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Cover illustration: Cover illustration: The floating plant *Cobbania corrugata* (LESQUEREUX) STOCKEY et al. from the Upper Cretaceous of North America inspected by an *Ornithomimus* dinosaur. The quarry in the Dinosaur Provincial Park, Alberta (Canada), produced numerous complete specimens of this plant and the most complete skeleton of the dinosaur (Reconstruction by Marjorie LEGIN). For details, see BOGNER, J.: The free-floating Aroids (Araceae) – living and fossil, pp. 113–128 in this issue.

Umschlagbild: Umschlagbild: Ein *Ornithomimus* Dinosaurier betrachtet die Schwimmpflanze *Cobbania corrugata* (LESQUEREUX) STOCKEY et al. aus der Oberkreide Nordamerikas. Im Steinbruch des Dinosaur Provincial Park, Alberta (Kanada), wurden mehrere komplette Exemplare dieser Pflanze und ein nahezu vollständiges Skelett des Dinosauriers gefunden (Rekonstruktion Marjorie LEGIN). Für weitere Informationen siehe BOGNER, J.: The free-floating Aroids (Araceae) – living and fossil, S. 113–128 in diesem Heft.

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Globicultrix nugax nov. gen. et nov. spec. (Chytridiomycota), an intrusive microfungus in fungal spores from the Rhynie chert

By

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Abstract

Fungal spores from the Lower Devonian Rhynie Chert are known to harbor a wide variety of parasitic and saprotrophic microfungi. However, only a few of these intrusive organisms have been documented in detail. This paper describes a previously unknown microfungus contained in fungal spores from the Rhynie chert; it consists of tenuous branched filaments and terminal, globose, usually apophysate sporangia with a single discharge pore or papilla. This complement of features is similar to the rhizomycelial and zoosporangial morphology seen in certain extant polycentric chytrids, and thus the fossil is provisionally placed in the Chytridiomycota.

Key words: Apophysis, Chytridiomycota, fossil fungi, Early Devonian, Rhynie chert, zoosporangium

Zusammenfassung

Pilzsporen aus dem unterdevonischen Rhynie chert beherbergen ein Reihe parasitischer und saprotropher Mikropilze, von denen allerdings nur wenige bislang detailliert dokumentiert worden sind. In dieser Arbeit wird ein bislang unbeschriebener Mikropilz aus Pilzsporen im Rhynie chert vorgestellt, der aus zarten verzweigten Filamenten und endständigen, kugeligen, meist apophysaten Sporangien mit einer einzelnen Austrittspore oder -papille besteht. Die Morphologie dieses fossilen Pilzes ähnelt der des Rhizomyzels und der Zoosporangien einiger moderner polyzentrischer Chytridien; auf Grund dessen wird das Fossil vorläufig zu den Chytridiomycota gestellt.

Schlüsselwörter: Apophyse, Chytridiomycota, fossile Pilze, Rhynie Chert, Unterdevon, Zoosporangium

1. Introduction

The Early Devonian Rhynie chert has preserved a diversity of microorganisms, including bacteria (KIDSTON & LANG 1921), cyanobacteria (e.g., CROFT & GEORGE 1959; KRINGS et al. 2007, 2009), microalgae (EDWARDS & LYON 1983; DOTZLER et al. 2007), peronosporomycetes (TAYLOR et al. 2006), and fungi (surveyed in TAYLOR et al. 2004). Many of these life forms were fossilized so that associations and interactions with other organisms can be directly examined. This is especially true of the fungi, which, as heterotrophs, are intricately involved with other organisms in saprotrophic, parasitic, and/or mutualistic associations (TAYLOR & TAYLOR 2000). While some of the fungal associations from the Rhynie chert are known in great detail (e.g., endomycorrhizae; see TAYLOR et al. 1995, 2005), others continue to be incompletely understood because some of the morphology, life history, spatial distribution, systematic affinities, and/or diversity levels of the fungal partner(s) cannot be reconstructed in sufficient detail or demonstrated on a consistent basis.

