similarities between* R. bicornis *and the extant* Rhizophydium goniosporum *and* R. transversum *(Rhizophydiales) are used to suggest affinities of the fossil to the Chytridiomycota.*

Keywords: discharge papilla, fossil fungi, Lower Devonian, *Rhizophydium goniosporum*, zoosporangium

INTRODUCTION

Chytrid-like morphologies are common among the fungi preserved in the Early Devonian Rhynie chert (Taylor *et al.* 1992, 2004, Berbee *et al.* 2017). They indicate that chytrids (*i.e.* members of the phylum Chytridiomycota) and chytrid-like organisms (*i.e.* forms that resemble chytrids morphologically but cannot be safely assigned on the basis of morphological features; see Strullu-Derrien 2018) played important ecological roles in early terrestrial ecosystems. Most helpful in the study of these roles is the fact that the chytrid-like fossils in the Rhynie chert are almost always preserved in situ, and thus allow the context in which the organisms once lived to be examined directly (e.g., Strullu-Derrien *et al.* 2016, Krings *et al.* 2017, Krings 2022).

The vast majority of chytrids and chytrid-like organisms described to date from the Rhynie chert are associated in one form or another with either land plants (e.g., Illman 1982, Taylor *et al.* 1992b, Krings *et al.* 2017, 2021), the charophyte alga *Palaeonitella cranii* (Taylor *et al.* 1992a, Strullu-Derrien *et al.* 2016, Garcia Cabrera & Krings 2024), or other fungi, especially Glomeromycota (e.g., Hass *et al.* 1994, Krings & Harper 2018, 2019a, 2020, Krings 2022, 2024). One of the best-documented Rhynie chert chytrids is *Rhizophydites matryoshkae*, which occurs on spores of the land plant *Horneophyton lignieri* (Krings *et al.* 2021). Thalli are monocentric and consist of an inoperculate zoosporangium with one or several discharge papillae or short tubes, and a rhizoidal system that arises from a single site on the sporangium. Several specimens comprise two or more successive generations of zoosporangia, a feature that allows for a direct comparison with present-day *Rhizophydium* (Rhizophydiales). Although *Rhizophydium* is one of the larger genera of the chytrids today (Letcher & Powell 2012), further species of the fossil-genus *Rhizophydites* have not yet been described.

Here, I present *Rhizophydites bicornis* nov. sp., a newly discovered Rhynie chert fungus that corresponds to *R. matryoshkae* in several structural features, but differs in that the zoosporangia typically are broadly citriform, ovoid, or inversely triangular, and have two lateral opposite discharge papillae.

GEOLOGICAL SETTING, MATERIAL, AND METHODS

The Rhynie chert Lagerstätte is located in the northern part of the Rhynie outlier of Lower Old Red Sandstone in Aberdeenshire, Scotland, within a sequence of sedimentary and volcanic rocks (Garwood *et al.* 2020). The chert occurs in the Rhynie Block of the Dryden Flags Formation northwest of the village of Rhynie. The Lagerstätte is made up of fossiliferous beds containing lacustrine shales and chert that have been interpreted as ephemeral pools within a geothermal wetland (Channing 2017, Trewin & Kerp 2017). Preserved in the chert are both aquatic facies from the pools and subaerial soil/litter horizons with in situ plants that grew along the margins of the pools; preservation is thought to have taken place as a 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 biota are regarded as 411.5±1.3 to 407.6±2.6 million years old according to Mark *et al.* (2011) and Parry *et al.* (2011), and Pragian-earliest Emsian according to Wellman (2006, 2017) and Wellman *et al.* (2006).

The fossils described below are present in a thin section prepared by cementing a wafer of the Rhynie chert to a glass slide, and then grinding the wafer until it was sufficiently thin to transmit light (for details on thin section preparation, see Hass & Rowe 1999). The slide belongs to a series of 42 thin sections prepared from one chert block. All materials (chert block, offcuts, and thin sections) are deposited in the Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) in Munich, Germany, under accession SNSB-BSPG 2016 XII; the slide containing the fossils has the number SNSB-BSPG 2016 XII 16. Fossils were examined using transmitted light microscopy (Leica); digital images were captured with a Jenoptik Gryphax Naos camera and processed in Adobe Photoshop (for details on microscopy and image processing, see Krings *et al.* 2021).

