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Entophysalis in the Rhynie chert (Lower Devonian, Scotland): implications for cyanobacterial evolution

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Abstract

The ~407-my-old Rhynie chert of Scotland contains exquisite body fossils of land plants, animals and microorganisms, which provide our earliest reasonably complete snapshot of a Phanerozoic terrestrial ecosystem. These fossils have been instrumental to our understanding of the ‘greening of the land’, a major transition in the history of the Earth–life system. Among the primary producers preserved in the chert are cyanobacteria, of which only a fraction have been formally described. Here, we report the occurrence of the colony-forming cyanobacterium *Eoentophysalis* in the Rhynie chert. To our knowledge, this represents the first bona fide record of Entophysalidaceae from any post-Cambrian fossil assemblage or any non-marine fossil assemblage of any age. The Rhynie *Eoentophysalis* appears remarkably similar in appearance both to modern marine and freshwater *Entophysalis* ssp. and to *Eoentophysalis belcherensis*, a shallow-marine fossil from the ~2 Ga Belcher Group of Canada that is perhaps the oldest convincing cyanobacterium on record. Darkened cell envelopes in the Rhynie *Eoentophysalis* correspond well with both *E. belcherensis* and modern *Entophysalis*, whose cell envelopes often contain the photoprotective brown pigment scytonemin. The occurrence of *Eoentophysalis* in the Rhynie chert supports previous claims that the fossilisable traits of entophysalid cyanobacteria are evolutionarily static through geological time. These organisms may be such effective generalists that major changes in their environment – in this case, the transition to a fully non-marine habitat – have not imposed significant selection pressure on these traits.

1. Introduction

Cyanobacteria represent ‘arguably the most important group of organisms ever to appear on our planet’ (Knoll, 2008). They have dominated prokaryotic primary production in diverse marine and terrestrial environments since they originated in the Archean eon. They were instrumental in oxygenating the atmosphere, oceans and groundwater in the Proterozoic, and continue to play a major role in Earth’s carbon, nitrogen and oxygen cycles; they were also the endosymbionts that engendered the plastids of all phototrophic eukaryotes (Demoulin *et al.* 2019). Thus, the cyanobacterial fossil record is primary evidence for the evolution of the Earth–life system over time. This archive is more remarkable as a record of stasis than one of change. Among the oldest unequivocal fossil cyanobacteria that can be directly related to a modern equivalent is a colonial coccoid with gelatinous extracellular envelopes from the ~2 Ga-old Belcher Group of Nunavut, Canada, which was formally described by Hofmann (1976) as *Eoentophysalis belcherensis*. Its morphology, pattern of growth and even pigmentation are indistinguishable from the modern genus *Entophysalis* (family Entophysalidaceae, order Chroococcales) (Golubic & Hofmann, 1976; Schopf, 1994), a fact which has often been cited in work on the tempo of evolution (e.g. Knoll, 1989; Schopf, 1992, 1994).

Most cyanobacterial fossils with established taxonomic names come from the Precambrian (Sergeev *et al.* 2012). Of these, the majority are known from three-dimensional carbonaceous fossils silicified within chert, a transparent matrix that can be thin-sectioned for optical microscopy. The decline of shallow-marine silicification at the end of the Precambrian (a function of falling silica concentrations in the oceans) greatly restricts our view of later cyanobacterial diversity. Many Phanerozoic cyanobacteria are auto-mineralised calcifiers that lack the fine detail necessary for a close comparison with modern forms (Riding, 1982; Golubic & Seong-Joo, 1999). The highly diverse microbiota of the ~407 Ma-old Rhynie chert (including

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the original Rhynie chert and the nearby, coeval Windyfield chert) of Scotland provides an important counterexample. Located near the village of Rhynie in Aberdeenshire, this deposit is formed by the precipitation of silica from hydrothermal spring waters (Rice *et al.* 2002; Trewin & Kerp, 2017; Wellman, 2019). The silica, now transformed into transparent chalcedony with a slight amber colouration, encased and permineralized diverse early land plants, fungi and many protists, meiofauna and bacteria in their life positions, commonly with intact cellular and some subcellular details (see the papers in Edwards *et al.* 2018; Garwood *et al.* 2020). In addition to the exceptional quality of preservation, the assemblage is notable for capturing our earliest near-complete view of a fully non-marine ecosystem (Strullu-Derrien *et al.* 2019; Wellman, 2019). As such, it provides important insight into the Early Devonian ‘greening of the land’ by plants, a transition which shifted the balance of Earth’s biomass from prokaryotic to eukaryotic dominance and permanently altered the planet’s atmosphere, soil and climate (Lenton *et al.* 2016; McMahon & Parnell, 2018)

