Nova Hedwigia Vol. 99 (2014) Issue 3–4, 403–412 **Article**
published online May 15, 2014; published in print November 2014

An unusual fossil microfungus with suggested affinities to the Chytridiomycota from the Lower Devonian Rhynie chert

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With 2 figures

Abstract: Land plant and fungal spores from the Lower Devonian (~410 Ma) Rhynie chert are known to have been colonized by a wide variety of microfungi, however, only a few of these organisms have been formally described. Thalli of *Illmanomyces corniger* nov. gen. et sp., a distinctive microfungus on certain types of fungal spores from the Rhynie chert, consist of a spheroid epibiotic sporangium with 4–5 prominent, conical discharge tubes. The endobiotic rhizoidal system originates from a single, proximal protrusion on the sporangium. Rhizoidal and sporangial morphology suggest affinities of *I. corniger* to the Chytridiomycota.

Key words: monocentric chytrid, preservation, rhizoidal system.

Introduction

The Early Devonian Rhynie chert, a fossilized (silicified) ~410-million-yr-old hot spring ecosystem in northern Scotland, is today widely known as one of the most important sources of information on the morphology and biology of early non-marine animals and various types of plants (e.g., Kerp & Hass 2004, Trewin & Rice 2004). Moreover, the Rhynie chert has contributed substantially to our concept of the roles that fungi have played in shaping and sustaining the early continental ecosystems (Taylor & Taylor 2000; Taylor et al. 2004, 2014). This is due primarily to the fact that many of the Rhynie chert fungi were fossilized in situ so that associations and interactions with other components of the ecosystem can be directly analyzed.

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 DOI: 10.1127/0029-5035/2014/0205

www.borntraeger-cramer.de
0029-5035/2014/0205 $ 2.50

One of the frequently encountered fungal associations in the Rhynie chert are microfungi that colonize the spores of land plants and other fungi. Several examples of these associations have been described (e.g., Kidston & Lang 1921; Illman 1984; Taylor et al. 1992; Hass et al. 1994; Krings et al. 2009, 2010a), including one type consisting of spheroid or flask-shaped sac-like structures, some with discharge openings, that are attached to the outer surfaces of spores (e.g., Kidston & Lang 1921: pl. VI, fig. 71; Taylor et al. 1992: figs 25, 35–45). These structures have been interpreted as zoosporangia of monocentric chytrids (Taylor et al. 1992, Hass et al. 1994). However, the vast majority of these structures lack diagnostic features that are consistent (or consistently recognizable) among several specimens, and thus cannot be directly compared with modern equivalents. Moreover, no information is available to date on host preferences and the significance of this association in the functioning of the Rhynie ecosytem. Documentation of new microfungi is therefore critical in developing a comprehensive understanding of the Rhynie paleoecosystem. Especially important are the fossil forms that do not only display a set of features which can be related to those of extant organisms, but also suggest a consistent pattern of association with other organisms that in turn can provide the platform necessary to explore fungal diversity and help define patterns of ecological functioning (Krings et al. 2010b).

This paper describes *Illmanomyces corniger* nov. gen. et sp., an unusual microfungus that occurs on certain types of fungal spores in the Rhynie chert. The fossil consists of an epibiotic spheroid sporangium with prominent discharge tubes and an endobiotic rhizoidal system. Based on morphology, *I. corniger* is suggested as representing a monocentric chytrid (Chytridiomycota).

Geological setting, material and methods

The Rhynie chert 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. The cherts occur in the so-called Rhynie Block of the Dryden Flags Formation, located northwest of the village of Rhynie. 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 in the cherts are both aquatic (freshwater) facies from the pools and subaerial soil/litter horizons with in situ plants that are hypothesized to have grown along the edges of the pools. Preservation is suggested to have taken place as a result of temporary flooding of silica-rich water, or by groundwater high in silica percolating to the surface. The cherts have been dated as Pragian, perhaps earliest Emsian, based on dispersed 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) for the fossilized biota.

