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Mini-review

Archean microfossils: a reappraisal of early life on Earth

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Abstract

The oldest fossils found thus far on Earth are c. 3.49- and 3.46-billion-year-old filamentous and coccoidal microbial remains in rocks of the Pilbara craton, Western Australia, and c. 3.4-billion-year-old rocks from the Barberton region, South Africa. Their biogenicity was recently questioned and they were reinterpreted as contaminants, mineral artefacts or inorganic carbon aggregates. Morphological, geochemical and isotopic data imply, however, that life was relatively widespread and advanced in the Archean, between 3.5 and 2.5 billion years ago, with metabolic pathways analogous to those of recent prokaryotic organisms, including cyanobacteria, and probably even eukaryotes at the terminal Archean.

Keywords: Archean; Early life; Microfossils; Stromatolites

1. Introduction

The time period and the environment surrounding the appearance of the oldest fossils on Earth provide important insights into the origins of life. The Precambrian Earth history, from the beginning of our planet c. 4.56 billion years ago (Ga = Giga annum) to c. 0.545 Ga, when the first skeletal shelly fauna appeared, is divided into the older Archean lasting until 2.5 Ga and the younger, subsequent Proterozoic. When carrying out research on the origin of life, Precambrian palaeontology serves as a test for theoretical considerations and experimental data, and helps to assess our understanding of evolutionary pathways and molecular clocks. With a boost in the general interest in exobiology (astrobiology), a discipline yet barren of a true study object, the understanding of early life on Earth, and particularly of Archean microfossils, also becomes increasingly important for exploring the possibility of extraterrestrial life.

Three main lines of evidence in the search for early Archean life exist: Chemical evidence (carbon-isotopic and biomarker detection), morphological evidence (microscopic detection of microfossils) and biosedimentological interpretation of structures like stromatolites.

Chemical evidence of carbon isotopes (RuBisCO-type fixation of ^{12}C in higher proportions than ^{13}C) reported from Archean rocks of Greenland suggests that life existed on Earth as early as 3.8 billions years ago [11,20,25,26]. These reports of ancient life, however, were repeatedly criticised as detection of traces of later rock colonialisation by contaminating (endolithic) bacteria, or as not in agreement with the results of detailed mapping and geological interpretation of rock formations (i.e., the rocks are younger than 3.8 billion years) [21,36,42].

The earliest microscopically recognisable microfossils were reported from the 3.49 Ga Dresser Formation [35] and from the 3.46 Ga Apex Chert of the Pilbara craton, Australia. From the Apex sedimentary rocks, eleven taxa of cellularly preserved filamentous microbes were described [28]. Recent studies, however, have questioned the validity of some of the Earth's oldest fossils from the 3.5 to 3.4 Ga rocks of South Africa and Australia, implying that the structures mimicking bacterial fossils may be contaminants, fluid inclusions [1,2], or carbon threads formed abiologically in hydrothermal environments [6]. The controversy and the public debate on these findings have attracted much attention in the scientific community [9,10,15]. Any report of the record of early

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life, therefore, must hold up to the most rigorous inspection before the findings can be accepted as genuine and authentic.

The earliest assured cyanobacterial microfossils were reported from Neoarchean rocks (2.7–2.5 Ga). The earliest cyanobacterially/bacterially mediated biomineralisation was reported from 2.6 Ga carbonate rocks [4,14,17,19]. Furthermore, the startling findings of biomarkers like methylhopanes and steranes [7] in the 2.7 Ga shales of the Fortescue Group, Pilbara Craton, Western Australia indicate oxygenic photosynthesis, and the existence of eukaryotes already in the Neoarchean. Hence the metabolism of the Neoarchean biota was essentially similar to that of modern organisms, and included anaerobic fermentation, anoxygenic photosynthesis, oxygen-producing photosynthesis, and aerobic respiration in autotrophs and heterotrophs. These data are consistent with estimations of minimal divergence times of the major bacterial and archaeal phyla [33].