Previous studies have identified more than a dozen distinct cyanobacterial morphologies in the Rhynie chert. Two forms, of which one is coccoid and *Gloeocapsa*- and *Chroococciopsis*-like, the other filamentous, allegedly heterocystous, and suggested to belong to the Nostocales, occur as photobionts of the putative cyanolichen *Winfrenatia reticulata* (Taylor *et al.* 1997; Karatygin *et al.* 2009). A further eight forms are filamentous, including *Archaeothrix oscillatoriformis* and *A. contexta* (Kidston & Lang, 1921; Krings *et al.* 2009; Krings, 2021a); *Kidstoniella fritschii*, *Langiella scourfieldii* and *Rhyniella vermiformis* (Croft & George, 1959; recently merged into one taxon, *L. scourfieldii*, by Strullu-Derrien *et al.* 2023); *Croftalania venusta* (Krings *et al.* 2007; Krings, 2021b); *Palaeolynghya kerpilii* (Krings, 2019) and the complex, *Stigonema*-like *Rhystigonema obscurum* (Krings, 2021c). Loron *et al.* (2023) illustrate what may be another *Stigonema*-like form. Four forms are coccoid and colony-forming. *Rhyniococcus uniformis* produces unistratose colonies resembling of the modern *Merismopedia* (Edwards & Lyon, 1983; Krings & Harper, 2019), while colonies of *Rhyniosarcina devonica* are cuboidal, spheroidal or irregular sarcinoid and resemble modern chroococceans such as *Cyanosarcina* (Taylor & Krings, 2015). *Rhyniotaxillus devonicus* and *Rhyniotaxillus minutulus* both occur as solitary cells and packages of cells arranged within prominent gelatinous envelopes or sheaths (Krings & Sergeev, 2019; Krings, 2021d). Cells of *R. minutulus* are only 0.6–1.2 µm in diameter whereas those of *R. devonicus* are larger (2.5–3.5 µm). *Rhyniotaxillus* resembles to a certain extent both *Eucapsis* (Synechococcales) and *Entophyalis* (Chroococcales), but the true affinities are uncertain.

Here, we describe a new colony-forming coccoid cyanobacterium from the Rhynie chert that can safely be assigned to the fossil genus *Eoentophyalis*. To our knowledge, this fossil is the first post-Cambrian entophyalid and the first unambiguously non-marine entophyalid in the rock record (modern entophyalids occur in both marine and freshwater environments).

2. Material and Methods

The fossils described in this study were identified in a single standard polished, ~100 µm thick thin-section (labelled GCCR7) obtained from a block of Rhynie chert supplied by the National Museums of Scotland (accession number NMS G.2015.33.11.1). The section was studied (a) in Edinburgh, using a Leica DM2700 P petrographic microscope (configured for Koehler illumination

with a 100× oil-immersion objective), and photographed in transmitted light with a Leica DFC 420c camera and (b) in Munich, using a Leica DM LB2 microscope with a Jenoptik Gryphax Naos camera. Images obtained were processed in the Leica Application Suite v. 4.0 software with additional enhancement of brightness and contrast in Adobe Photoshop (for details of microscopy and image optimisation, refer to Krings *et al.* 2021). Cell unit diameters were measured with the freeware ImageJ software (<https://imagej.nih.gov/ij/>). Confocal Laser Scanning Microscopy (CLSM) images were acquired at 512 x 512 pixel resolution with a Zeiss LSM880 CLSM equipped with an Airyscan detector (Zeiss, Germany). Z-stacking was not successful. We used a 40× oil-immersion objective and 1.3 numerical aperture in Airyscan mode. Autofluorescence of the sample was excited with 488 nm and 561 nm lasers, and emission was collected with a long pass 605 nm emission window. CLSM Images were processed using ImageJ to convert from CZI to TIF with minor brightness and contrast adjustment (no noise removal).