The specimens of the new microfungus were identified in a series of 4 thin sections, each approximately 100 µm thick, prepared from a single chert block (~4 × 4 × 5 cm). Thin sections were prepared by cementing wafers of the block to glass slides and then grinding the rock slices until the section was sufficiently thin to transmit light. Slides are deposited in the Bayerische Staatssammlung für Paläontologie und Geologie at Munich, Germany, under accession numbers SNSB-BSPG 2013 V 1–4. Slides were analyzed using normal transmitted light microscopy equipment; digital images were captured with a Leica DFC-480 camera.

Systematic paleomycology

Chytridiomycota incertae sedis

Fossil genus ***Illmanomyces*** M.Krings et T.N.Taylor **nov. gen.**

MycoBank MB 808057

DIAGNOSIS: Monocentric, zoosporangium epibiotic, more or less spheroid, with >3 prominent, conical discharge tubes; rhizoidal system endobiotic, arising from single site on sporangium.

ETYMOLOGY: The genus is proposed in honor of Dr. William I. Illman for his contributions to our understanding of the biodiversity of Rhynie chert microfungi.

TYPE SPECIES: *Illmanomyces corniger* nov. sp., hic designatus

Illmanomyces corniger M.Krings et T.N.Taylor, **nov. sp.**

Mycobank MB 808058

DIAGNOSIS: Zoosporangium spheroid to slightly dorsiventrally compressed, >60 µm in diameter, with proximal papilla-like protrusion attached to host; zoosporangium with 4–5 discharge tubes, each >20 µm long; 4 discharge tubes arranged around circumference of sporangium in single plane; if 5th tube present it may be located outside this plane; rhizoidal system originating from tip of protrusion, extending into host spore lumen; *host:* fungal spores, probably glomeromycotan.

ETYMOLOGY: The epithet (Lat. corniger, -a, -um = horned, having horns) refers to the prominent horn-like discharge tubes.

DETAILED DESCRIPTION: *Illmanomyces corniger*-host spore complexes occur in the chert matrix, within a loose accumulation of small fragments of degraded land plant tissue, various types of land plant and fungal spores, pieces of the charophyte *Palaeonitella cranii* (Kidst. et W.Lang) Pia, and fungal hyphae and rhizomorphs. The following description is based on a total of 7 specimens of *I. corniger* (Figs 1, 2).

The microfungus occurs attached to relatively thin-walled, unornamented spherical structures, 150–165 µm in diameter (Figs 1a, 2f), which based on size probably represent glomeromycotan spores. In one specimen, several smaller spheroid structures (probably other microfungi) are also attached to the host spore (arrows in Fig. 1c). The thallus of *Illmanomyces corniger* consists of an epibiotic spheroid to slightly dorsiventrally compressed structure, 60–75 µm wide and >60 µm high. It is relatively thin-walled, unornamented, and in all specimens except one [i.e., Fig. 1a (lower specimen)] lacks any internal inclusions. The mode of attachment to the host spore consists of a proximal, papilla-like protrusion ~28 µm wide and ~25 µm high (arrows in Fig. 2h). From the tip of this protrusion a rhizoidal system consisting of tenuous, branched filaments extends through the wall into the lumen of the host spore (Fig. 2f–h). All specimens of *I. corniger* possess 4 or 5 prominent, horn-like, conical discharge tubes, each up to 35 µm long, proximally >15 µm wide, and open at the tip (Figs 1, 2a–g). The wall of the tubes appears to be thinner than the wall of the spheroid from which they arise (e.g.,