SYSTEMATIC PART

Phylum **Chytridiomycota** Doweld, 2001
Fossil-genus ***Rhizophydites*** M. Krings et C.J. Harper, 2021 [in Krings *et al.* 2021]
Mycobank: MB 834563
Type species: *Rhizophydites matryoshkae* M. Krings et C.J. Harper, 2021; Lower Devonian, Rhynie chert, Scotland

Species ***Rhizophydites bicornis*** nov. sp.
Plate I
Mycobank: MB 852566
Etymology: The epithet (Lat. adj. *bicornis* = two-horned, having two horns or horn-like parts) refers to the two prominent discharge papillae.
Locality: Rhynie chert site, Aberdeenshire, Scotland, UK National Grid Reference NJ 494276 (57°20'09.97" N, 002°50'31.83" W).
Stratigraphic horizon: Dryden Flags Formation.
Age: Early Devonian; early (but not earliest) Pragian to earliest Emsian (Wellman 2006, 2017), 411.5 ± 1.3 Ma (Parry *et al.* 2011), 407.1 ± 2.2 Ma (Mark *et al.* 2011).
Holotype: Specimen shown in Plate I, fig. j; in slide SNSB-BSPG 2016 XII 16, SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.
Additional studied material: Additional thalli in slide SNSB-BSPG 2016 XII 16.
Diagnosis: Zoosporangia sessile or with a small proximal protrusion, smooth-walled, symmetrical or asymmetrical, typically wider than high (long axis more or less perpendicular to point of insertion on host), broadly citriform or spindle-shaped, ovoid, inversely drop-shaped, triangular or trapezoidal, or irregular, upper surface flattened; variable in size, less than 10 to 25 μm high and up to 35(–40) μm wide (including discharge papillae); with two (very rarely only one) lateral opposite discharge papillae or short tubes located in distal half of sporangium; size and shape of both papillae equal or unequal; primary rhizoidal axis prominent, apophysis may be present; secondary zoosporangia may grow from walls of old zoosporangia; secondary sporangia small, usually irregularly shaped.
Description: *Rhizophydites bicornis* is three-dimensionally preserved (silicified) within a heavily degraded early land plant axis of unknown affinity (Plate I, fig. a). Cells and tissues of the axis have disintegrated into a more or less homogeneous, beige to light-brown mass, except for the central water-conducting strand (ct in Plate I, fig. a) and the cuticle (cu in Plate I, fig. a), which are still in place and appear to be at least partially intact.