3. Results

Thin section GCCR-7 was obtained from a hand sample of dark, massive chert (‘texture (1)’ of Trewin, 1994) and contains organic-rich laminae studded with grains of quartz and mica (Figure 1a). These laminae are draped and compressed around irregular inclusions (here called ‘fenestrae’) of clear chert containing uncompressed fossils, mostly plant material and fungi in a variable state of decay. The fossil material described in the paragraph below occurs in only one such fenestra (Figure 1a). The chert in this fenestra is pervaded by brown fossil organic matter of variable density, interspersed with clearer regions containing black clots presumably composed of organic matter.

The fossil material of interest is arranged in a continuous formation, approximately 260 µm in maximum dimension, which resembles a long cumulus cloud with a flat ‘base’ and a lobed and mammillated ‘top’ (Figure 1 a,b), oriented perpendicular to the prevailing lamination direction in the host chert (such that the mammillations face the centre of the fenestra). Within the lobes are more than 100 overlapping organic-walled spheres 3.6–6.4 µm in diameter (median = 4.7 µm; mean = 4.7; standard deviation = 0.6; n = 40; see online Supplementary Material at <http://journals.cambridge.org/geo> for histogram), interpreted as cell units (i.e. gelatinous polysaccharide envelopes faithfully preserving the shapes of the actual cells; for details, refer to Krings & Harper, 2019), which are moderately well preserved in the centre of the colony but become increasingly faint and indistinct towards the margins (Figure 1a–c). Some of the cell units are disseminated randomly in the matrix within the fenestra but outside of the main lobes. The organic material is more faintly and diffusely preserved than in other cyanobacteria present in Rhynie chert thin sections prepared from the same block (see Loron *et al.* 2023). As a result, resolution of fine structural features is generally impeded; the outer boundaries of many cell units are ambiguous and the cell contents are amorphous. Nevertheless, objects resembling paired cells (dyads), tetrads, and equatorially constricted, dividing cells can be distinguished in some areas (Figure 1e–h). Moreover, stratified envelopes either suggesting encapsulation or simply reflecting the sequence of cell divisions are visible in some of the dyads (Figure 1g). Dark inclusions probably representing the conglomerated actual cells are common within the cell units (e.g. Figure 1f, h). The lobes of the formation are rimmed by organic shrouds with dark boundaries, interpreted as the remains of a colonial mucilage. Both the cell surfaces and surrounding envelopes appear dark in

