

Organically preserved microbial endoliths from the late Proterozoic of East Greenland

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Diverse microorganisms ranging from cyanobacteria to eukaryotic algae and fungi live endolithically within ooids, hardgrounds and invertebrate shells on the present-day sea floor. These organisms are involved in the mechanical destruction of carbonates, and are useful ecological indicators of water depth and pollution¹⁻³. The Phanerozoic history of microbial endoliths has been elucidated through the study of microborings (the trace fossils of endolithic microorganisms) and rare cellularly preserved individuals^{1,3,4}, but nothing was known of the possible Precambrian evolution of comparable microorganisms until Campbell⁵ documented the occurrence of microborings in late Proterozoic ooids from central East Greenland. We now report the discovery of large populations of organically preserved endolithic microorganisms in silicified pisolites from the 700–800-Myr-old Limestone–Dolomite Series of East Greenland. This fossil assemblage is significant for three reasons: (1) It confirms the prediction⁵ that oolites, pisolites and hardgrounds—the substrates for pre-Phanerozoic endoliths—provide a hitherto poorly explored but rewarding set of environments into which the search for early microfossils must be broadened; (2) the assemblage is diverse, containing about 12 taxa of morphologically distinct and previously unknown endolithic cyanobacteria, plus associated epilithic and interstitial populations; and (3) at least six of the fossil populations are indistinguishable in morphology, pattern of development, reproductive biology and inferred ecology from distinctive cyanobacterial species that bore ooids today in the Bahama Banks.

The Eleonore Bay Group comprises some 7,000 m of unmetamorphosed sedimentary rocks that lie beneath latest Proterozoic glaciogenic beds in the coastal fjordlands of central East Greenland⁶⁻⁸. Carbonates occur principally in the upper part of this sequence, particularly in the 1,200-m-thick Limestone–Dolomite 'Series'. The Limestone–Dolomite succession documents a prolonged period of carbonate deposition along an extensive peritidal platform not unlike that of the present-day Bahama Banks. Flat-laminated, hemispherical and columnar stromatolites abound in this sequence, and these are intimately associated with oolites, pisolites, catagraphs, intraformational conglomerates and rippled to flat-laminated carbonate mudstones⁹. On biostratigraphic grounds, the Limestone–Dolomite sequence is considered to be predominantly late Riphean (perhaps 700–800 Myr)¹⁰, although the uppermost beds of the unit, above the horizons of interest here, may be Vendian.

The fossils in question occur in silicified pisolites from Bed 18 of the Limestone–Dolomite Series exposed on Ella Ø (72°53' N, 25°8' W) and 87 km to the north in exposures along the east flank of Grejsdalen (73°33' N, 25°5' W). Individual pisoids within the pisolites average 6–9 mm in diameter, but grains up to 14 mm have been observed. In both localities, the pisolites are cross-bedded, rippled and well-sorted, often grading into conventionally sized oolites. Although the pisoids have been affected to various extents by silicification, neomorphism, dolomitization and calcitization, petrographic fabric analysis and strontium content determinations suggest that they consisted originally of concentric laminae of tangentially oriented aragonite crystals⁹. In all sedimentological, petrographic and

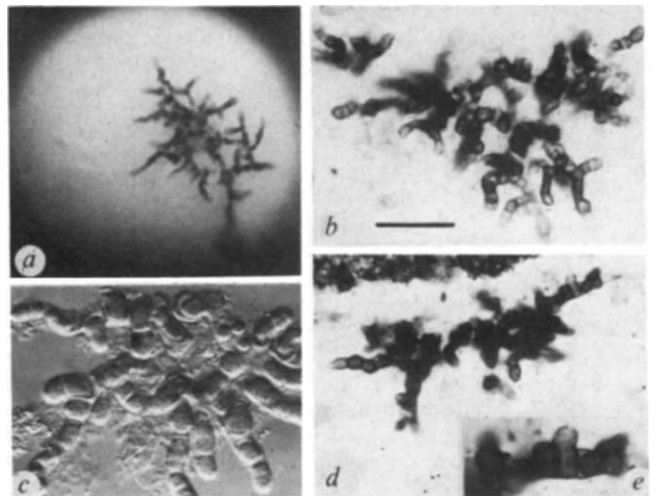


Fig. 1 a, Modern endolithic cyanobacterium *Hyella gigas* in ooid from the Bahama Banks ($\times 90$; scale bar in b = 115 μm). b, d, Fossil endolithic microorganisms comparable in morphology, development, reproduction and inferred ecology to modern *H. gigas* ($\times 128$; scale bar in b = 80 μm). c, Modern *H. gigas* freed from ooid to show details of morphology ($\times 255$; scale bar in b = 40 μm). e, Detail of d showing branch initiation ($\times 500$; scale bar in b = 40 μm).