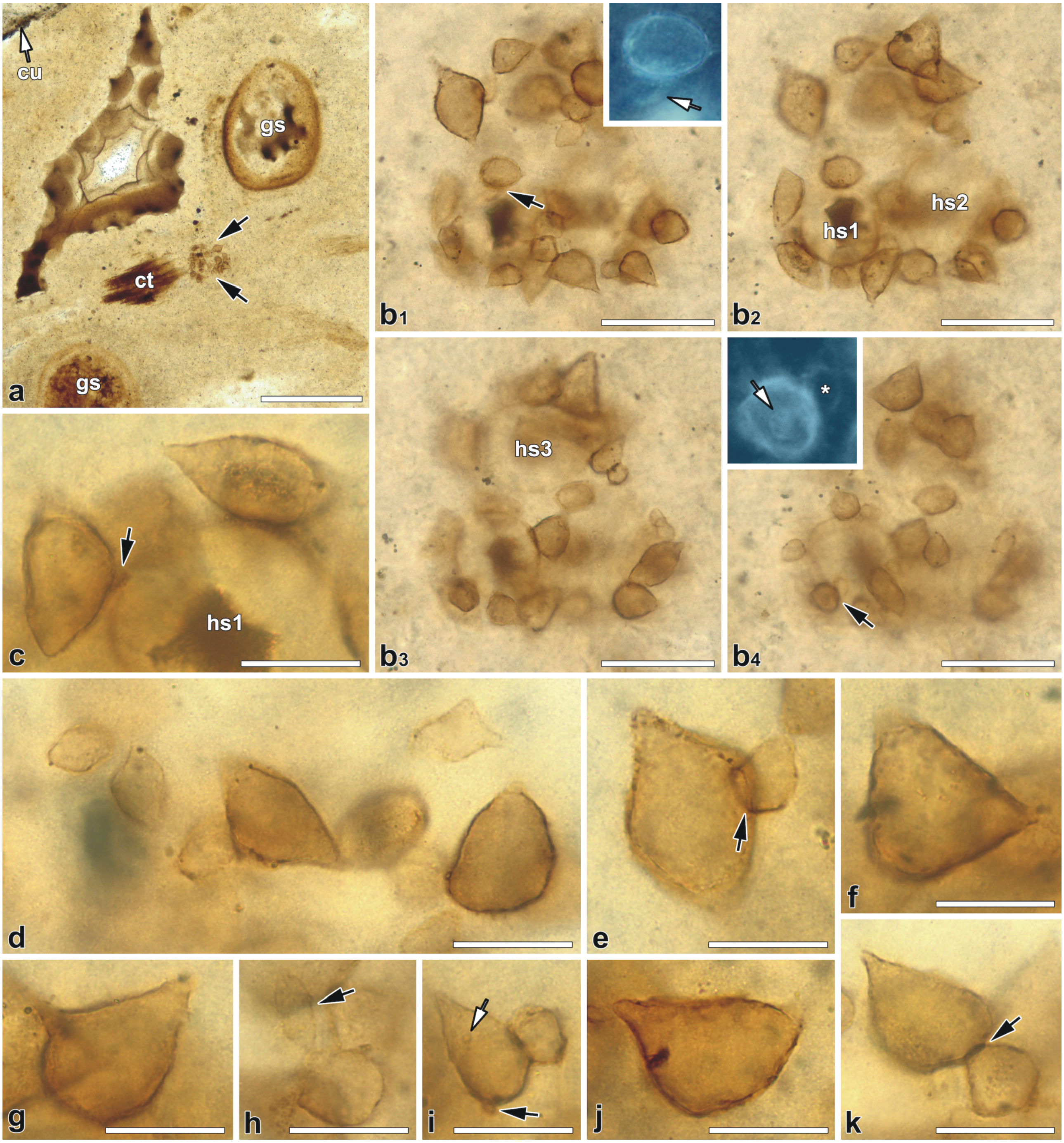

Plate I. *Rhizophydites bicornis* nov. sp. from the Lower Devonian Rhynie chert, Scotland. **a** – Plant axis (slightly oblique cross section) with intact cuticle (cu) and central strand of water-conducting tissue (ct); other cells and tissues disintegrated into homogeneous mass; gs = glomeromycotan spores; arrows indicate population of *R. bicornis* [magnified in Figure $1b_{1-4}$]; scale bar, 300 μm. $\mathbf{b_{1-4}}$ – Population of *R. bicornis* distributed over three thin-walled fungal spores (hs1, hs2, and hs3) in four different focal planes; arrows in Figure b_1 and b_4 indicate position of sporangia shown in insets; inset of Figure b_1: primary rhizoidal axis; inset of Figure b_4: cluster of oblong bodies (arrow) and putative apophysis (*); scale bars, 50 μm. **c** – Zoosporangia on hs1, the left one with a proximal protrusion (arrow), the right one sessile; scale bar, 20 μm. **d** – Normal and smaller, distinctly thinner-walled zoosporangia; scale bar, 20 μm. **e** – Zoosporangium (viewed from above) with a small secondary sporangium (arrow); scale bar, 20 μm. **f** – Inversely triangular zoosporangium; scale bar, 20 μm. **g** – Sporangium with one larger and one smaller discharge papilla; scale bar, 20 μm. **h** – Small, thin-walled, and almost colorless sporangium (arrow); scale bar, 20 μm. **i** – Sporangium containing spheroidal body (white arrow); note secondary sporangium; black arrow indicates proximal protrusion; scale bar, 20 μm. **j** – Holotype; scale bar, 20 μm. **k** – Sporangium with a rhomboidal secondary sporangium (arrow); scale bar, 20 μm.

