



THREE MICROPROBLEMATICA OF OCCASIONAL OCCURRENCE IN THE LOWER DEVONIAN RHYNIE CHERT

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Krings, M. (2026): Three microproblematica of occasional occurrence in the Lower Devonian Rhynie chert. – *Fossil Imprint*, 82(1): 1–12, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (online).

Abstract: The Lower Devonian Rhynie chert of Scotland contains a wealth of fossils of various types of microorganisms; however, the forms described so far represent only a fraction of the diversity that actually existed in the Rhynie ecosystem. Here I describe three different types of enigmatic structures in the μm range that have been preserved in the chert after they detached or were released from the systems on or in which they had developed. All three can be characterized very precisely morphologically and show similarities to the spores of certain Fungi; however, affinities with algae, animals, and slime molds cannot be ruled out either. Since the biological nature and relationships of the structures are unclear, they are referred to as microproblematica. Regardless, each of these structures represents a previously unknown fossil organism, and thus expands our knowledge of the diversity of microbial life in early terrestrial ecosystems.

Key words: dispersal, early terrestrial ecosystem, fossil fungi, life cycle, microbial diversity, microfossil, reproduction

Received: September 18, 2025 | Accepted: November 14, 2025 | Issued: October 7, 2026

Introduction

The Lower Devonian Rhynie chert of Scotland is unquestionably the most illustrative testimony to the microbial diversity in early terrestrial ecosystems (Kidston and Lang 1921, Taylor and Krings 2005, Dotzler et al. 2009, Strullu-Derrien et al. 2019b, Krings and Kerp 2023). Numerous fungi and fungus-like organisms, cyanobacteria, and microscopic algae, as well as microscopically small animals, have been described and documented in detail using fossils from the Rhynie chert, many of which are preserved (petrified) in the exact places where the organisms once lived and show even the subtlest details of their morphology (e.g., Krings et al. 2012, 2021, Strullu-Derrien et al. 2017, 2019a, 2023a, Krings 2021, 2022a, b, 2024a, b, Garcia Cabrera and Krings 2024). Nevertheless, anyone who takes a closer look at the Rhynie chert will quickly realize that the microorganisms described so far only represent a fraction of the diversity that actually existed in the various facies of the ecosystem.

There is a considerable – and only too understandable – bias towards forms of which, on the one hand, particularly informative specimens are available (e.g., those that are complete and distinctive, or characteristically interacting

with other organisms) and which, on the other hand, can be classified with some confidence by direct comparison with present-day equivalents. In addition to these informative fossils, however, there are many other remains in the form of single cells, cell clusters, colonies, and propagules that also bear witness to the microbial diversity in the Rhynie ecosystem, but which have received little attention to date, mainly because their characteristics are usually not sufficient to determine their biological nature and systematic affinity (Krings and Harper 2023). In order to have a better understanding of such fossils and eventually take them into account and incorporate them when assessing the significance of microorganisms in early ecosystems, it is necessary, as a first step, to describe and document them thoroughly, to compile an inventory of their morphological diversity, and to find present-day equivalents.

To contribute to this admittedly arduous task, in this study I present three enigmatic microscopic structures that I have occasionally encountered in the course of my work with the Rhynie chert. Due to their unknown biological nature and systematic affinity, I refer to them as microproblematica (*sensu* Krings et al. 2010). All three structures are morphologically distinct and can be easily recognized under

a microscope at sufficiently high magnification. They each represent a type of microorganism that has not previously been recorded for the Rhynie chert, and thus contribute to our conception of microbial diversity in the Rhynie ecosystem.

Geological setting

The Rhynie chert is located in the northern part of the Rhynie outlier of Lower Old Red Sandstone in Aberdeenshire, Scotland, within an extensive sequence of sedimentary and volcanic rocks. The chert occurs in what is known as the Rhynie Block of the Dryden Flags Formation, located northwest of the village of Rhynie. The deposit consists of fossiliferous layers containing lacustrine shales and chert and has been interpreted as a geothermal wetland with temporary freshwater pools (Channing 2017) fed by alkali-chloride hot springs, which were part of a complex hydrothermal system in a region affected by volcanic activity (Rice et al. 2002, Trewin and Fayers 2016). The chert preserves both aquatic (freshwater) facies from the pools and subaerial soil and litter horizons with in situ plants that probably thrived at the edges of the pools. It is assumed that the biota was preserved by temporary flooding with silica-rich water or by the percolation of silica-rich groundwater high to the surface (Powell et al. 2000). The biota of the Rhynie chert has been dated to the early (but not earliest) Pragian to earliest Emsian based on spore assemblages (Wellman 2006, 2017, Wellman et al. 2006). High-precision age constraints for the Rhynie deposit have yielded an absolute age of 407.1 ± 2.2 Ma (Mark et al. 2011) and 411.5 ± 1.3 Ma (Parry et al. 2011), respectively. Details on the geology and paleontology of the Rhynie chert deposit can be found in the publications by Trewin and Kerp (2017) and Garwood et al. (2020), and in the special volume on the Rhynie chert edited by Edwards et al. (2018).

