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Sulfur-oxidizing bacteria prior to the Great Oxidation Event from the 2.52 Ga Gamohaan Formation of South Africa

Andrew D. Czaja[1]*, Nicolas J. Beukes[2], and Jeffrey T. Osterhout[1†]
[1]Department of Geology, University of Cincinnati, PO Box 210013, Cincinnati, Ohio 45221-0013, USA
[2]CIMERA, Department of Geology, University of Johannesburg, P.O. Box 524, Auckland Park 2006, South Africa

ABSTRACT

The first 2 b.y. of Earth's history was an important time for life when microbes evolved and diversified into essentially all of the metabolic forms that now exist. Because of feedbacks between biology and the surface environment, understanding Earth's biological history can help us understand the evolution of Earth itself. The morphological and geochemical evidence for this ancient biological history is sparse but is increasing. Here we report evidence for 2.52 Ga exceptionally large, organic, smooth-walled, coccoidal microfossils preserved in a deep-water black chert in the Gamohaan Formation of the Kaapvaal craton of South Africa. These fossils occur mainly as compressed solitary coccoids that range in size from 20 to 265 µm but occasionally occur in short chains of cells. Morphologically these fossils are similar to Proterozoic and Phanerozoic acritarchs and to certain Archean fossils interpreted as possible cyanobacteria. However, their exceptionally large size, simple cell wall microstructure, and paleoecological setting, as well as multiple sulfur isotope systematics of pyrite within the unit, suggest that the Gamohaan Formation fossils were sulfur-oxidizing bacteria similar to those of the modern genus *Thiomargarita*, organisms that live in anoxic and sulfidic deep-water settings. These are the oldest reported fossil sulfur bacteria and reveal a diversity of life and ecosystems, previously only interpreted from geochemical proxies, just prior to the Great Oxidation Event, a time of major atmospheric evolution.

INTRODUCTION

The evidence of life in the Archean Eon, >2.5 Ga, is well established, even back to ca. 3.5 Ga (e.g., Schopf, 2006), and geochemical proxies and molecular clock analyses suggest that not only is life ancient, but the major microbial metabolisms originated during this time (e.g., Zerkle et al., 2005). Despite this knowledge, the known diversity of fossil life from the Archean is low relative to more recent Earth history, largely because of preservational biases. The Archean fossil record includes only a few dozen occurrences of fossil microorganisms (microfossils) spanning 1 b.y. of Earth history (3.5–2.5 Ga). The record includes rod-shaped, filamentous, and coccoidal cells that are ≤30 µm in diameter (Schopf, 2006), as well as large spindle-shaped coccoids (e.g., Sugitani et al., 2007) and extra-large coccoids (30–300 µm; Javaux et al., 2010; Sugitani et al., 2015). All of these occurrences, however, represent shallow water organisms and/or have been interpreted as phototrophs. As a result, our knowledge of deep marine microbial ecosystems from this time is lacking. Below, we present evidence for exceptionally large coccoidal microorganisms preserved in a deep-water facies of a Neoarchean carbonate platform slope that are interpreted as fossil sulfur-oxidizing bacteria, the first ever reported from the Archean. This study provides an important check for geochemical proxies of microbial sulfur cycling at a time of major change in Earth's surface conditions, just prior to the Great Oxidation Event (GOE) when atmospheric oxygen levels began to rise and sulfur cycling likely increased in importance (e.g., Kaufman et al., 2007).

MATERIALS AND METHODS

Fossil microstructures reported here were collected from a finely laminated black chert in the upper portion of the Gamohaan Formation from the Griqualand West Basin of the Kaapvaal craton, South Africa. The chert was sampled from five sites at two localities in the Northern Cape Province: four sites at a locality 12.5 km northwest of the town of Kuruman, and one site from a locality 8.5 km north-northeast of the town of Danielskuil (Fig. 1A). The stratigraphy of the Gamohaan Formation is described in detail by Beukes (1987). The age of the chert is well constrained by a tuffaceous bed dated at 2521 ± 3 Ma (Sumner and Bowring, 1996) located a few meters stratigraphically above the chert layer (Fig. 1B). This portion of the Gamohaan Formation is interpreted to have been deposited in the deep subtidal (and probably sub–photic zone)