One of the more frequently encountered fungal associations in the Rhynie chert are microfungi inhabiting the spores of other fungi. Several examples of these interfungal associations have been described (KIDSTON & LANG 1921; TAYLOR et al. 1992; HASS et al. 1994), one of which consists of glomeromycotan spores containing varying numbers of small gametangia, (resting) spores, or sporangia of other, intrusive fungi (e.g., Fig. 1). The systematic affinities of most of the intrusive fungi remain elusive. However, differences in size and wall composition of the gametangia, spores, or sporangia, together with differences in the morphology of occasionally present subtending hyphae or filaments, suggest that a wide variety of microfungi in the Rhynie paleoecosystem lived, reproduced, and/or produced resting stages inside the spores of other fungi (KIDSTON & LANG 1921). Thus, detailed knowledge about these organisms represents an important component of fully understanding the roles that fungi played in the Rhynie paleoecosystem.

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This paper describes a previously unknown intrusive microfungus in fungal spores from the Rhynie chert that is characterized by apophysate sporangia positioned terminally on tenuous filaments. Structural correspondences between the fossil and members of the extant genera *Cladochytrium* NOWAK. and *Nowakowskiella* J. SCHRÖT. (in ENGLER & PRANTL) suggest affinities of the fossil with the Chytridiomycota, order Chytridiales.

2. 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. The cherts occur in the upper part of the Dryden Flags Formation, in the so-called Rhynie Block, a few hundred metres northwest of the village of Rhynie. The Lagerstätte consists of at least 10 fossiliferous beds containing lacustrine shales and cherts interpreted as a series of ephemeral freshwater pools within a hot springs environment (e.g., RICE et al. 2002). Preserved are both aquatic (freshwater) facies from the pools and subaerial soil/litter horizons with *in situ* plants around the edges of the pools; the latter became preserved as a result of temporary flooding of silica-rich water, or by silica-rich groundwater percolating to the surface. Based on dispersed spore assemblages and redefinition of the Pragian/Emsian boundary by the IUGS, WELLMAN (2006) and WELLMAN et al. (2006) date the cherts as Pragian-?earliest Emsian. Detailed information about the geological setting, sedimentology, and development of the Rhynie chert Lagerstätte can be found in RICE et al. (2002), and TREWIN & RICE (2004).

The infected fungal spores were identified in a thin section prepared by cementing a piece of chert to a glass slide and then grinding the slice until it is thin enough to be examined in transmitted light. The slide is part of the HIRMER collection (accession number BSPG 1964 XX 24), which is today deposited in the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG), Munich (Germany).

3. Systematic paleontology

Chytridiomycota M. J. POWELL, 2007, *incertae sedis*

Morphogenus *Globicultrix* nov. gen.

Mycobank number: MB 512268 (cf. <http://www.mycobank.org>)

Diagnosis: Thallus polycentric; vegetative system (rhizomycelium) composed of branched filaments; zoosporangia terminal, apophysate or non-apophysate, at maturity with a single discharge pore or papilla.

Type: *Globicultrix nugax* M. KRINGS, DOTZLER et T. N. TAYLOR (this paper)

Globicultrix nugax nov. spec.
(Figs 1[arrow], 2.1–9)

Mycobank number: MB 512269 (cf. <http://www.mycobank.org>)

Holotype: Specimen illustrated in Figure 2.1: Slide no. BSPG 1964 XX 24, deposited in the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG), Munich (Germany).

Specific diagnosis: Thallus endobiotic, in spores of other fungi; rhizomycelial filaments tenuous, <1–2 µm wide, apparently ephemeral; zoosporangia spherical, up to 10(–15) µm in diameter, usually apophysate, wall non-ornamented; apophysis inconspicuous or prominent, bulb-shaped or somewhat pyriform, up to 3 µm long; discharge pore or papilla in apical or subapical position, <1.5 µm in diameter.

Etymology: The generic name *Globicultrix*, a combination of the Latin words *globus* (= globe, sphere) and *cultrix* (= dweller, occupant), refers to the occurrence of the microfungus in a large, globose glomeromycotan spore; *nugax* (Lat.) = cute.

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

Age: Pragian-?earliest Emsian (Early Devonian), according to WELLMAN (2006) and WELLMAN et al. (2006)

Description: *Globicultrix nugax* occurs in a single, sub-spherical glomeromycotan spore, 185 µm long and ~160 µm wide (Figs 1[arrow], 2.1), which is positioned on a somewhat bulbous base (Fig. 2.1[arrow]) of the vegetative or parental hypha. The host spore occurs in the cortex of a degraded land plant axis where it is associated with several other glomeromycotan spores containing intrusive microfungi. However, fungal remains displaying the same complement of features as *G. nugax* have not been detected in any one of the other spores, nor do they occur in the plant tissues and matrix surrounding the spores.