micropalaeontological aspects, the pisoids are essentially large ooids and not diagenetic structures formed in the vadose zone⁹. Chert occurs as irregular nodules that loosely parallel bedding; field and petrographic observations indicate that the silica is an early diagenetic replacement of primary carbonate sediments⁹. All organically preserved endoliths occur within the outer rim of individual pisoids, suggesting that preservation was made possible by the rapid burial of pisoids following a period of extensive endolithic colonization.

Among the more common constituents of the endolith assemblage is a population of relatively large, branching filamentous microfossils that radiate inward from their points of entry into pisolites (Fig. 1b, d). Like most other fossils in the Limestone–Dolomite assemblage, these specimens are preserved largely as extracellular envelopes that only rarely contain highly degraded cell contents; however, envelope morphologies preserve a record of divisional patterns and approximate original cell size. Filaments are predominantly uniserial, 8.5–101 μm long (mean 42.5 μm ; s.d. 23.8 μm ; $n = 37$) by 7.5–21 μm wide (mean 12 μm ; s.d. 2.5 μm), and consist of the extracellular envelopes of coccoidal cells 8.5–21 μm long (mean 13 μm ; s.d. 3.5 μm ; $n = 125$) by 6.5–21 μm wide (mean 11 μm ; s.d. 2 μm). Terminal cells may be slightly longer than intercalary cells. Because the cells of endolithic cyanobacteria are constrained by their extracellular envelopes and essentially do not move after division, developmental pattern can be reconstructed from individual specimens¹¹ and corroborated by observations of younger specimens in the same assemblage. Filaments evidently grew by transverse cell division and branching originated by cell slippage within filaments and by longitudinal divisions of intercalary cells (Fig. 1e). Reproduction occurred by the formation of baeocytes (reproductive cells produced by repeated binary divisions without intervening cell growth) from cells near the pisid surface.

In cell and envelope size and shape, branching morphology, developmental pattern and mode of reproduction, these fossils are indistinguishable from populations of the modern endolithic cyanobacterium *Hyella gigas* Lukas and Golubic¹² which occur today as endoliths in oolitic shoals of the Bahama Banks (Fig. 1a, c). Marine ooids have narrowly circumscribed conditions of formation, and except for the more vigorous agitation implied by their larger size, the East Greenland pisolites appear

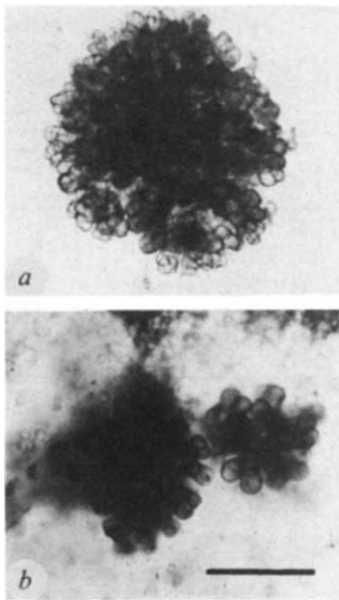


Fig. 2 *a*, Undescribed modern endolithic cyanobacterium freed from Bahamian ooid; view is essentially that seen from the interior of the substrate ($\times 140$; scale bar in *b* = 100 μm). *b*, Two specimens of fossil endolithic microorganisms comparable in morphology, development and inferred ecology to the living population illustrated in *a*; the fossil on the left is seen in longitudinal view, while the smaller individual on the right is viewed from the direction of the pisolith interior ($\times 350$; scale bar, 40 μm).

to have accumulated under sedimentary conditions much like those found today in the Bahamas. Thus, the morphological and reproductive similarity between *H. gigas* and its fossil counterpart is paralleled by a close environmental congruence between the modern and Proterozoic sediments in which the two taxa have been found.