2. Identification of the problem

Although several decades have passed since the first description of Archean microfossils, the palaeontological record of the Archean is disappointingly scanty, accounting only for about 30 accepted taxonomic occurrences. Archean rocks, although rather widespread in old cratonic cores, are usually strongly altered, often beyond recognition of their primary structure and composition, by geological processes of denudation, low temperature recrystallization (and weathering diagenesis), tectonism (including plate tectonics), and thermal and pressure alteration (metamorphism). Imperceptibly metamorphosed rocks, particularly from the early Archean (>3.0 Ga), are extremely rare and occur mainly on the Kaapvaal craton of South Africa (Barberton greenstone belt) and on the Pilbara craton of Western Australia. All known rocks older than 3.5 Ga are severely metamorphosed, including those of the Isua greenstone belt of Greenland, and underwent metamorphism and tectonism under temperatures reaching 600 °C and high pressure (>5 kbar). Under such conditions new minerals form in the rocks and possible organic content alters to graphite and amends its isotopic biosignature [36]. Nonetheless, morphological, geochemical and isotopic data from rocks 3.5 Ga and younger imply that Archean life forms were widespread and relatively advanced, having entered metabolic pathways that serve analogous organisms today.

The clearest macroscopic witnesses of Archean life are stromatolites occupying and building carbonate platforms and reef-type bioherms (limestone, $CaCO_3$ and dolomite, $CaMgCO_3$ or chert rocks, SiO_2). Stromatolites are defined as lithified biosedimentary structures, growing through accretion of laminae by the entrapment of sediment and/or by direct precipitation of carbonate, as the result of the activity of microbial organisms [40]. Other definitions also include possible and pure chemical precipitates [12]. In the latter case, stromatolites, of course, do not necessarily evidence life. Stromatolite researchers are thus divided into different groups, those who follow the biological approach to stromatolites and others who treat stromatolites rather as sedimentary or biosedimentary structures. Naturally, these groups also differ in their opinion on the stratigraphic usefulness of stromatolites in the Precambrian. Those who view stromatolites as sedimentary or biosedimentary structures are today in the majority and stromatolites are preferably regarded as environmental rather than stratigraphic indicators. They do not represent fossils sensu strictu, but are rather lithified associations of sediment and microbial mats. Nevertheless, stromatolites bear witness to the early evolution of life, as far back as 3.5 Ga, and may contain fossil microbial remains of that age. They occur in a vast range of shapes and sizes, as microstromatolites (Fig. 1), recognisable only in microscopic thin section, in small, patchy lithoherms, and within widespread stromatolitic lithostromes, up to tens or hundreds of metres in thickness and hundreds of kilometres in lateral extent (Fig. 2). Shallow pools and peritidal realms or evaporitic and hydrothermal basins are envisaged as the main sites of stromatolite growth. However, from the Precambrian rock record, microbial mats thriving in deep, aphotic conditions were also reported. In Archean stromatolites microfossil preservation is extremely exceptional. Stromatolites bearing microfossils are termed “biophoric”, whereas microbially influenced fossilised biosedimentary structures are named “biogenic” stromatolites. Non-biogenic stromatolites, precipitated chemically, and biogenic stromatolites can be biophoric if they contain chemical precipitate which has trapped and fossilised organisms in the environment (comp. Altermann [2] and references therein).

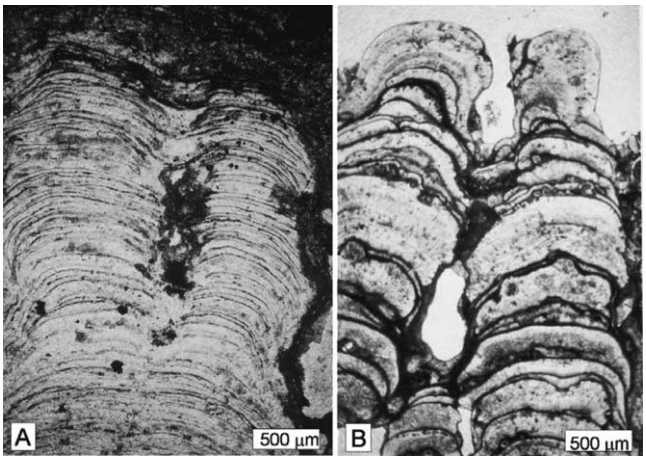

Fig. 1. (A) Late Archean digitate microstromatolitic structures (Kogelbeen Fm., Kathu borehole, South Africa) composed of silicified, darker and lighter calcium carbonate laminae. (B) Almost identical modern calcareous microstromatolitic structure from quasi-marine crater Lake Motitoi, on Satonda Island (central Indonesia) composed of similarly alternating lighter and darker laminae originating from in vivo (darker calcitic laminae) and early post mortem (lighter aragonitic laminae) calcification of coccoid cyanobacteria. Cyanobacterial capsules are occasionally excellently preserved due to early diagenetic silicification. (Thin section micrographs in transmitted light.)