The fungus consists of a vegetative system composed of narrow, branching filaments <1–2 µm wide (Fig. 2.1). Septae, intercalary swellings, and rhizoids extending from the filaments have not been observed. Spherical sporangia, up to 10(–15) µm in diameter, occur terminally on the filaments. The wall of these structures is typically <0.5 µm thick, slightly darker than the wall of the subtending filament, and non-ornamented. Most of the sporangia are empty, while a few contain amorphous material that appears to have undergone shrinkage (Fig. 2.2[white arrow], 4), probably as a result of osmotic water loss during fossilization. Sporangia are usually subtended by an inconspicuous or prominent swelling of the parental filament (Fig. 2.3, 8, 9). This subsporangial swelling is bulb-shaped or somewhat pyriform, up to 3 µm long and 1.5–3 µm wide. In some of the specimens, it appears that the swelling is separated from the parental filament by a constriction of the filament or by a septum (e.g., Fig. 2.4[white arrow]). Other sporangia lack the subsporangial swelling of the filament (e.g., Fig. 2.2[black arrow]). Many sporangia display a single circular discharge pore (<1.5 µm in diameter) or slightly elevated (<1 µm high), papilla-like orifice in apical or subapical position (Fig. 2.5–8[arrows]). One specimen appears to have a single circular

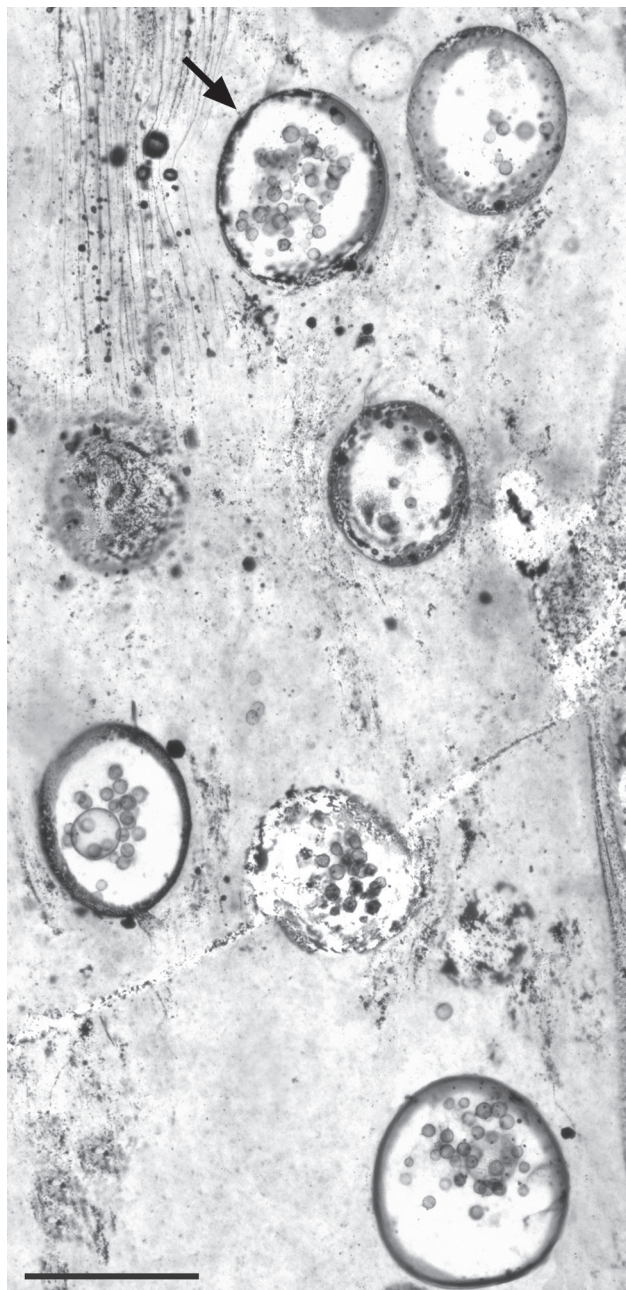


Figure 1: Large fungal (glomeromycotan) spores in the cortex of a degrading land plant axis; note that most spores contain large numbers of small gametangia, spores, or sporangia of intrusive microfungi, one of which is *Globicultrix nugax* [arrow]; slide no. BSPG 1964 XX 24; bar = 150 μ m.