Other fossil populations in the Limestone-Dolomite assemblage also compare closely with extant microorganisms that occur in Bahamian ooids. These include fossils resembling the modern taxa *Plectonema terebrans*, *Cyanosaccus* spp., *Solentia foveolarum* and unnamed coccoidal endoliths described by Harris *et al.*¹³. Perhaps the most interesting population is one composed of densely branched microfossils like that shown in Fig. 2*b*. These fossils have a high cell density, giving the appearance of a hemispherical cell cluster from which many short filaments radiate into the pisolith. Filaments are uniseriate or biseriata, only a few cells long, and often terminated by a pair of end cells. Branches tend to be club shaped, widening towards the pisolith interior. Filaments are 20–47 μm long (mean 33.5 μm , s.d. 8 μm ; $n = 20$) and have a maximum width of 12.5–16 μm (mean 14.5 μm ; s.d. 1.5 μm). Cell dimensions are 8.5–21 by 5–19 μm (mean 12.3 \times 12 μm ; s.d. 3.4 \times 3.7 μm ; $n = 62$). Baeocyte formation has not been demonstrated for this fossil. This taxon is a common constituent of the East Greenland endolith assemblage, but it has no precise counterpart among described species of modern endolithic cyanobacteria. Our comparative studies of Bahamian ooids have revealed the presence of a locally common and hitherto undescribed blue-green (Fig. 2*a*) that is remarkably similar in morphology and development to the fossil population in question. This demonstrates that palaeobiological knowledge of late Proterozoic microfossils has become sufficiently refined to be of use to systematic and ecological studies of modern coastal marine microorganisms.

Equally well-preserved remnants of at least five other intertidal and shallow subtidal communities occur in silicified carbonates and shales of the Limestone-Dolomite Series¹⁴. Although the organisms in these assemblages lived contem-

poraneously with those found in the pisolites, there is essentially no taxonomic overlap between the endolithic and other biotas. Endolithic microfossil assemblages clearly document communities that differed significantly from those of the microbial mat and phytoplankton biotas usually reported from Precambrian rocks; thus, they add significantly to our knowledge of early microbial diversity.

The Limestone-Dolomite fossil endolith assemblage provides new and compelling examples of the close resemblance between Proterozoic prokaryotes and their modern counterparts^{15–17}, in this case a comparison that begins with morphology and extends to reproductive, developmental and ecological similarity. Most important, the comparisons relate several co-occurring fossils from a single Proterozoic assemblage to taxa that occur today as part of a single community in a physically equivalent environment. Collectively, Limestone-Dolomite fossils demonstrate that endolithic cyanobacteria were abundant, diverse and apparently quite modern in shallow marine environments well before the radiation of either grazing or skeletonized metazoans.

This study was funded in part by NSF grants DPP-83-01226 (K.S.), BSR 85-16328 (A.H.K.) and EAR-83-06179 (S.G.). We thank the Commission on Scientific Research in Greenland for permission to do field work in East Greenland, R. Ginsburg for samples of Bahamian ooids and S. Campbell for helpful comments.

Received 13 January; accepted 7 April 1986.

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More than one event in the late Triassic mass extinction

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The recent hypothesis that mass extinctions are discrete phenomena that have occurred with great regularity during the history of life^{1,2} is testable in several ways. Two essential elements of the hypothesis are (1) that each extinction event represents a significant departure from normal, or 'background', rates of extinction, and (2) that such mass extinction events are spaced equally in time. The analyses of the cyclicity of mass extinctions so far have concentrated on the past 250 Myr, with the first event occurring at the Permian-Triassic boundary, 245 Myr ago^{1–5}. The second event followed 26–33 Myr later^{1–6}, in the late Triassic. Here I present a detailed analysis of the fossil record of marine and non-marine life during the late Triassic which suggests that there were at least two phases of mass extinction during that time, separated by 12–17 Myr.

The late Triassic has long been recognized as an important time of mass extinction^{7–11} (approximately equivalent in magni-