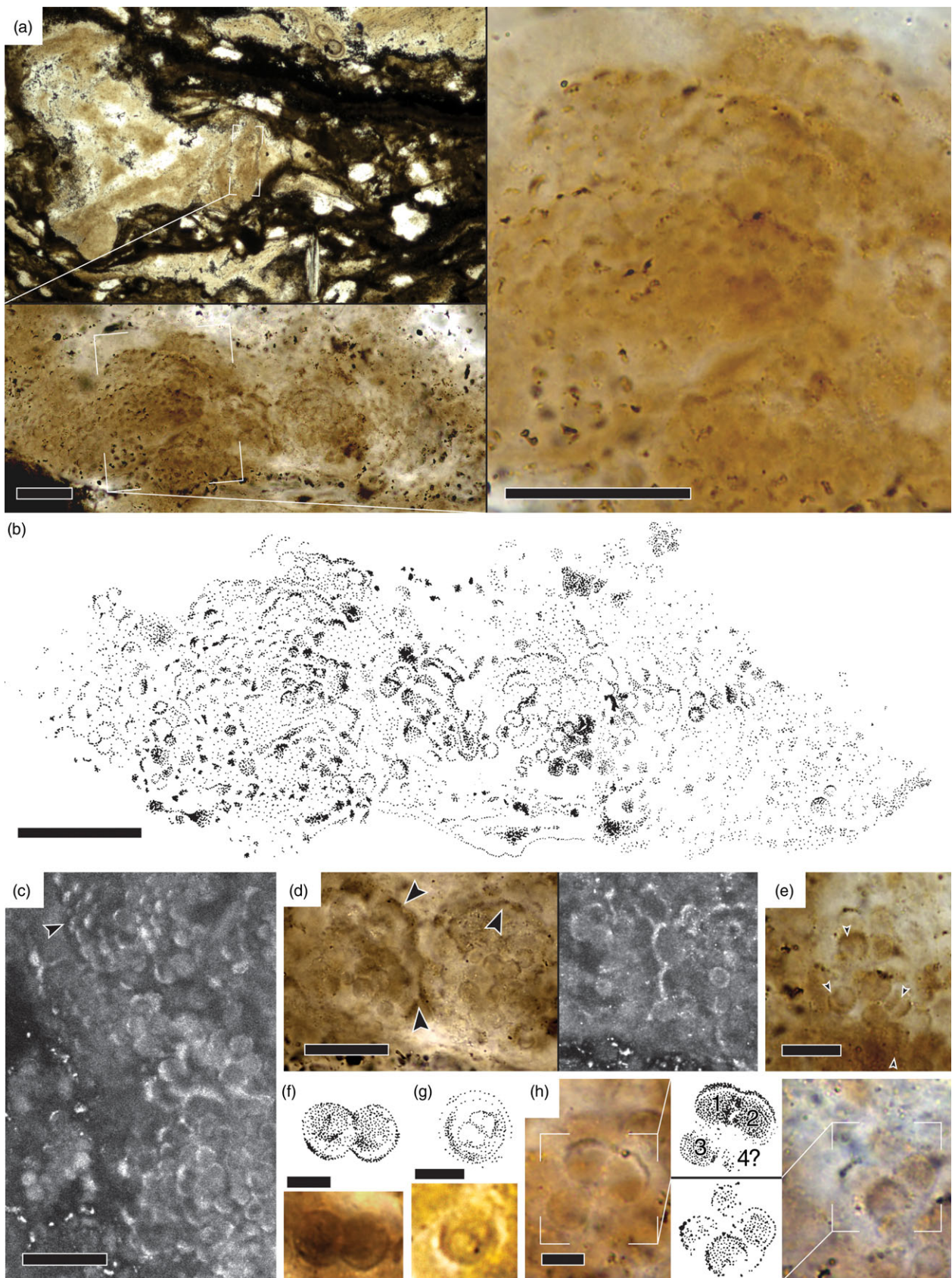


Figure 1. (Colour online) *Eoentophysalis* sp. in the Rhynie chert (a) Nested photomicrographs showing silicified fenestrae between clay- and organic-rich laminae, with location of *Eoentophysalis* formation highlighted. Note diffuse brown colour surrounding cells. (b) Stipple drawing of colony. (c) Confocal laser-scanning micrograph of *Eoentophysalis* colonies. Arrow shows a region where fluorescing organic material (likely the remains of the actual cells, perhaps augmented by residues of pigment) is consistently oriented on one side of the cell units, creating a 'fish-scale' pattern. (d) Close-up showing colony boundaries (arrowed) interpreted as mucilaginous; these appear dark in photomicrographs (left) and bright in confocal laser-scanning micrographs (right). (e–h) Dyads, possible tetrads and dividing cells in shared and in part stratified envelopes suggestive of encapsulation. Dark intracellular inclusions in (f) and (h) suggest contraction of the actual cells during decay. Scale bars: 25 μm (a,b), 20 μm (c,d), 10 μm (e) and 5 μm (f–h).

transmitted light but fluoresce strongly in confocal laser-scanning imagery (Figure 1c,d); the boundaries are especially fluorescent. Many of the cell units are darker on the mammillated side of the formation, and some regions of the envelopes are also pervasively stained.

4. Discussion

Recent additions to the inventory of cyanobacteria from the Lower Devonian Rhynie chert have greatly expanded our understanding of cyanobacterial paleobiodiversity in early non-marine ecosystems. The specimen described in this study further extends the list of interesting cyanobacterial fossils documented from the Rhynie chert.