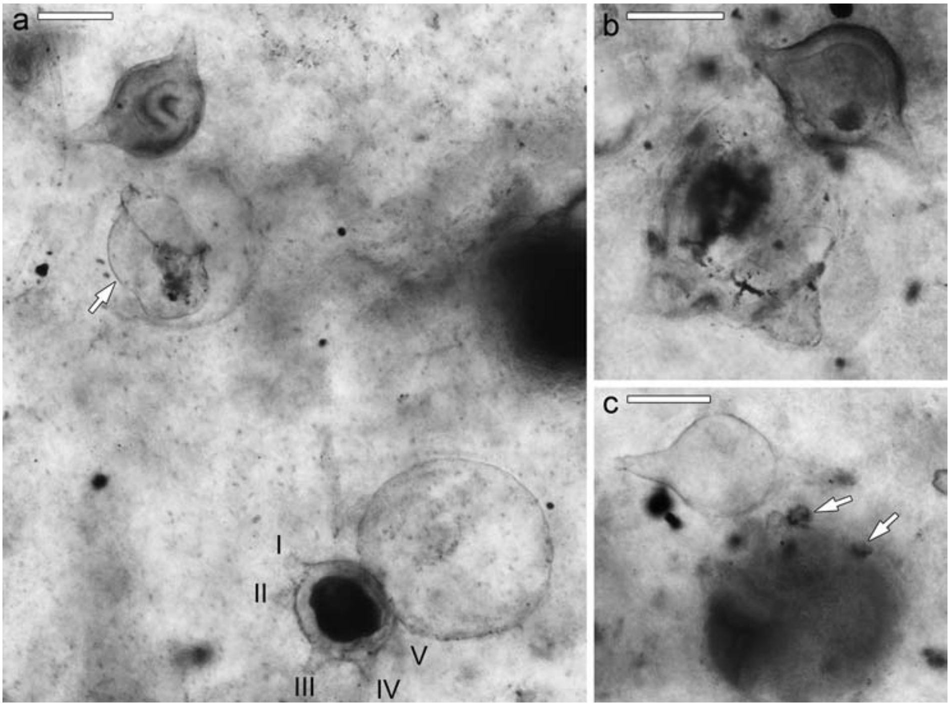

Fig. 1. *Illmanomyces corniger* nov. gen et spec., a putative chytrid colonizing fungal spores from the Lower Devonian Rhynie chert. a. Two host spores with attached zoosporangia; upper sporangium (median longitudinal section), showing 3 discharge tubes; lower specimen (oblique top view), showing all 5 tubes (I–V); arrow in upper specimen indicates second structure attached to host spore. Slide SNSB-BSPG 2013 V 2. Scale bar = 50 µm. b. Zoosporangium (median longitudinal section), showing discharge tubes in proximal half. Slide SNSB-BSPG 2013 V 4. Scale bar = 50 µm. c. Zoosporangium with lateral discharge tubes; note small spherules also attached to the host spore (arrows). Slide SNSB-BSPG 2013 V 3. Scale bar = 50 µm.

Fig. 2a). The discharge tubes are straight to slightly curved, and occur in the distal half of the spheroid in 6 of the specimen (e.g., Fig. 2a, c–e). In one specimen, however, the tubes occur in the proximal half of the spheroid and are curved in the opposite direction (Fig. 1b). We are uncertain whether this specimen represents morphological variability of the discharge tubes or is simply a preservational artifact. The arrangement of the discharge tubes is best recognizable in those specimens that provide an oblique surface view (e.g., Figs 1a [lower specimen], 2a & b), or by viewing the complete spheroid in multiple focal planes (e.g., Fig. 2c–e). These specimens reveal that 4 of the discharge tubes are typically arranged in a single horizontal plane around the circumference of the spheroid (I–IV in Fig. 1a, I–IV in Fig. 2a & b, I–IV in Fig. 2c–e); if the 5th tube is present it is located outside this plane (e.g., V in Fig. 1a, V in Fig. 2c–e).

Six of the host spores have only a single individual of *Illmanomyces corniger* on the surface, while one specimen shows a second sac-like structure apparently attached