Material and methods

All fossils described in this study are available in thin sections from the collections of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany (SNSB-BSPG). The sections were prepared by cementing wafers of the chert onto glass slides and then grinding them until they were thin enough (usually 60–80 μm thick) to allow light to pass through (for details on the preparation of thin sections, see Hass and Rowe 1999). The fossils were examined using transmitted light microscopy (Leica) and the highest practicable magnification (400 $\times$ or 1000 $\times$ total magnification of the microscope). Digital images were captured using a Leica DFC-480 camera or a Jenoptik Gryphax Naos camera and edited in Adobe Photoshop CS5 for brightness and contrast. Details on microscopy and image optimization can be found in the publication by Krings et al. (2021). The accession numbers for all specimens shown are provided in the figure captions.

Results

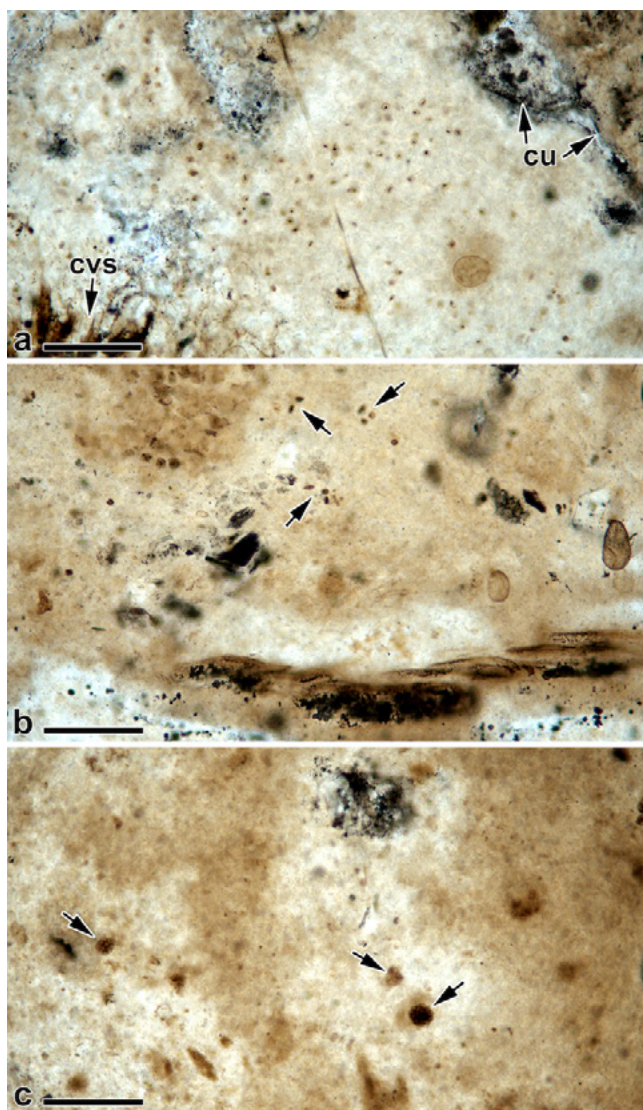
Preliminary remark

The structures described in the paragraphs below can all be characterized very precisely morphologically, but their biological nature and systematic affinities remain unknown due to the uncertain diagnostic value of the available characteristics and the fact that nothing is known about their parent organisms. If the structures had been discovered in palynological preparations, they would be treated as non-pollen palynomorphs (NPPs; e.g., Shumilovskikh and Van Geel 2020, Marret et al. 2021, Kuoppamaa 2025) and could be directly compared with other NPPs. Determining whether the silicified fossils from the Rhynie chert correspond to any NPP taxon is difficult due to the very different modes of preservation. To adequately deal with these limitations, the fossils are informally designated as *microproblematica* types 1–3. Because the Rhynie chert is a very rich fossil deposit, however, I assume that the producers of the structures will also be found at some point, which will enable a biologically sound formal description using the correct terminology and, if possible, a classification. For the time being, therefore, the informal designation proposed here seems most appropriate to me.

Context

The fossils occur dispersed (i.e., disconnected from the structure on or in which they developed) in the chert matrix or in degraded land plant parts, all within aquatic or wet facies of the ecosystem characterized by abundant fragmented and partially to largely degraded land plant remains (litter accumulations), coccoid and filamentous cyanobacteria and algae, various types of fungal hyphae and reproductive units, scattered remnants of arthropod exuviae, land plant spores, unidentifiable organic matter, and varying amounts of sediment.