4.1 Comparison with modern and other fossil Entophysalis

Several lines of morphological evidence suggest that the fossil described above is a representative of the family Entophysalidaceae (Chroococcales), of which the best-known modern genus is *Entophysalis*. *Entophysalis* is globally distributed in pools and intertidal zones, on rocky seashores, in inland lakes and in other marine and non-marine habitats (Kaštovský *et al.* 2011; Hauer & Komárek, 2022). *Entophysalis* forms gelatinous, irregular, granular, microscopic to macroscopic colonies that typically cover the substrate. Young colonies are polarised and attached to the substrate, whereas older ones are composed of sub-colonies, which are radially or serially arranged in aggregates (Komárek & Anagnostidis, 1998), or laterally interlinked to form pustulate laminae or mats, or stromatolites (e.g. Golubic, 1983; Foster *et al.* 1989; Golubic & Abed, 2010). Cells or their groups within the colonies are arranged in radial or erect rows and possess their own gelatinous envelopes. Dissemination mainly occurs through groups of cells or small colonies that dislodge from the parental colony. The long, flat 'base' of the Rhynie chert fossil described here (Figure 1a, b) may correspond to the substrate to which the colony was attached and from which it grew towards the light. Such a growth pattern is typical of *Entophysalis* and distinguishes it from other envelope-forming coccoid cyanobacteria such as *Gloeocapsa* or *Gloeotheca* (Golubic & Abed, 2010). Interpretation of the fossil as an entophysalid is also supported by the fact that many of the cell units appear to be richer in organic material on the side facing away from the base and towards what was presumably the light. This material is dark in transmitted light microscopy (Figure 1a) and fluoresces brightly in confocal imagery (Figure 1c, d). Its distribution may reflect the original distribution of a pigment secreted by the cells into their gelatinous envelopes; in modern *Entophysalis*, the UV-screening pigment scytonemin is similarly concentrated in the upper, illuminated side of the colony (Golubic & Abed, 2010).

Fossil cyanobacteria resembling modern *Entophysalis* are usually referred to as the fossil genus *Eoentophysalis*. *Eoentophysalis* is a major constituent of numerous Proterozoic Lagerstätten but has also been reported from a few Cambrian deposits (e.g. Sergeev, 1989). The type species, *E. belcherensis*, was initially described by Hofmann (1976) from the Belcher Group of Arctic Canada and was recently dated to 2016.5 Ma (Hodgskiss *et al.* 2019). As originally described, it consists of cells 3–5 µm in diameter organised into palmelloid colonies in which dyads and tetrads commonly occur within enveloping sheaths. In the revised taxonomy of Sergeev *et al.* (2012), *E. belcherensis* has been synonymised with several other proposed species, expanding the diameter range to 2–10 µm

(e.g. Muir, 1976; Knoll & Golubic, 1979; Lo, 1980; Mendelson & Schopf, 1982; McMnamin *et al.* 1983). Sergeev *et al.* (2012) accept only one other *Eoentophysalis* species as valid, namely *E. dismallakesensis*, which was first reported in the Dismal Lakes Group of Arctic Canada by Horodyski & Donaldson (1980). The form resembles *E. belcherensis* in its patterns of cell division and colony formation but is somewhat larger (11–22 µm; Sergeev *et al.* 2012).

There is also a relatively high level of morphological correspondence between the Rhynie entophysalid and a fossil formally described as *Coccostratus dispergens*, which occurs along with *E. belcherensis* in the cherts and silicified carbonates of the Mesoproterozoic Gaoyuzhuang Formation (1.4–1.5 Ga) of Hebei Province, China (Seong-Joo & Golubic, 1999). Cells of *C. dispergens* are 'conspicuously spherical' with a mean diameter of 2–6.5 µm, divide by binary fission following equatorial constriction, and form mats or mammillate formations of loosely attached cell units above which dispersed cells can be identified. All of these features are shared by the Rhynie fossil. Because *C. dispergens* lacks distinct sheaths and its cells are loosely attached and not apparently encapsulated, it is regarded by Seong-Joo & Golubic (1999) as different from *E. belcherensis* and indeed placed within the family Chroococcaceae rather than Entophysalidaceae. However, Sergeev *et al.* (2012) place *C. dispergens* within the Entophysalidaceae and remark that the supposed differences may be due to different ecological conditions in the respective habitats of growth. In any case, since the Rhynie fossil displays cells and cell groups suggestive of encapsulation (e.g. Fig 1e), there is no reason not to assign it to Entophysalidaceae. Additionally, the darkened envelopes on the outward-facing side of the cell units in the Rhynie chert fossil correspond well not only with the photoprotective adaptation described in *Entophysalis* but also with the characteristically darkened envelopes reported in *Eoentophysalis belcherensis* from the type locality and elsewhere (Hofmann, 1976; Sergeev *et al.* 1995; Knoll & Golubic, 1992; Golubic & Abed, 2010).