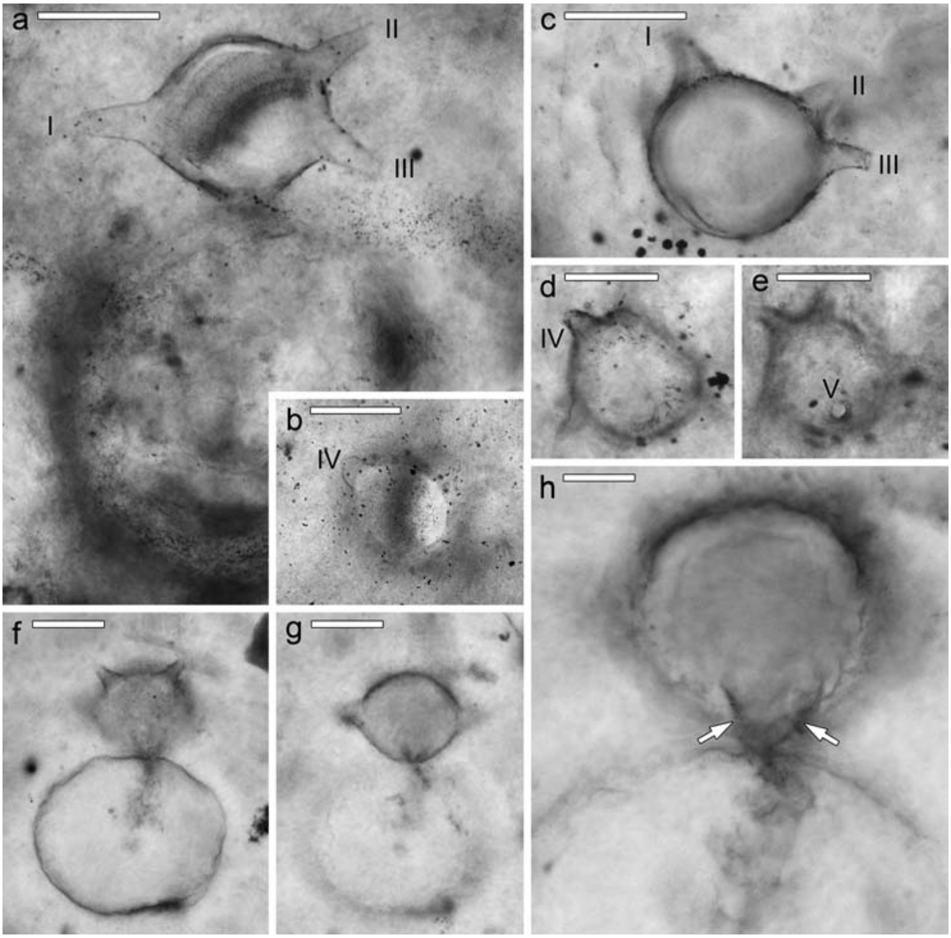

Fig. 2. *Illmanomyces corniger* nov. gen et spec., a putative chytrid colonizing fungal spores from the Lower Devonian Rhynie chert. a & b. Zoosporangium (oblique top view) in two different focal planes, showing 4 discharge tubes (I–III in a, and IV in b). Slide SNSB-BSPG 2013 V 1. Scale bars = 50 µm. c–e. Zoosporangium (lateral view) in three different focal planes, showing 5 discharge tubes (I–III in c, IV in d, and V in e). Slide SNSB-BSPG 2013 V 4. Scale bars = 50 µm. f–h. Holotype specimen (oblique bottom view) in three different focal planes, showing 4 discharge tubes (two visible in f, two others in g), proximal protrusion (arrows in h), and endobiotic rhizoidal system extending into host spore lumen (g & h). Slide SNSB-BSPG 2013 V 2. Scale bars = 50 µm (f & g) and 20 µm (h).

to the host spore (arrow in Fig. 1a). Since a discharge tube is visible in this sac-like structure, we believe that it belongs to an old, degenerated thallus of *I. corniger*.

Repository: Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; accession numbers SNSB-BSPG 2013 V 1, 2013 V 2 (holotype), 2013 V 3, and 2013 V 4.

Locality: Rhynie, Aberdeenshire, Scotland, National Grid Reference NJ 494276

Age: Early Devonian; Pragian, 411.5 ± 1.3 Ma (Parry et al. 2011), 407.1 ± 2.2 Ma (Mark et al. 2011).