Microproblematicum type 1 (hereafter referred to as *mpt1*) has been found in more than 50 thin sections from the SNSB-BSPG holdings, either in the chert matrix or in degraded plant parts, almost always as single specimens or in small assemblages of 2–4 unconnected individuals. A single assemblage of several hundred specimens was found in the cortex area of a largely decayed land plant axis (Text-fig. 1a), of which only the cuticle (cu in Text-fig. 1a) and the central strand of water-conducting tissue (cvs in Text-fig. 1a) are recognizably preserved. *Microproblematicum* type 2 (hereafter *mpt2*) occurs in the chert matrix, in most cases in close association with partially decayed plant material (arrows in Text-fig. 1b) and *Scytonema*-like filamentous cyanobacteria; several thousand specimens have been recorded to date in more than 50 thin sections. *Microproblematicum* type 3 (hereafter *mpt3*) occurs singly or in small groups in the chert matrix (Text-fig. 1c). The form is generally rare and has been found in less than 10 thin sections to date, but there is one section that contains an assemblage of ca. 50 specimens.



Text-fig. 1. Microproblematica from the Lower Devonian Rhynie chert: context of discoveries. **a:** Numerous *mpt1* specimens in the decayed cortex of a land plant axis, of which only the cuticle (cu) and the central strand of water-conducting tissue (cvs) are still recognizable; slide SNSB-BSPG 2016 IX 14; scale bar = 200 μm . **b:** Small groups of *mpt2* specimens (arrows) in the chert matrix among land plant fragments, detritus, fungal remains, and sediment; slide SNSB-BSPG 2016 XII 13; scale bar = 200 μm . **c:** Specimens of *mpt3* (arrows) in the chert matrix among plant remains, organic particles, and sediment; slide SNSB-BSPG 2016 XII 2; scale bar = 200 μm .

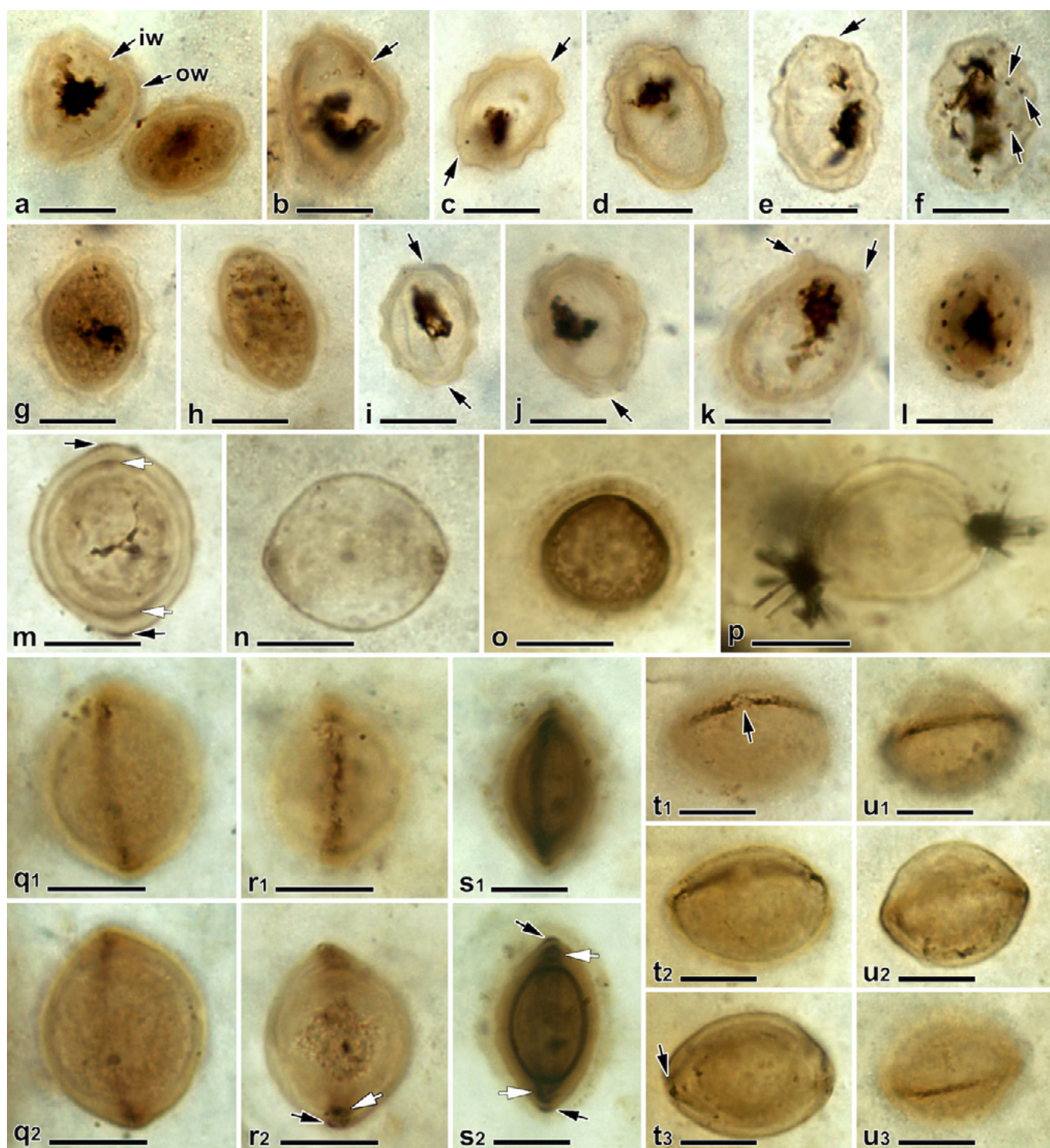
mpt1 (Text-fig. 2a–l)