The Rhynie chert fossil described here is the first post-Cambrian documented record of a cyanobacterial fossil that fits the definition of *Eoentophysalis*. All previous records of *Eoentophysalis* come from shallow-marine settings (Hofmann, 1976; Knoll & Golubic, 1979; Knoll *et al.* 1991; Sergeev *et al.* 1995), whereas the Rhynie chert fossil lived in a non-marine, albeit not necessarily freshwater environment (for a discussion on salinity levels in the aquatic portions of the Rhynie ecosystem, refer to Channing, 2018). Because of the striking similarities to *Eoentophysalis*, we feel confident in assigning the Rhynie chert fossil to this genus. We do not, however, formally describe it as a new species even though it differs greatly in age and habitat from other reported instances of *Eoentophysalis* because there is only one specimen currently available and this specimen does not possess sufficiently definitive morphological traits to demarcate it at the species level. For the same reason, we do not assign the Rhynie *Eoentophysalis* to the species *E. belcherensis* (nor would we claim that this fossil necessarily corresponds to a real biological species that survived from the Mesoproterozoic to the Devonian), but retain it in open nomenclature as *Eoentophysalis* sp.

Affinities to the Entophysalidaceae have previously been considered for two other cyanobacterial fossils from the Rhynie cherts, namely *Rhyniotaxillus devonicus* and *Rhyniotaxillus minutulus*, but neither of them has been formally assigned to this family (Krings & Sergeev, 2019; Krings, 2021d). *Rhyniotaxillus devonicus* occurs singly or in clusters in the chert matrix, and is characterised by cuboid to irregular colonies of up to 64 cells

surrounded by prominent gelatinous envelopes. The colonies are very similar to the cell groups and small colonies that make up larger formations in *Entophysalis* and serve as dissemination units. However, no evidence has been found of substrate-covering colonies or more extensive formations. Conversely, *R. minutulus* occurs within lobed and pustulate formations composed of what appears to be a mucilaginous substance. Present in the mucilage are multiple dyads, groups of four or eight cells and larger colonies of *R. minutulus*, each surrounded by a gelatinous envelope. Specimens occur predominantly along the margins of the mucilage and in the pustules, where they are, in places, regularly aligned and closely spaced. The formations containing *R. minutulus* are similar to specimens of pustulate (mammillate) mats of *Eoentophysalis belcherensis* figured by Butterfield (2015: fig. 2A). Moreover, cell groups, packages and colonies of *R. minutulus* situated at the surface of the mucilage often possess darkened envelopes that correspond to the pigmented envelopes seen in both *Entophysalis* and *Eoentophysalis*.

4.2 Implications for the Rhynie ecosystem

Eoentophysalis in Palaeo- and Mesoproterozoic deposits is usually abundant and widespread, which raises the question: How abundant and ecologically important were entophysalid cyanobacteria in the Rhynie ecosystem? The fact that formations as the one described in this study have not previously been reported from the Rhynie cherts, notwithstanding the intensive research that has been conducted on this Lagerstätte for more than 100 years, could suggest that entophysalids were rare constituents of the Rhynie ecosystem. It is also possible, however, that these cyanobacteria occurred only in certain areas of the ecosystem that did not become preserved in the chert, or that are not represented by the chert blocks examined to date (Krings, 2021c). On the other hand, larger cyanobacterial colonies and formations held together by mucilage may rapidly disaggregate into individual cells and small cell groups after burial such that no evidence of an entophysalid affinity remains (Sergeev *et al.* 2012). Thus, the characteristic entophysalid formations are perhaps not regularly encountered in the Rhynie chert simply because they hardly ever became preserved. If this is accurate, then it raises the question of what made it possible that the specimen described here nevertheless became preserved, albeit somewhat poorly? This specimen comes from a small fenestra or inclusion of clear chert situated amidst silicified substrate. Well-preserved specimens of two other cyanobacteria from the Rhynie cherts, namely *Palaelyngbya kerprii* and *Rhyniococcus uniformis*, have previously been described from clear chert inclusions within silicified substrate (Krings, 2019; Krings & Harper, 2019). Krings & Harper (2019) suggest that a special micro-environmental setting was imperative for the fragile, unistratose colonies of *R. uniformis* to become preserved intact and that the substrate appears to have served as a preservation trap by shielding organisms enclosed in small inclusions between substrate layers from destructive mechanical forces and taphonomic alteration. Krings & Kerp (2019) demonstrate that part of the clear chert inclusions were once land plant axes based on shape and because they are surrounded by cuticles, and hypothesised that microbial life thriving on substrate surfaces and prostrate plant axes regularly became buried by new sediment layers. Within the consolidating sediment, the plant axes decayed and eventually turned into voids, in places still bounded by cuticles and containing remnants of the interior tissues. Microbial life associated with the plant axes, or washed into the voids from the vicinity, became protected in this way from mechanical destruction by water or sediment.