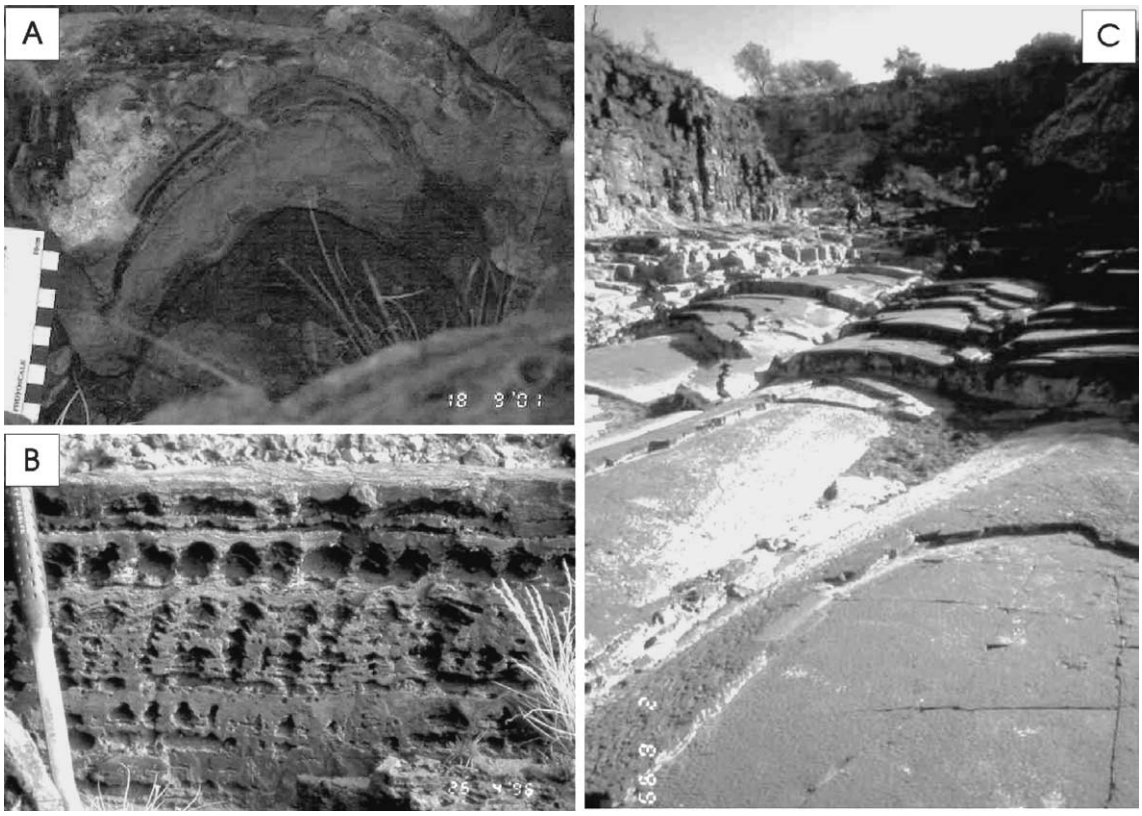

Fig. 2. Field occurrence of Archean stromatolites: (A) Small domical to columnar stromatolite in partly silicified carbonate rocks of the 3.45 Ga Warrawoona Group, Western Australia (scale in cm). (B) 2.7 Ga pseudocolumnar, laterally linked, silicified stromatolites in volcanic, tuffaceous rocks of the Ventersdorp Supergroup, South Africa (40 cm long hammer handle for scale). (C) Giant stromatolitic domes of the 2.5 Ga Campbellrand Subgroup. These subtidal domes can attain over 50 m length and 20 m height and 2 m of synoptic relief and are parallel to palaeocurrents. The stromatolitic beds (reefs) are traceable for tens of kilometers laterally.