Specimens are prolate spheroidal or ovoid in shape, in some cases slightly asymmetrical, and between 15 and 25 μm long and 12–19 μm wide (Text-fig. 2a–l). They consist of a central lumen surrounded by a two-layered wall. The wall layers are clearly distinguishable from each other. The outer layer (ow in Text-fig. 2a) is whitish, appears somewhat translucent, and is up to 1.5 μm thick (without ornamentation); its outer surface is covered with sculptural elements in the form of prominent verrucae and short ridges. In some cases, this wall layer appears to be stratified; moreover, minute black bodies may be embedded in the wall layer (Text-fig. 2f [arrows], l). Some of the individuals show a flattened area at one of the

poles (arrows in Text-fig. 2c, e, i, j) or, more rarely, at both poles (arrows in Text-fig. 2c, i), in which the outer wall layer is either normally formed (upper arrow in Text-fig. 2c) or thinner (upper arrow in Text-fig. 2i), or even absent (arrow in Text-fig. 2e). If it is missing, the outer wall layer is in some cases thickened around the flattened area to form a collar-like rim (arrows in Text-fig. 2k). The inner wall layer (iw in Text-fig. 2a) is darker than the outer layer and on average c. 1 μm thick; its outer surface is smooth, while the inner surface facing the lumen is somewhat diffuse in most cases. An additional, light yellowish layer can sometimes be seen between the inner and outer wall layers in the microscopic image (Text-fig. 2a, b [arrow]). However, this layer is not visible in all specimens and is incomplete in others, and is therefore probably an artifact of microscopy. The lumen of most specimens is empty, with the exception of an amorphous mass of almost black matter (Text-fig. 2c–f, i–k). However, there are also specimens that contain a relatively homogeneous mass consisting of lighter and darker brownish areas (Text-fig. 2a [right-hand specimen], h). Some individuals also appear to represent a transitional stage between these two states, with an irregular central dark mass (possibly in the process of formation) surrounded by brownish matter (Text-fig. 2a [left-hand specimen], b, g).

Remarks

I know of no convincing contemporary equivalent to this fossil. The flattened polar region(s) could indicate that the structure was formed terminally or intercalarily on a parental system, and that the polar regions represent the attachment sites to this parental system. The structure was perhaps a thick-walled fungal spore (conidium, chlamydospore) that developed on a hypha. I am not aware of any modern fungal spore that matches the fossils in size and shape, but there are some that are at least somewhat similar in overall morphology. For example, certain species in the genus *Aspergillus* P. MICHELI ex HALLER (Ascomycota) produce conidia with a surface ornamentation comprised of verrucae, spikes, and ridges (Silva et al. 2011: fig. 2, Sugui et al. 2014: figs 2E, 4E, 5G, H). Similar warty conidia also occur in the ascomycete genus *Trichoderma* PERSOON (Samuels et al. 1999: figs 1, 2). However, these conidia are all much smaller than the *mpt1* specimens. On the other hand, the ascospores of certain truffle-like fungi of the genus *Genea* VITTADINI (Pezizales) and the urediniospores of some rust fungi (Basidiomycota) are more like the size of the fossils and often also have a similar shape and ornamentation (Ellis 2001–2025a, Kumru et al. 2025). Urediniospores are vegetative spores produced on a dikaryotic mycelium several times during the growth period of the host plant (Baka and Rabei 2013). In *Puccinia melanocephala* SYDOW et P. SYDOW, the ornamentation of those spores is not as pronounced as in the fossils, but the walls are layered and they show a flattened attachment site (Prasher et al. 2015: fig. 2A–C). Nevertheless, a biological relationship between *mpt1* and rust fungi seem rather unlikely, not least because rust fungi are obligate biotrophs with a complex life cycle and close relationship with their host plants, which probably originated from a common ancestor during the Cretaceous (Zhang et al. 2024). Finally, chlamydospores of similar size



Text-fig. 2. Microproblematica from the Lower Devonian Rhynie chert. a–l: *mpt1* [specimens in a–e and g–k shown in a sectional view, specimens in f and l in face view]; iw = inner wall layer, ow = outer wall layer; arrows point to what could be an additional wall layer between the inner and outer wall layers (in b), flattened polar areas (in c, e, i, j), black bodies in outer wall layer (in f), and thickened outer wall layer forming rim around flattened polar area (in k) [further explanations in the text]; all specimens in slide SNSB-BSPG 2016 IX 14; scale bars = 10 μ m. m–u: *mpt2* [specimens in m and n shown in a sectional view perpendicular to the equator (m rotated by 90°), the specimen in o in a sectional view parallel to, but not through, the equator, the specimen in p shows crystals growing from pores, and the specimens in q–u shown in lateral views (q, r, and s rotated by 90°) in two and three different focal planes, respectively]; arrows point to superimposed dark bands, one peripherally and one further inside the thickening (black and white arrows in m, r2, s2), and pores in the thickening (in t1, t3) [further explanations in the text]; slides SNSB-BSPG 2016 XII 6 (r), 2016 XII 12 (u), 2016 XII 13 (m, o, q, t); 2016 XII 21 (s), 2016 XII 29 (n), and 2016 XII 39 (p); scale bars = 10 μ m.

to the *mpt1* fossils are known, which are ornamented with various types of warts and short ridges, for example in the nematophagous ascomycete *Arthrobotrys flagrans* (DUDD.) MEKHT. (Wang et al. 2024: fig. 3).