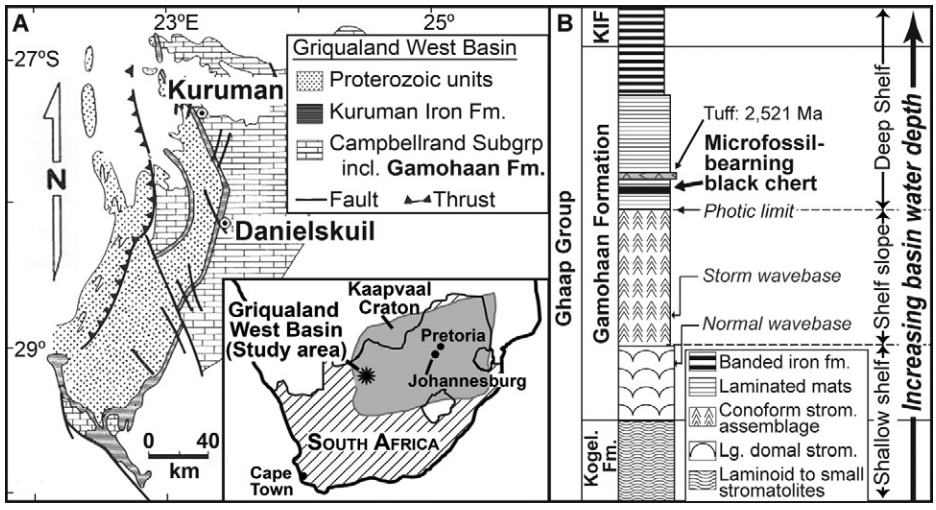

Figure 1. Geologic context of sampling locations. A: Simplified geologic map of Griqualand West Basin (South Africa) showing relative locations of two sampling localities, near towns of Kuruman and Danielskuil (adapted from Klein et al., 1987). Fm.—Formation. Inset: Map of South Africa showing location of Kaapvaal craton and Neoarchean Griqualand West Basin. B: Simplified stratigraphic column of Gamohaan Formation showing increasing basin water depth during deposition and position of fossiliferous chert unit (adapted from Beukes and Gutzmer, 2008). Kogel.—Kogelbeen; KIF—Kuruman Iron Formation; Lg.—large; strom.—stromatolite.

*E-mail: andrew.czaja@uc.edu
†Current address: Department of Earth, Planetary, and Space Sciences, University of California, Los Angeles, 595 Charles E. Young Drive East, Los Angeles, California 90095-1567, USA.