3. Criteria and methods for microfossil identification

Several workers attempted to set up criteria for recognising genuine Archean microfossils and distinguishing such findings from younger fossilised bacterial contaminants, pseudofossils and artefacts [8,30]. To ensure the authenticity of Archaean microfossils the samples must be of firmly established Archean provenance and age, the fossils must be indigenous to the rock and syngenetic with its deposition (i.e., not introduced by later colonisation of cracks and pores in the rock [42]), and allowing for morphological recognition of assured biological origin. Several lines of positive evidence like fossil morphology, the presence of carbonaceous matter, isotopic signatures, biomarkers and mineralogy need to be combined in such a testimony. Petrographic thin sections that can provide clear evidence of the relationship between fossil-like objects and their encompassing rock matrix, are best suited study objects and must always be combined with at least the first three abovementioned positive pieces of evidence (morphology, carbon, isotopes). They may be supported by electron microscopy (SEM), laser Raman spectroscopy, atomic force microscopy (AFM) and isotopic investigations, performed preferably on individual fossils.

Techniques like SEM or AFM expose only the surface of the rock and do not reveal the relationship of the supposedly biogenic structure to the rock itself, as petrographic thin sections do. Petrographic studies and understanding of the diagenetic and metamorphic history of the sample are, however, crucial evidence and must be presented in order to demonstrate that the sample is potentially suitable for authentic microfossil preservation and is indeed microfossiliferous. Laser Raman spectroscopy can demonstrate that the microfossils in question are made of carbonaceous matter. The crystallinity of carbon, if detectable, should actually correspond to the diagenetic and metamorphic history of the rock itself—a criterion that has rarely been fully discussed yet, because of insufficient laser Raman analysing techniques [23,31]. AFM usage on Precambrian microfossils is still an experimental technique currently applied only to previously assured microfossil occurrences. Coccoid microfossils investigated with the AFM, combined with laser Raman spectroscopy, were found to consist of kerogenous walls composed of stacked, platy, angular polyaromatic hydrocarbon subunits ∼200 nm in size, oriented perpendicular to the cell walls [16]. It has yet to be demonstrated to what extent this feature is typical and characteristic of microfossil preservation.

Although the identification of isotopic and organic biomarkers provides indispensable information on the early life traces preserved in rocks, such studies are to be treated with caution. Rocks can be colonised by microbial communities long after their formation, when exposed to subsurface or surface environments, and such colonies can become fossilized by migrating fluids and their precipitates. Organic compounds can be introduced into the rock by percolating ground water. Younger bituminous matter and fluids can also be trapped in microscopic fluid inclusions, in minerals filling open spaces, e.g., pores and cracks, when the rocks are exposed to low hydrothermal fluid migration. Therefore, in situ studies on particular microfossils are better evidence than bulk rock analyses, but are extremely difficult to perform on structures of only a few μm across, and are therefore still very rare [13].

Taxonomic classification of Precambrian microfossils is based on morphometrics of often badly preserved specimens**,** and on their morphological comparisons to representatives of modern taxa. The main characteristics used in classification include shape and size of cells, form of filament and thallus, patterns of cell growth and division, presence or absence of extracellular sheaths or envelopes, form of extracellular structures and of wall ornamentation, and presence or absence of colonial organisation. Schopf [27] suggested that fossil septate filaments <1.5 μm wide can be regarded as probable bacteria and those >3.5 μm wide as probable cyanobacteria. The range between these two classes was referred to as "undifferentiated prokaryotes". Coccoid microfossils larger than 60 μm in diameter were assigned to "assured eukaryotes". However, because the size ranges of extant and fossil bacteria, cyanobacteria and alga overlap, this subdivision is not inevitably correct, nor do morphological similarities necessarily imply similar metabolism. However, no better, unequivocal criteria have been found thus far.