Yet another comparison is the spores of certain members of the Entorrhizomycota, a group of plant pathogens today associated with roots of Cyperaceae and Juncaceae, whose evolutionary origins are believed to date back at least 500 Ma (Bauer et al. 2015, Zhao et al. 2017, Riess et al. 2019). In several representatives of the genera *Entorrhiza* C.A. WEBER and *Juncorrhiza* K. RIESS et PIĄTEK, the spores (teliospores) are spherical to ellipsoidal and characterized by a prominent ornamentation comprised of verrucae and tubercula (Denchev and Denchev 2019: figs 2–5, Riess et al. 2019: figs 3, 8, 10, van Steenwinkel and Vanderweyen 2022: 3, 4 [particularly similar to *mpt1* in size, shape, and ornamentation], 6, 7).

An alternative interpretation views the flattened polar regions in the fossils as preformed openings through which something could emerge or hatch, and thus that *mpt1* was an algal spore or resting cyst (e.g., Worobiec 2014, Shang et al. 2019, Permann et al. 2023) or the egg of an animal. Regarding the latter, *Ascaris lumbricoides* L., a parasitic roundworm of the phylum Nematoda, produces resistant, thick-walled eggs that typically are much larger than *mpt1*, but may otherwise be quite similar in shape and ornamentation (Foster 1914: figs 1–3, Morandi 2018: fig. 4L, Sohn and Chai 2024: fig. 5A–D).

***mpt2* (Text-fig. 2m–u)**

These fossils resemble a lemon in lateral view (limoniform; Text-fig. 2n), in some cases also a spindle (e.g., Text-fig. 2s), and are up to 24 µm long (high) and 19 µm wide. In face view, however, they are more or less round or elliptical (Text-fig. 2o). They are thus reminiscent of lentils or biconvex optical lenses (Text-fig. 2m–u). Since the radius of curvature is often smaller on one side than on the other, many specimens are slightly asymmetrical in lateral view (e.g., Text-fig. 2n, r, u). The surrounding wall is up to 1.5 µm thick, clearly demarcated on the outside and inside, and bears no ornamentation. Its most characteristic feature is a single more or less pronounced thickening or ridge that surrounds (girdles) the entire structure in the equatorial plane, and in which the wall reaches a thickness of up to 2.6 µm. The thickening appears (significantly) darker than the rest of the wall, due probably to the accumulation of a light-refracting substance. In most specimens, two narrow or relatively broad dark bands can be seen one above the other, one at the periphery of the thickening and one further inside (black and white arrows in Text-fig. 2m, r2, s2), while in others the thickening appears (almost) uniformly dark (Text-fig. 2n). Some specimens have one or more roundish pores within the thickening (arrows in Text-fig. 2t1, t3), and in one partially degraded specimen, crystals have formed in the areas of such pores and grown outward from there (Text-fig. 2p). The lumen usually contains a mass that appears brownish under the microscope with irregular outer boundaries (e.g., Text-fig. 2m, q2, r2), probably the shrunken contents of the cell. A few specimens are surrounded by a diffuse gelatinous layer or sheath with inclusions of unknown nature (Text-fig. 2s).

Remarks

In terms of their overall shape, these fossils resemble certain ascospores, e.g., those of some species of genera *Chaetomidium* (ZOPF) SACC. (Greif et al. 2009: figs 8, 13, Doveri 2011: figs 78, 79) and *Chaetomium* KUNZE (Doveri 2008: figs 3e, f, 6a–d, 12e, g), as well as their Quaternary fossil counterparts (e.g., Van Geel and Aptroot 2006: pl. I, 9). Unfortunately, the number of pores, which can be an important diagnostic trait, cannot be determined in the fossils. The most characteristic structural feature of *mpt2* is the equatorial ridge. Similar equatorial thickenings, rims, or ridges are found in the ascospores of several species of the present-day genera *Gymnoascus* BARAN. emend. ARX (Mathur and Thirumalachar 1970: figs 1–10, Orr et al. 1977: fig. 12, von Arx 1986: fig. 1, Zhou et al. 2016: fig. 7q) and *Talaromyces* C.J. BENJAMIN (Eliades et al. 2006: fig. 1E, Han et al. 2022: fig. 4f, h, Sharma and Nonzom 2022: fig. 2e–g), among other genera, but also in the spores of a few slime molds (Myxomycetes; e.g., Gmoshinskiy et al. 2025: figs 2B, C, F, 3B). The equatorial ridge must be distinguished from a germination slit, which appears in a range of ascomycetes as a short or long, straight or spiral groove or furrow in the ascospore wall, and through which the germ hypha emerges during germination (e.g., Beckett 1979, García et al. 2006, Damm et al. 2010, Fournier et al. 2015). A germ slit was not found in any of the *mpt2* specimens.