Present within the mass in the cortical portions of the axis are two large glomeromycotan spores (gs in Plate I, fig. a), as well as a cluster of three considerably smaller and thinner-walled, spheroidal or ovoid fungal (probably glomeromycotan) spores (arrows in Plate I, fig. a; hs1–hs3 in Plate I, fig. b). More than 50 thalli of *R. bicornis* were found as colonizers of these latter spores.

Rhizophydites bicornis is eucarpic and monocentric. Thalli consist of a smooth-walled epibiotic vesicle, for which henceforth the term zoosporangium is used in anticipation of the interpretation of the fossil as a member of the Chytridiomycota, and an endobiotic rhizoidal system; the latter, however, is very rarely preserved. The zoosporangia are symmetrical or asymmetrical, broadly citriform or spindle-shaped, ovoid, inversely drop-shaped, triangular or trapezoidal, or irregular, between less than 10 and 21(–25) μm high and up to 35(–40) μm wide (including discharge papillae), and most have a flattened upper surface (Plate I, figs c–g, i–k). They usually lie with their long axis perpendicular to the point of insertion on the host, and are either sessile (e.g., right sporangium in Plate I, fig. c) or attached to the host spore via a proximal protrusion up to 2 μm high (black arrows in Plate I, figs c, i). A few smaller and distinctly thinner-walled and lighter-colored (nearly translucent in some cases) zoosporangia are also present (Plate I, fig. d; arrow in Plate I, fig. h); as to whether these sporangia are mature but underdeveloped, or aborted, or still developing remains unknown. Nearly all zoosporangia possess two (very rarely only one) lateral opposite discharge papillae or short tubes, in some cases up to 4.5 μm long, and closed or open at the tip. The papillae occur in the distal half of the sporangium (e.g., Plate I, figs c, g, j, k), and their walls appear to be thinner than the wall of the sporangium from which they arise. In some cases, one of the papillae is (slightly) larger and differently shaped than the other (Plate I, figs f, g). No evidence of opercula was found. Rhizoidal systems are usually not recognizable; if remnants of them have been preserved, they appear as a primary rhizoidal axis that extends into the lumen of the host spore (inset of Plate I, fig. b_2). One specimen was found indicating the presence of an endobiotic subsporangial apophysis (inset of Plate I, fig. b_4).

While the vast majority of zoosporangia are empty, one or two contain one to several tiny spherical or oblong bodies with a diameter of c. 1 μm (white arrows in Plate I, fig. i and in the inset of Plate I, fig. b_4), which are probably (encysted) zoospores. Several specimens indicate that new (secondary) zoosporangia could develop from the walls of old sporangia (arrows in Plate I, figs e, k). Secondary zoosporangia are always smaller and more irregularly shaped than the parental sporangia.

DISCUSSION

The abundance and morphological diversity of fungal spores and reproductive units is one of the paleontological hallmark features of the Rhynie chert (Krings *et al.* 2017). No less astonishing is the fact that a great many of these propagules demonstrably served as a habitat and carbon source for a diverse array of other fungi (Krings & Harper 2018). Several examples of such fungi, which occur either in the lumen of their hosts or on their surfaces (or both), or extend out between individual host wall layers, have been described (surveyed by Krings 2022).