Morphologically representative measurements and statistical comparison to extant species are thus fundamental. Simple coccoid forms, single or arranged in clusters, and corresponding in size to extant species, must be treated with scepticism. This is especially valid if such structures are not found in the samples by means other than SEM or AFM, i.e., the relationship to embedding rock matrix is unclear, and if no easily discernible cell walls are recognisable. Silica often crystallises to spheroidal aggregates of a few μm to sub-μm in diameter. Such spheroids may contain carbon from migrating bituminous fluids or simply from their CO_2 content. True coccoid microfossils may exhibit shapes reflecting cell division and traces of the EPS surrounding such benthic colonies. The morphology of filamentous fossils offers more definite characteristics, including distinct terminal cells, cylindrical shapes with robust cell walls, septation, and a typical range of widths (<0.5 to $\sim$100 μm) and of lengths, of a few tens to a few hundred μm, to some degree comparable to the sinuosity of the filaments [30].

Generally the microfossils found in Precambrian rocks tend to increase in size with time. Those found in rocks of 3.5 to 3.0 Ga are often smaller than 10 μm in diameter, those at around 2.5 Ga can be larger than 10 μm, and "assured eukaryotes" >60 μm appear only in the Proterozoic. However, considering the scarcity of reports of authentic early Archean microbes, this observation might be fallacious. Schopf [29] has noticed that the early evolution of life is characterised by morphological conservatism, evidenced in the extremely slow evolutionary progress of the prokaryotes. This "hypobradytelic evolution" and the deficient fossil record consequently imply that prokaryotes are of no stratigraphic significance for the Archean.

4. The Archean fossil record

Extensive morphometric studies of $\sim$2000 cells in $\sim$180 specimens have demonstrated a systematic correlation between cell shape, filament diameter, and taxon-specific terminal cell morphology for each of the 11 filamentous species described from the 3.46 Ga Apex Chert [28]. Suggestions that the Apex fossils might be thermally degraded remnants of ensheathed benthic colonies of coccoid cyanobacteria [15] need further investigations on the original material. Interpretation of these fossils as remnants of inorganic Fischer–Tropsch-type synthesis of carbon within hydrothermal systems [6] can only be considered when demonstrated that such inorganic carbon synthesis can produce microfossil-like structures of similar isotopy and kerogen crystallinity in chert.

From the early Archean fossil record, Schopf [30] has identified only a few reports that fulfill the criteria listed above. These microfossiliferous occurrences from eight 3.2 to 3.5 Ga Archaean formations of Western Australia and South Africa can be accepted as authentic ancient fossils and provide firm evidence that 3500 Myr ago microbial life was flourishing and presumably widespread. These oldest findings contain spheroidal or filamentous microfossils [5,24,27, 28,32,35,38,39]. One sampling location [5] from 3.45 Ga old rocks of Western Australia could not be found again [30] and remains to be verified. Carbon isotopic analyses and laser-Raman spectroscopy, however, support the interpretation of the structures found in this sample as authentic microfossils. Negative carbon isotopic values, typical of Precambrian biogenic kerogens, (up to $-36‰$) have been measured on the carbonaceous components and individual fossils of the oldest of these findings. Few reports [18,22,37,38,41] were classified [30] as being of possibly uncertain fossil content. Some of these findings, however, are now supported by additional carbon isotopic and laser Raman spectroscopy analyses and thus can, at least in part, be accepted as probable microfossils [1,18,30,38,41].

To the above listed early Archean findings, reports of ascertained younger Archean fossils can be added [4,14,17,19]. Colonial coccoid cyanobacteria have not yet been discovered in rocks older than about 2.6 Ga, although their very early origin is suggested by molecular phylogenetic analyses [34].