Remarks: Almost nothing is known about the range of morphological plasticity in the Rhynie chert microfungi that colonize spores. One morphological difference present between some of the specimens of *Illmanomyces corniger* relates to the size of the discharge tubes (e.g., compare upper and lower specimen in Fig. 1a, and Fig. 2a with Fig. 2c). This probably has little systematic significance because zoosporangial and discharge structure morphology in extant chytrids may be variable even within the same species (Karling 1977). As a result, we have described the fossils as representing a single species, with the caveat that the taxon might represent several biological species that are simply impossible to distinguish based on the material at hand. Since none of the epibiotic microfungi on fungal spores from the Rhynie chert have previously been formally described, establishment of a new genus to accommodate the fossils is required.

Discussion

Evidence of microfungi utilizing the spores of land plants and other fungi as a habitat and/or source of carbon is present in almost every Rhynie chert thin section, indicating that this association was widespread and ecologically significant in the Rhynie ecosystem. Several different types of microfungi based on size and morphology, and associated with the spores of other organisms in the Rhynie chert, have already been documented (Kidston & Lang 1921; Illman 1984; Taylor et al. 1992; Hass et al. 1994; Krings et al. 2009, 2010a). However, only two mycelial thalli, both growing in the lumen of glomeromycotan spores, have been formally described and named, i.e., *Globicultrix nugax* M.Krings et al. (2009) and *Kryphiomyces catenulatus* M.Krings et al. (2010a).

Microfungi growing on the outer surfaces of Rhynie chert spores are represented by various sac-like sporangia, some with distal or lateral discharge openings, papillae or tubes; in some of these fossils also rhizoidal filaments extending into the host are preserved (Taylor et al. 1992, Hass et al. 1994). However, those morphological features of microfungi that are distinctive and that are consistent in a way that makes it possible to interpret a type as one species with some degree of confidence are exceedingly rare among these fossils. The lack of a suitable suite of distinctive characters in general makes it difficult to evaluate the range of diversity and ecological significance of microfungi in the Rhynie ecosystem. This is aggravated by the small size of the fossils. Moreover, their occurrence in a solid chert matrix, together with the inherent restrictions imposed using thin sections to study the fossils, makes it difficult to record and evaluate the details of the specimens from multiple sides and angles, and trace structural details. In addition, thin sections often contain a relatively high percentage of incomplete individuals which do not exhibit the entire features of the organism. Adding more uncertainty to the evaluation of fossil microfungi is convergent evolution of morphological characters, which is extensive in certain lineages of fungi, and thus renders interpretation of the systematic affinities of fungal fossils based exclusively on morphological data speculative. Certain (ultra-)structural and life history features, together with molecular and genetic data, are used routinely today to determine the precise systematic position of extant microfungi. This degree of resolution is not available when evaluating fossils (Krings et al. 2010b).

Illmanomyces corniger is defined by a combination of four structural features: (i) epibiotic spheroidal sporangia 60–75 µm in diameter; (ii) 4–5 prominent conical (horn-shaped) discharge tubes; (iii) 4 of the discharge tubes arranged around the circumference of the sporangium in a single horizontal plane; and (iv) an endobiotic rhizoidal system originating from the tip of a proximal protrusion in the sporangium. Based on these features, *I. corniger* is most similar morphologically to a monocentric chytrid (Chytridiomycota), perhaps within the extant orders Rhizophydiales or Spizellomycetales. Zoosporangia exhibiting several prominent discharge papillae or conical tubes are known to occur in a number of extant chytrids that colonize spores and pollen grains (e.g., Sparrow & Dogma 1973; Karling 1946, 1968, 1977; Letcher & Powell 2012). For example, *I. corniger* closely resembles a specimen of *Rhizophydium haynaldii* (Schaarschm.) A.Fisch. on pine pollen figured by Chen & Chien (1995: fig. 2c). Specimens of *Rhizophydium anomalum* Canter with lateral discharge tubes (Canter 1950; Letcher & Powell 2012: pl. 25, fig. 10) also resemble some of the specimens of *I. corniger* (e.g., Fig. 1b, c). Moreover, the endobiotic rhizoidal system of *I. corniger* originates from a single site on the sporangium, a condition that is found in most extant representatives of *Rhizophydium* Schenk (Sparrow 1960). Another extant chytrid that may appear similar to the fossil is *Spizellomyces pseudodichotomus* D.J.S.Barr. A zoosporangium of this fungus attached to a pine pollen grain (image available online at http://www.bsu.edu/classes/ruch/msa/barr/4-14.jpg) has discharge papillae/tubes arranged in a single horizontal plane, precisely as *I. corniger*. Moreover, most members in the Spizellomycetales possess a distinctive subsporangial swelling (apophysis) from which the rhizoids originate (e.g., Barr 1980). What we interpret as a papilla-like protrusion in *I. corniger* (Fig. 2h) may in fact represent the apophysis. Arguing against this hypothesis, however, is the fact that the apophysis is part of the rhizoidal system (i.e., is a subsporangial swelling of the rhizoid axis) and usually occurs endobiotically, not epibiotically as the protrusion in *I. corniger*.