An equatorial slit is also characteristic of the conidia of some members of the ascomycete genus *Arthrimum* KUNZE. These conidia are more or less lens-shaped, and they possess a pale slit-like marking that runs along the equator (e.g., Scheuer 1996: fig. 2e, f, Agut and Calvo 2004, Pintos et al. 2019: figs 7F, G, 10M, 12E). However, in some *Arthrimum* species, such as *Arthrimum saccharicola* F. STEVENS, the slit has been described as at times appearing like a ridge of paler pigment (Crous and Groenewald 2013). Conversely, the ridge in the *mpt2* specimens contains one or two superposed dark bands, which appear to be due to the incorporation of a light-refracting substance. Although it is impossible to determine the chemical composition of this substance, it is quite conceivable that it is melanin. Melanin protects fungi from environmental stressors, such as UV radiation, heavy metals, desiccation, hydrolytic enzymes, oxidative agents, heat, and cold (Pombeiro-Sponchiado et al. 2017, Ramachandra et al. 2023, Suthar et al. 2023). Moreover, it plays a crucial role in cell development in filamentous fungi that produce melanized structures such as appressoria, sclerotia, conidia, and reproductive structures. In addition, melanin can enhance fungal virulence by promoting adhesion, penetration, and evasion of the host immune response. Therefore, if the *mpt2* fossils are indeed ascospores, the presence of melanin in the spore walls seems to make perfect sense due to the properties of this substance.

***mpt3* (Text-fig. 3a–n)**

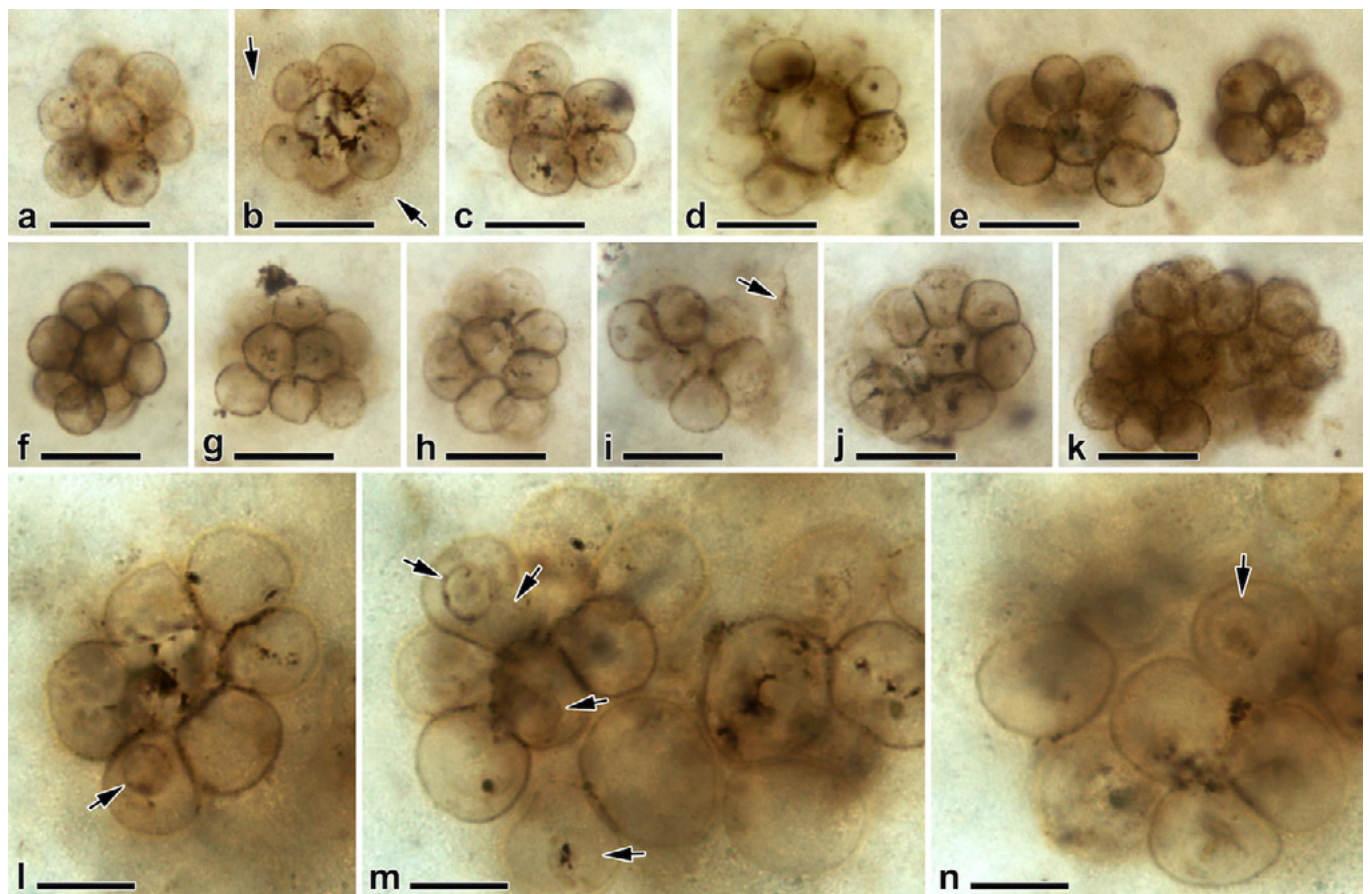
This fossil type occurs in the form of compact clusters of 8 to more than 50 spheroidal or ovoid vesicles that appear to be firmly joined together. The vesicles are (9–)10–15(–20)