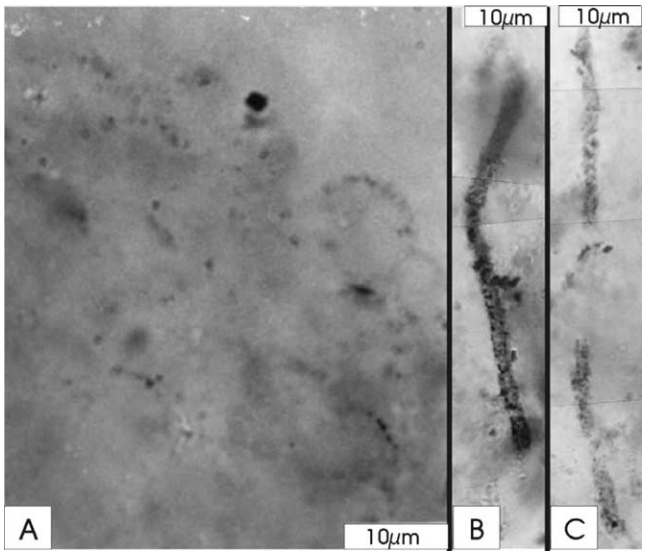

Fig. 3. Microfossils from stromatolitic, early diagenetically silicified limestones of the 2.55–2.52 Ga Campbellrand Subgroup, South Africa, in petrographic thin section. (A) Faint fossil ghosts interpreted as remnants of EPS of entophysalidacean benthic coccoids assigned to *Eoentophysalis* sp. [4]. (B) and (C) filamentous, cyanobacterial nonseptate sheaths assigned to *Eomycetopsis* cf. *filiformis* [4].

Recognition of Neoarchean and Proterozoic fossils raises comparably minor problems because fossils are more abundant and often much better preserved. They can be so similar in morphology to modern microbial taxa that both their biogenicity and biological affinities can be readily established. The better preservation of Neoarchean to Proterozoic rocks plays an important role therein. The environmental setting for all Archean fossiliferous units ranges from shallow marine intertidal to subtidal, to hydrothermal.

Most reports of Archean microfossils are from diagenetically silicified carbonates or primary cherts (Fig. 3). Carbonate rocks are conventionally excluded as a potential source of microfossils because of the crystallization force of carbonate minerals, which is believed to be responsible for destruction of prokaryotic cell-sized structures. In one reported exception, the filaments described as *Siphonophycus transvaalensis* were partly preserved in late diagenetic, euhedral dolomite crystals, in parallel with their preservation in chert [17]. These cyanobacteria-like filaments display minute needles (originally aragonite?) within sheaths, that were interpreted as possible remains of cyanobacterial calcification.

Non-silicified occurrences of carbonate rocks are rare in early Archean successions, including the 3.5 Ga Warrawoona Group. Thick and extensive stromatolitic carbonate platforms appear in the geologic record only at about 2.9 to 2.6 Ga and the mechanism of biocalcification and carbonate precipitation is highly debated for the entire Precambrian. Wright and Altermann [43] reported on possible microbial mediation in calcification and dolomitisation processes in microbial laminites and oolites. Rates of sediment accumulation and organic production on Neoarchean carbonate platforms were comparable to those on modern carbonate platforms and in recent microbial mats [3,19]. The first direct morphological evidence for biomineralisation by benthic coccoid Archean cyanobacteria was presented from the Campbellrand Subgroup of South Africa [14]. The biostructures obtainable in the SEM images are essentially similar to capsules and common mucilage sheaths of modern benthic cyanobacteria classified within the orders Chroococcales (particularly the family Entophysalidaceae) and Pleurocapsales (comp. Fig. 4). The characteristic feature of all these cyanobacteria is the capsular organisation of their mucilaginous sheaths surrounding individual cells and cell clusters forming colonies. The process of early postmortem mineralization in the ca. 2.6 Ga Neoarchean cyanobacteria probably reflects the action of heterotrophic bacteria upon the dead cyanobacterial biomass. The lytic action of the heterotrophic bacteria might have led to liberation of Ca and Mg cations stored (complexed) in the cyanobacterial EPS and glycocalyx during their lifetime. This, in turn, might have enhanced precipitation of carbonate minerals within the extracellular polymers and in spaces occupied earlier by the cytoplasm, by increasing calcium carbonate oversaturation. It has been proposed [14] that taphonomic and fossilisation processes similar, if not identical, to those acting today were in operation in the early history of life. The abundant cyanobacterial mats in the peritidal deposits of Neoarchean formations suggest mass production of fine-grained calcium carbonate by benthic coccoid cyanobacteria. This process explains the finely laminated nature of most Archean (particularly stromatolitic) calcareous sediments.