discharge pore and one discharge tube (Fig. 2.7 [black and white arrows]), but the latter might also represent a filament fragment adhering to the sporangial wall. It is interesting to note that discharge pores or papillae have not been observed in any of the sporangia containing amorphous material. However, one of these specimens shows what appears to be an operculum (Fig. 2.4 [black arrow]), but this structure might also represent an artifact of preservation. Figure 2.8 shows a swelling from which extends a well-developed sporangium with apical discharge pore [black arrow] and a smaller, bulb-like structure [white arrow] containing tiny spherules, which perhaps represents a second, immature sporangium.

Remark: Determining the exact systematic position of *Globicultrix nugax* is impossible at this time. We therefore refrain from formally referring the fossil to any one of the extant genera with which it is compared (see Discussion section below), but rather introduce a new morphogenus *incertae sedis*, *Globicultrix*, to accommodate this distinct Early Devonian microfungus until such a time that more specimens are available to increase the suite of diagnostic features.

4. Discussion

The Early Devonian Rhynie chert contains the oldest fossil evidence for microfungi inhabiting the spores of other fungi (KIDSTON & LANG 1921; TAYLOR et al. 1992; HASS et al. 1994). Especially abundant are fungal spores containing one to several small spherical gametangia, (resting) spores, or sporangia of other fungi. The most detailed account on this type of association was provided by KIDSTON & LANG (1921). These authors describe several types of intrusive microfungi based on the size and morphology of the gametangia, spores/sporangia, and occasionally the presence of subtending hyphae or filaments. However, none of the organisms has been formally described and named, due perhaps to the fact that the fossils do not normally display many features that could be used for comparison with modern taxa.

Globicultrix nugax is characterized by spherical sporangia that are exclusively terminal, usually positioned on a distinct swelling of the subtending filament (Fig. 2.3,8,9), and have a single apical or subapical discharge pore or papilla (Fig. 2.5–8 [arrows]). The most important structural features distinguishing this form from the previously described intrusive microfungi in fungal spores from the Rhynie chert (see KIDSTON & LANG 1921; HASS et al. 1994) are the subsporangial swellings and the single discharge pores/papillae. However, nothing is known about the range of morphological plasticity and life history of *G. nugax*, and thus we cannot rule out that some of the specimens described by KIDSTON & LANG (1921) and HASS et al. (1994) are conspecific with *G. nugax*, despite the fact that they are morphologically different.

The morphology and dimensions of *Globicultrix nugax* are reminiscent of certain modern chytrids (Chytridiomycota), especially the polycentric genera *Nowakowskiella* and *Cladochytrium* (Chytridiales, *Cladochytrium* clade [cf. JAMES et al. 2006]). *Nowakowskiella* consists of a branched rhizomycelium constructed of delicate filaments bearing operculate zoosporangia in terminal or intercalary position. Within this genus zoosporangia may be apophysate or non-apophysate, and usually are broadly or narrowly pyriform in shape, but may also be spherical. At maturity, zoospores are liberated via a short or long neck or discharge papilla (e.g., KARLING, 1977; MARANO et al. 2007; PIRES-ZOTTARELLI & GOMES 2007). *Cladochytrium* represents the inoperculate counterpart of *Nowakowskiella* (KARLING 1977; DAYAL 1997), in which zoospores are released through a discharge tube, papilla, or simple pore. Correspondences in basic structure between the rhizomycelial and zoosporangial morphology of these modern chytrids and *G. nugax* suggest that the fossil represents a polycentric chytrid in the order Chytridiales. The vegetative parts of *G. nugax* can be interpreted as remains of a branched rhizomycelium,