Rhizophydites bicornis described in this study is one more in the expanding list of fungal colonizers of fungal spores in the Rhynie ecosystem. Well-suited present-day morphological equivalents of this fossil are species in the "traditional" (*i.e.* morphology based) genus *Rhizophydium* (Chytridiomycota), especially *R. goniosporum* and *R. transversum* (Letcher & Powell 2012, p. 137/138, pl. 32, figs 12–15 and pl. 33, figs 13–16). Scherffel (1926, p. 20, pl. 1, figs 40–42 and pl. 2, figs 43–50) states that the zoosporangia of *R. goniosporum*, when viewed from the side, have the shape of a lying lemon, or rather that of a bread roll, which lies parallel to the host surface with its longitudinal axis. The ventral side of the sporangium is usually less curved than the dorsal side, but it also happens that the ventral side is strongly curved and the dorsal side is flattened. The two opposite tips of the sporangium [*i.e.* the discharge papillae] protrude in a teat-like manner. Deviations from this typical shape, such as a lying ovoid or somewhat irregular shapes, are often found. Most characteristic is that the sporangium is always wider than high. Similarly, Braun (1856, p. 44/45, pl. IV, figs 1–6) describes the young zoosporangia of *R. transversum* (as *Chytridium transversum*) as spherical or somewhat compressed dorsi-ventrally (oblate), and the older ones as having two opposite, laterally protruding [discharge] papillae. The apparent morphological correspondences between these two present-day chytrids and the fossil strongly suggest that the latter is also a member of the Chytridiomycota, and one that can be directly compared with certain species of *Rhizophydium*. It therefore seemed justified to me to accommodate this form in the genus *Rhizophydites*, which is used for chytrid-like fossils that are morphologically similar or even identical to present-day *Rhizophydium* (Krings *et al.* 2021).

The characteristic zoosporangia with two opposite discharge papillae distinguish *Rhizophydites bicornis* from all other chytrid-like fossils described to date. The form is distantly similar to *Illmanomyces corniger*, another monocentric chytrid-like colonizer of fungal spores in the Rhynie chert, in that the endobiotic rhizoidal system originates from a single, proximal protrusion on the sporangium, and that the discharge apparatus is comprised of prominent papillae or tubes (Krings & Taylor 2014). On the other hand, *I. corniger* is up to two times larger than *R. bicornis*. Moreover, secondary sporangia growing from the walls of old sporangia are not known for *I. corniger*. However, such secondary sporangia have been described for *Rhizophydites matryoshkae* (Krings *et al.* 2021, fig. 2D, F), which is characterized by inoperculate zoosporangia of approximately the same size as *R. bicornis*, but which are predominantly spheroidal and have between one and four discharge papillae.

Only one population of *Rhizophydites bicornis* (c. 50 thalli on three closely spaced fungal spores) has been found so far. The form thus belongs to those fungal morphologies in the Rhynie chert that have been described on the basis of single or relatively few specimens or assemblages (e.g., Krings *et al.* 2009, 2010, Krings & Taylor 2014). On the other hand, there are also multiple fungi in the Rhynie chert, of which large sample sets of several hundred, if not a thousand specimens are available (see Krings *et al.* 2017). This raises the question as to whether *R. bicornis* and the other "rare" forms were in fact rare constituents of the Rhynie ecosystem, or have rarely been preserved or recognized. There are several possible explanations for the scarcity of evidence of *R. bicornis*. Krings (2024) suggested that the chytrids and chytrid-like organisms in the Rhynie ecosystem completed their life cycles within relatively short periods of time, and thus provided only small windows for preservation in recognizable form. Moreover, the thalli probably were readily destroyed unless they either were particularly small, simple, and robust (as for instance *Perexiflasca tayloriana*; see Krings *et al.* 2017), or there was some form of protection from destructive mechanical forces (e.g., a surrounding plant axis or a microbial mat) prior to and during the fossilization process (e.g., Krings & Harper 2019b). It is also conceivable that *R. bicornis* thrived only in certain areas of the Rhynie ecosystem (or its vicinity) that did not become preserved in the chert, or that are not represented by the chert blocks examined to date. The one plant axis containing the specimens of *R. bicornis* could have been transported into its burial site from elsewhere.

Although Rhynie chert fossils have been intensively studied for more than 100 years, new and previously understudied specimens still offer many opportunities to refine and advance the broader discussion of the diversity of life in this early terrestrial ecosystem. I hope that this report will promote interest in the fungal component of the Rhynie ecosystem, and that further specimens of *R. bicornis* will be discovered that can be used to better understand the ecological role of this chytrid in associations and interactions with other organisms.

Acknowledgments

I gratefully acknowledge H. Martin and S. Sónyi (both Munich, Germany) for technical assistance and Hans Kerp (Münster, Germany) and A. Mihai F. Tomescu (Arcata, CA, USA) for their comments on the manuscript.

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