Only one fossil resembling *Illmanomyces corniger* has previously been documented from the Rhynie chert (Taylor et al. 1992, fig. 43). However, the discharge tubes in the latter fungus appear to be arranged in a different manner. Despite the fact that Rhynie chert fungi have been studied intensively during the last decades (see Taylor et al. 2004, 2014), and that *I. corniger* is easily recognizable, only a few specimens of this fungus have been discovered to date. We wonder if this is because *I. corniger* was a rare element of the Rhynie mycoflora, or it was host-specific and colonized exclusively one rare type of fungal spore. It is also possible that sporangial morphology was variable in this fungus, and sporangia with prominent discharge tubes were seldom formed.

Spores and pollen grains are excellent host substrates and habitats for a variety of extant chytrids (e.g., Schenk & Nicolson 1977; Tzean et al. 1983; Czeczuga & Muszyńska, 2001, 2004a, b). Based on size (i.e., 150–165 µm in diameter), it is very likely that the hosts to *Illmanomyces corniger* represent glomeromycotan spores. If *I. corniger* colonized the spores while they were viable, then this association would represent a form of mycoparasitism. It is interesting to note that chytrids commonly parasitize spores of extant glomeromycotan fungi, and, as a result, can negatively affect the development of these fungi and their performance in mycorrhizal colonization and function (e.g., Ross & Ruttencutter 1977, Syliva & Schenk 1983, Wakefield et al. 2010). However, there is no evidence of a parasitic relationship in the form of a host response of the fossil host spores described here. In other Rhynie chert glomeromycotan spores, a frequent type of host response to mycoparasite intrusion is in the form of callosities (Hass et al. 1994). These structures are also common in extant Glomeromycota where they are effective in inhibiting intrusive chytrids and other soil microorganisms (e.g., Boyetchko & Tewari 1991, Purin & Rillig 2008). In the absence of any observable host response it is also possible that *I. corniger* represents a saprotroph that colonized non-viable spores or spores which had already germinated.

Illmanomyces corniger demonstrates that some of the microfungi colonizing land plant and fungal spores in the Rhynie paleoecosystem possess structural features that are consistent, and can be used to produce suites of characters which make it possible to recognize distinctiveness among these organisms. We believe that, as work on the Rhynie chert continues, additional distinctive microfungal morphologies will be discovered and described, and that this will ultimately lead to a more accurate understanding of the biodiversity of microfungi in the Rhynie chert, including information on the life history biology of these organisms. Information of this type is critical in not only documenting microfungal diversity within this ancient ecosystem, but also in establishing the full compliment of biological interactions that took place in the Rhynie ecosystem some 410 Ma ago.

Acknowledgments

Funds were provided by the National Science Foundation (EAR-0949947), the Deutsche Forschungsgemeinschaft (KE 584/13-2), and the Alexander von Humboldt-Foundation. We gratefully acknowledge Ulrich Projahn, Stefan Sónyi, and Nora Dotzler (Munich, Germany) for technical assistance. The paper benefited from the constructive comments and suggestions of two anonymous referees.

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Manuscript submitted March 4, 2014; accepted April 8, 2014.