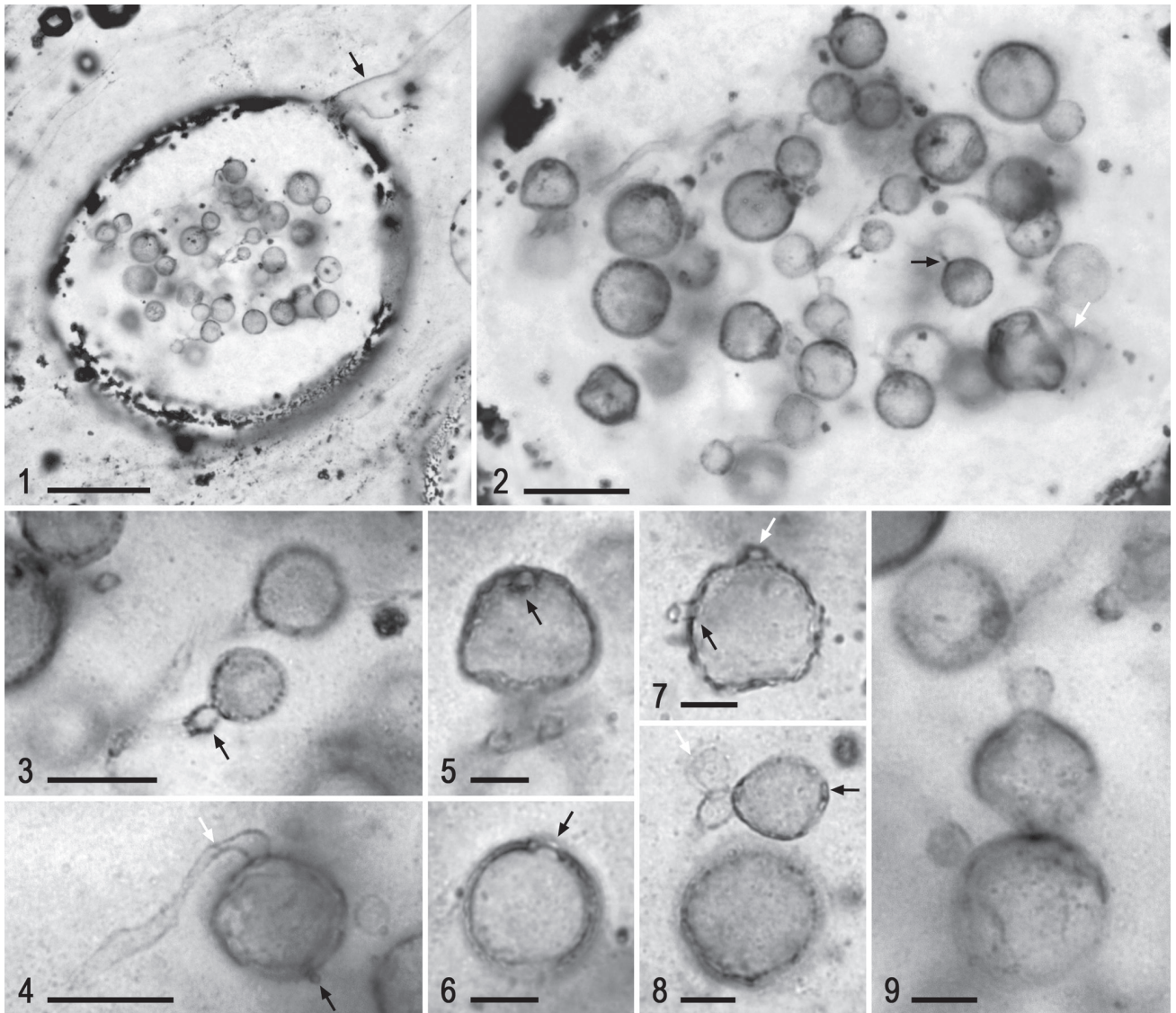


Figure 2: *Globicultrix nugax* nov. gen et nov. spec. from the Early Devonian Rhynie chert; slide no. BSPG 1964 XX 24. **2.1** Thallus within the spore (holotype); arrow points to the somewhat bulbose base of the host spore; bar = 50 μ m. **2.2** Detail of Figure 2.1, focusing on the intrusive thallus; black arrow indicates a non-apophysate zoosporangium, white arrow indicates a zoosporangium showing contents; bar = 20 μ m. **2.3** Filament branches bearing apophysate zoosporangia [one of the apophyses is indicated by an arrow]; bar = 10 μ m. **2.4** Filament with terminal, inconspicuously apophysate zoosporangium; note constriction of the filament (or septum?) immediately below the apophysis [white arrow] and what appears to be an operculum [black arrow] in apical position; bar = 10 μ m. **2.5** & **2.6** Zoosporangia with discharge pores in apical position [arrows]; bars = 5 μ m. **2.7** Zoosporangium with shallow discharge papilla [white arrow] and what appears to be a second, tube-like opening [black arrow]; bar = 5 μ m. **2.8** Apophysate zoosporangium with discharge pore in apical position [black arrow] and bulb-like structure (perhaps a second, immature zoosporangium) extending from the apophysis [white arrow]; bar = 5 μ m. **2.9** Two zoosporangia with prominent apophyses; bar = 5 μ m.