5. Conclusions

Microfossils from the Archean are extremely difficult to identify and are subject to continuous controversy. Archean stromatolites, although evidencing early life on Earth, cannot be viewed as fossils sensu strictu. The earliest microscopically recognisable microfossils were reported from the 3.49 Ga Dresser Formation and from the 3.46 Ga Apex Chert of the Pilbara craton, Australia. Although their biogenecity has recently been questioned, whole rock carbon isotopic compositions with RuBisCO-signatures and morphological affinity of microfossils to recent cyanobacteria and bacteria, together with laser Raman identification of carbon within the fossil bodies, testify to their authenticity. Certainly, life in a more primitive form must have existed on Earth before 3.5 Ga, but the key to proving it lies in finding older rocks or in utilising new methods allowing identification of cryptic organic remnants. When extrapolating to extraterrestrial conditions the difficulties in finding and recognising Archean microfossils, the prospect of finding and identifying microfossils in Martian samples seem extremely faint, and undisputed results can only be obtained on samples brought back to Earth's laboratories.

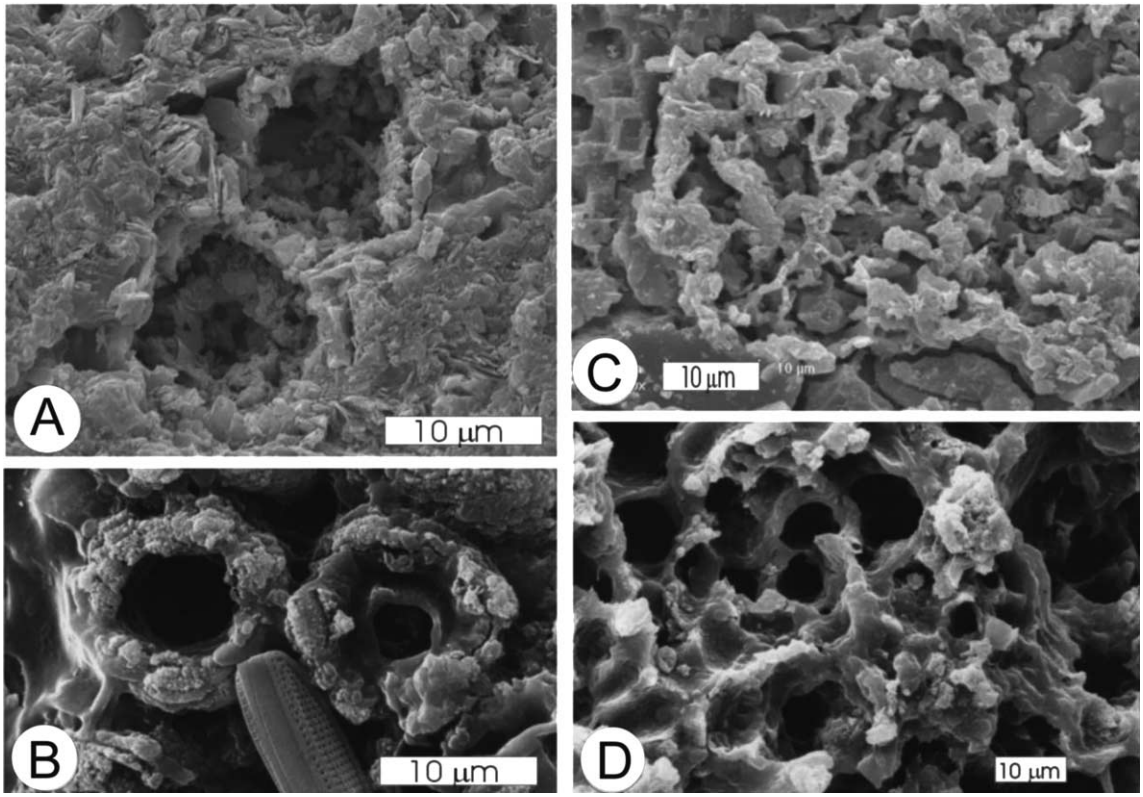

Fig. 4. (A) SEM image of mucilage capsules from the ~2.6 Ga old Nauga Fm. (South Africa) cyanobacterial mat mineralized by calcium carbonates and Al–Fe silicates. (B) Similarly mineralized modern capsules from Lake Vai Si'i, Tonga. (C) SEM image of etched section of the Archean mat, showing patterns resembling capsular mucilage sheaths of modern coccoid pleurocapsalean cyanobacteria, like those shown in (D) from the rocky shore of Sulejow Dam, central Poland. (The Archean sample was taken north of the Orange River at Prieska, approximately at 29°32′S/22°40′E.)

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