μm in diameter and surrounded by a smooth wall. The walls between adjacent vesicles are mostly straight (particularly clearly visible in Text-fig. 3j). The most common arrangement of vesicles within smaller clusters in the sectional view is that one central vesicle (in some cases two; see Text-fig. 3j) is surrounded and enclosed by others (Text-fig. 3a–f, l). In several cases, the central vesicle is slightly or even significantly larger than the surrounding vesicles and also appears to have a slightly thicker wall (Text-fig. 3d, f). In large clusters, the arrangement of the vesicles is less uniform and no general pattern is discernible (e.g., Text-fig. 3k). Most vesicles are empty, but some contain single (very rarely two or three; see Text-fig. 3m) small spheres with a diameter of 5.5–6.5 μm (arrows in Text fig. 3l–m). Some of the vesicle clusters appear to be surrounded by a diffuse, almost colorless gelatinous substance (arrows in Text-fig. 3b), while others have shreds of unknown origin attached to them (arrow in Text-fig. 3i), which could indicate the presence of a parental wall or sheath *in vivo*, but could just as easily be random attachments.

Remarks

It cannot be completely ruled out that the *mpt3* specimens are groups or colonies of algal cells or egg masses of some animal. A fossil resembling the specimen shown in Text-fig. 3d

was described by Strother et al. (2025: pl. X, fig. 15) from the Upper Ordovician of Saudi Arabia and interpreted as possibly a form of algal coenobium. However, I consider it much more likely that *mpt3* belongs to the fungi in the broadest sense. There are various structures in modern fungi that can be morphologically quite similar to the fossils, albeit not necessarily in terms of size. For example, various fungi produce bulbils, reproductive bodies of more or less definite form composed of a compact mass of homogeneous or heterogeneous cells that may be few or many in number (Hotson 1912, 1917, Lawrey et al. 2016). The bulbils of *Tengochaeta bulbillosa* Y. MARÍN ET BARR.-ADAME (Ascomycota), which are spherical to irregular, pale to dark brown, up to 70 μm in diameter, and composed of globose to ellipsoidal or irregularly globose cells (Barrera-Adame et al. 2025: fig. 2B–D), bear a striking resemblance to the large clusters shown here (Text-figs 1c, 3k). There are several ascomycetes in which the 8-spored asci superficially resemble the smallest of the *mpt3* clusters (e.g., Text-fig. 3a–c), including *Aphanoascus fulvescens* (COOKE) APINIS (Doveri 2006: fig. 7b–f, h, i), *Gymnoascus reessii* BARAN. (Orr et al. 1963: figs 5, 6), and *Kernia cauquensis* CALVIELLO (Doveri 2011: figs 45, 47). However, these structures are surrounded by the ascus wall and fall apart as soon as this wall breaks open. No evidence of the presence of an ascus wall was found in the fossils, although there were a few specimens in which shred-like attachments could possibly represent remnants of such a wall (Text-fig. 3i).



Text-fig. 3. Microproblematica from the Lower Devonian Rhynie chert. a–n: *mpt3* [all specimens shown in a sectional view]; arrows point to diffuse, almost colorless gelatinous substance surrounding a cluster (in b), a shred of unknown origin attached to a cluster (in i), and vesicles containing small spheres (in l–n) [further explanations in the text]; all specimens in slide SNSB-BSPG 2016 XII 2; scale bars = 20 μm (a–k), 10 μm (l–n).