the spherical sporangia as terminal zoosporangia with a single discharge pore or papilla, and the subsporangial swellings of the subtending filaments as apophyses. If these interpretations are correct, the zoosporangia with a well-developed discharge pore/papilla (Fig. 2.5–8[arrows]) may appear empty because zoospore liberation had occurred prior to fossilization. Conversely, the presence of amorphous material in sporangia lacking discharge openings (e.g., Fig. 2.2[arrow], 4) may indicate that zoospores had not (yet) developed and/or been released at the time of fossilization.

An alternative interpretation views *Globicultrix nugax* as a member of the Peronosporomycetes (Oomycota). In this

scenario, the sporangia represent terminal oogonia, while the swellings at the base of the sporangia are collar-like, amphigynous antheridia. However, the swellings appear to represent enlargements of the subtending filament, rather than being formed by an oogonial hypha growing through an antheridium. Moreover, oospores and parental hyphae giving rise to the antheridia have not been observed in any of the specimens. As a result, it is much more likely that *G. nugax* represents a member of the Chytridiomycota.

Although *Globicultrix nugax* is similar in basic structure to the modern chytrid genera *Nowakowskiella* and *Cladochytrium*, there are some basic differences. The rhizomycelia in both

5. References

extant taxa typically bear rhizoids and conspicuous intercalary swellings (KARLING 1977; DAYAL 1997). These structures have not been observed in the fossil. However, this may be due to the fact that the vegetative system is incompletely preserved in the fossil. The vegetative system of *G. nugax* was perhaps ephemeral and disintegrated rapidly upon maturation of zoosporangia. Alternatively, the main portion of the vegetative system may have been too delicate to become preserved in a recognizable manner. In addition, it cannot be determined whether the zoosporangia of *G. nugax* were operculate or inoperculate. A *bona fide* operculum has not been observed in any of the specimens, but the consistent absence of this structure may also be a result of preservation.

It is difficult to assess the nature of the association between *Globicultrix nugax* and its host. If the microfungus colonized the glomeromycotan spore while it was viable, this association would represent a form of mycoparasitism. Mycoparasites are fungi that derive the majority of their nutrients from other fungi that are alive at the time of infection (JEFFRIES & YOUNG 1994; PURIN & RILLIG 2008). Interpreting *G. nugax* as a mycoparasite seems reasonable, as parasitic interfungal interactions appear to have been widespread in the Rhynie paleoecosystem (HASS et al. 1994). Moreover, glomeromycotan spores, which are among the largest spores known in the fungal kingdom, certainly represented particularly suitable habitats for parasitic microfungi, because they contain abundant and easily accessible nutrients. However, there is no indication of a host response in the form of structural alterations or modifications of the spore wall, which would indicate evidence of a parasitic relationship between *G. nugax* and its host. In the absence of host responses, fossil mycoparasites are difficult to distinguish from saprotrophs, which colonize and utilize dead organic matter as a carbon source (see DIX & WEBSTER 1995). Therefore, it is also possible that *G. nugax* represents a saprotroph that colonized non-viable spores or spores that had already germinated. Most extant members of *Nowakowskiella* and *Cladochytrium* are aquatic and soil saprotrophs that thrive on/in decaying plant material (SPARROW 1960; KARLING 1977), but at least one species of *Cladochytrium* (i.e. *C. aneurae* THIRUM.) has been described as a parasite of liverworts from the genus *Aneura* DUMORT. (THIRUMALACHAR 1947).

The discovery of *Globicultrix nugax* in the Rhynie chert adds to our understanding of the biodiversity of late Paleozoic microorganisms, and contributes to a more sharply focused concept of the complexity of ancient non-marine ecosystems. As more information is obtained about this and other microbial life forms from the Rhynie chert, it will be possible to offer more detailed hypotheses that can be used in association with those described from modern communities to more accurately depict the role of fungi and their interactions with other organisms in the ecology and evolution of non-marine paleoecosystems.

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