4.3 Evolutionary implications

The striking morphological resemblance between Proterozoic cyanobacteria in the genus *Eoentophysalis*, the fossil reported here from the Rhynie chert, and modern members of the genus *Entophysalis* bears on debates about possible fossil evidence for evolutionary stasis in prokaryotes. Golubic & Hofmann (1976) noted the very strong resemblance between *Eoentophysalis belcherensis* and modern *Entophysalis*, and Schopf (1994) interpreted this resemblance as evidence of evolutionary stasis, i.e. the maintenance of an original phenotype across geological time. More generally, Proterozoic cyanobacteria-like fossils can be grouped into morphotypes that appear to be indistinguishable from modern cyanobacteria (Knoll & Golubic, 1979; Schopf, 1992, 1994). As Knoll & Golubic (1979) have remarked, ‘essentially all of the salient morphological features used in the taxonomic classification of living cyanobacteria can be observed in well-preserved fossils’. This may reflect the ecological flexibility of many cyanobacteria, which, as generalists, thrive in diverse environments without further specialisation or modification of their fossilisable traits (even through the transition from marine to non-marine environments suggested by the presence of *Eoentophysalis* in the Rhynie chert). However, Butterfield (2015) has cautioned that *Entophysalis*-like morphology might represent a ‘grade of organization’, which may be ‘prone to evolutionary convergence’ such that *Entophysalis*-like fossils are unable to inform hypotheses about the long-term evolutionary stability of particular lineages. Nevertheless, evolutionary convergence between disparate taxa seems most likely to occur when environmental factors select for similar traits. Proterozoic *Eoentophysalis* lived in tidally influenced marine environments (e.g. Hofmann, 1976; Knoll & Golubic, 1979; Knoll *et al.* 1991; Sergeev *et al.* 1995), whereas the Rhynie and Windyfield cherts formed in a fully non-marine fluvial-alluvial floodplain setting with ephemeral hot spring pools (Powell *et al.* 2000). Similarly, modern *Entophysalis* is found in tidal settings, with a preference for lower intertidal ranges (Golubic & Abed, 2010), but can also be found in freshwater environments (e.g. Tavera & Komárek, 1996; Kaštovský *et al.* 2011). It would be a surprising coincidence (although certainly not impossible) for natural selection to have driven the acquisition of such similar morphological traits, modes of growth and organisation and even habits of pigmentation by originally dissimilar ancestors in such disparate environments. The discovery of entophysalid cyanobacteria in the Rhynie chert may be better explained by the broad environmental tolerance of a single lineage than by a multidimensional evolutionary convergence among unrelated cyanobacteria.

5. Conclusion

This study reports the discovery of a colony-forming entophysalid cyanobacterium in the Lower Devonian Rhynie chert of Scotland, which we refer to as the fossil genus *Eoentophysalis*. In morphology, pigmentation and arrangement, the fossil resembles both modern *Entophysalis* and the many examples of *Eoentophysalis* known from Proterozoic shallow-marine cherts. Although we cannot exclude evolutionary convergence between unrelated organisms, the strength of this resemblance is more parsimoniously explained by the persistence across two billion years of a single lineage with a broad environmental tolerance. Continued work on the Rhynie chert will likely yield additional types of cyanobacteria that can be used to further elaborate on the similarities and differences between cyanobacteria in Proterozoic marine cherts, a 407-myr-old terrestrial Lagerstätte, and present-day ecosystems.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0016756824000049>

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Competing interests. All authors disclose no relevant relationships.

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