Equally interesting as possible modern equivalents are those fungi and fungus-like organisms in which the spores occur in groups called spore balls. Particularly impressive and sometimes complex spore balls can be found in smut fungi (Basidiomycota, Ustilaginomycotina; see Vánky 1998, 2012), and some of them are morphologically very similar to the *mpt3* fossils, e.g., those of *Thecaphora anthemidis* J.KRUSE et al. (Kruse et al. 2018: fig. 2E, F) and other species of the genus *Thecaphora* FINGERH. (Vánky and Lutz 2007: figs 7, 8, 10), although in many cases the spores are ornamented. *Thecaphora*-like subfossil spore balls have also been described in palynological samples from medieval cultural layers in Poland (Mazurkiewicz-Zapałowicz and Okuniewska-Nowaczyk 2015: fig. 5j, k). Spore balls in the plant-pathogenic smut genus *Urocystis* RABENH. ex FÜCKEL are in many cases characterized by consisting of one or more larger central teliospores surrounded by a protective layer of smaller sterile cells (Ellis 2001–2025b). The *mpt3* specimens with a larger central cell (Text-fig. 3b, d) are reminiscent of such a configuration. Finally, spore ball-like clusters are also seen in certain slime molds, and those of the genus *Badhamia* BERK. can be strikingly similar to the fossils (Pliszko and Bochynek 2017: fig. 2B, Kuhnt 2019: fig. 24, Prikhodko et al. 2023: fig. 3C, E, G, J). However, fossils of myxomycetes are extremely rare. The oldest bona fide body fossil of a slime mold consists of a group of *Stemonitis*-like sporocarps preserved in Cretaceous amber from Myanmar (Rikkinen et al. 2019). Indirect evidence of the existence of these organisms comes from the same amber in the form of slime mold beetles, which depend on slime molds for their life cycle (Li et al. 2021).

A peculiar structural detail of *mpt3* are the small spherical inclusions occurring in some of the vesicles (Text-fig. 3l–m). They are reminiscent of inclusions found in many cells of the presumed green alga *Hagenococcus aggregatus* M.KRINGS et al. from the Rhynie chert, where they were interpreted as pyrenoids (Krings et al. 2017: figs 1–3). If the spheres in the *mpt3* vesicles are also pyrenoids, they would indicate a relationship with algae. However, similar spherical inclusions have also been found in certain fungal propagules from the Rhynie chert (Krings and Harper 2019: fig. 1m–o). Due to the fact that subtending hyphae have also been preserved in some of them, they have been identified as reproductive units of an intrusive microfungus.

Summary discussion and conclusions

The preceding section describes three different types of microscopic structures that have been preserved in the Rhynie chert after they detached or were released from the systems on or in which they were formed. They are representative of a much larger variety of microfossils that are scattered almost everywhere in the Rhynie chert. These fossils are either complete organisms, such as single-celled or few-celled colony-forming cyanobacteria or algae, or, as is more likely in the cases presented here, life cycle stages related to reproduction, survival, or dispersal, such as spores, resting cysts, or eggs. Searches for possible comparisons for the fossils described here in the diversity of modern microbial life have yielded various microorganisms whose life cycles

feature structures with a greater or lesser degree of actual or perceived morphological similarity. The comparisons in the above subsections *Remarks* could undoubtedly be continued further. So, what to do with these fossils and the identified similarities with certain modern organisms?

The fossils – however diminutive they may be – expand our knowledge of the microbial diversity that populated the Rhynie ecosystem some 410 Ma ago. Each of them represents an organism and, together with other microbial life forms known only from fragmentary remains, such as various types of mantled fungal reproductive units (e.g., Moore and Krings 2025) and parts of algal (pseudo)filaments (Edwards and Lyon 1983, Wellman et al. 2019), provides insight into a subset of this diversity about which we know very little overall, but which was probably very extensive. Furthermore, each of them opens a window onto a little-understood segment of the ecological complexity of early terrestrial ecosystems (Krings and Harper 2023). For example, only one representative of the Ascomycota has been described in detail from the Rhynie chert (Taylor et al. 2005), and there is some evidence of the existence of two or three others (Honegger et al. 2017, Krings and Harper 2023, Strullu-Derrien et al. 2023b). However, geothermal ecosystems today are often remarkably rich in Ascomycota (e.g., Redman et al. 1999, Bazzicalupo et al. 2022, Bregnard et al. 2023, Yan et al. 2025). Given the heterogeneity of the environment and the multitude of potential carbon sources, it is therefore unlikely that there were only three or four representatives of this fungal lineage in the Rhynie ecosystem. There must have been others that have not yet been documented, and spores could be the first clues to their existence. If some (or all) of the fossils described here do indeed originate from Ascomycota, it is entirely conceivable that they come from plant parasites or pathogens, or from saprotrophs involved in the decomposition of organic matter, i.e., organisms that may have played important roles as drivers or maintainers in the Rhynie ecosystem. Documentation of these remains therefore not only supplements the inventory of microbial life, but can also – and perhaps more importantly – serve as an incentive to search for the parent organisms of these structures, and to learn more about the ecological role(s) of this hitherto largely obscure segment of the microbial life in the Rhynie ecosystem. Detailed comparisons of the fossils with similar present-day morphologies can help to create a search image that provides a better guidance of what the parent organisms might have looked like and what to pay particular attention to when further examining thin sections.

Acknowledgements

I thank H. Martin and S. Sónyi (both Munich, Germany) for technical assistance and two anonymous referees for their comments on the manuscript.

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