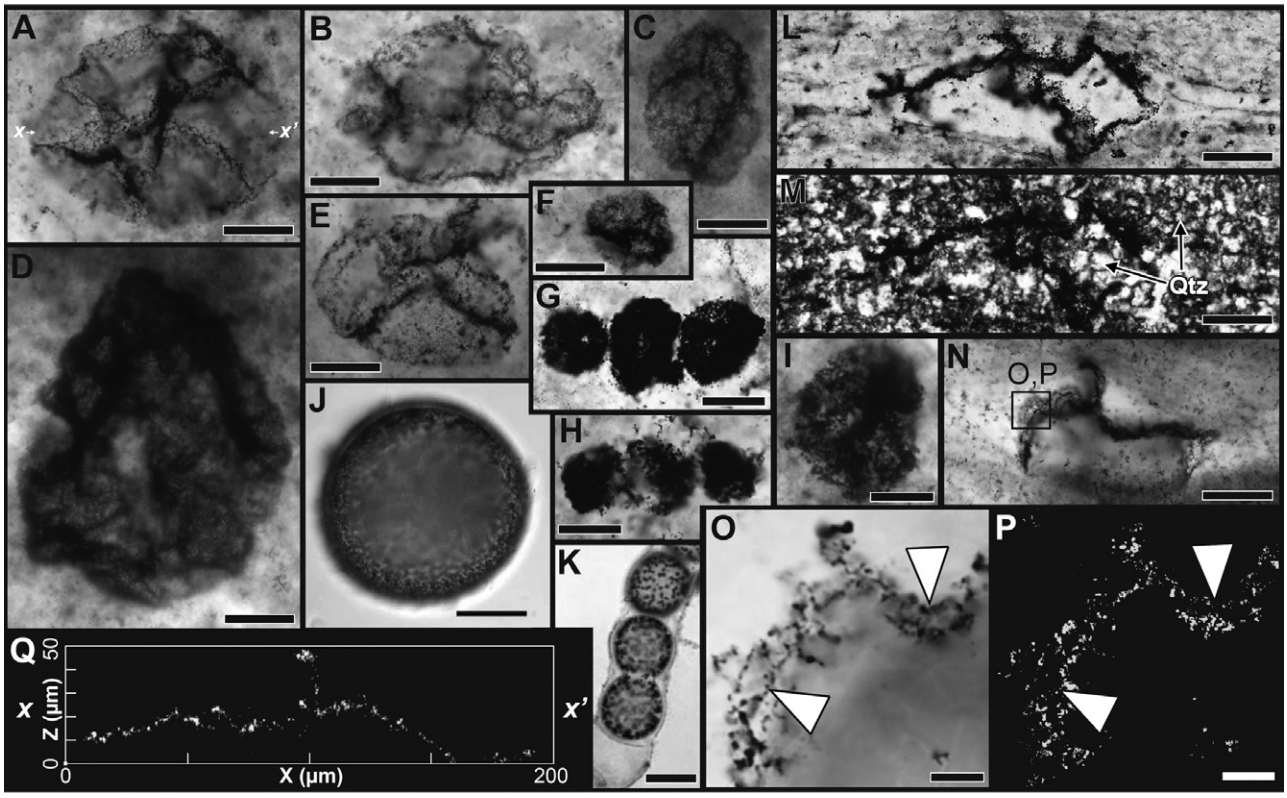

Figure 2. Photomicrographs of representative coccoidal microfossils from Gamohaan Formation (South Africa) and modern *Thiomargarita* sp. A–I: Fossils photographed in thin sections cut parallel to bedding showing approximate cross-sectional shape of organisms in life. J,K: Modern *Thiomargarita* sp. cells for comparison (J adapted from Kalanetra et al., 2005; K adapted from Schulz et al., 1999). L–N: Fossils photographed in thin sections cut perpendicular to bedding showing taphonomic compaction during burial. Image in M shows same specimen as that in L, but in plane polarized light to illustrate relationship between matrix quartz grains (Qtz) and fossilized organic matter. O,P: High-magnification photomicrograph (O) and confocal laser scanning micrograph (P) (both at same focal depth) of fossil pictured in N showing evidence of adpressed walls (white arrowheads). Q: Confocal laser scanning microscopy cross-section of fossil shown in A (transect x–x'). A–I, L, and N are transmitted white light photomicrographs taken with 20× or 40× objectives (A–F, L, N) or a 100× oil immersion objective (G–I, O). Image in M was taken with plane polarized light and 20× objective. Scale bars in A–F and L–N are 50 μm, in G–I are 20 μm, in O and P are 5 μm, and in J and K are 100 μm. See Figure DR2 (see footnote 1) for images of additional specimens. See Table DR1 for thin section numbers and stage coordinates for all imaged specimens.

region of the drowned Campbellrand-Malmani carbonate platform (Sumner, 1997; Beukes and Gutzmer, 2008). The chert bed occurs within the contorted laminated mat assemblage described by Sumner (1997), interpreted to be the deepest of the deep-water mat assemblages of the Gamohaan Formation. See Figure DR1 and supplementary text in the GSA Data Repository[1] for further geological and location details.

Specimens were located and photographed using transmitted light microscopy in unpolished thick sections of chert covered with a film of fluorescence-free immersion oil (Olympus Type-F). Microstructures were located in thin sections from all five sampling sites. Two- and three-dimensional images of selected specimens were acquired by confocal laser scanning microscopy (CLSM; Olympus FV1200) using 559 nm laser excitation and a 60× oil objective (NA [numerical aperture] = 1.42). The molecular structure of organic matter preserved in individual microstructures and in the chert matrix was measured using a Horiba T64000 Raman microscope and 457.9 nm excitation from a Coherent FreD 90C Ar+ laser with a spot size of ~2 μm. See the Data Repository for further details of CLSM and Raman data collection and processing.

RESULTS

The microstructures reported here have morphologies that are consistent with the remains of compressed coccoidal microorganisms. The structures range from ~20 to 265 μm in maximum diameter (mean: 124.3 μm, n = 62; Figs. 2 and 3; Fig. DR2). The flattened structures are typically more elliptical than circular in plan view and have a mean aspect ratio (length of short axis divided by length of long axis) of 0.82 ± 0.09 (1 standard deviation [s.d.]; Fig. DR4). The walls of the structures display a reticulate pattern typical of organic matter preserved in chert, and lanceolate folding patterns and wrinkles (e.g., Figs. 2A and 2Q). Rarely, cells were found in apparent short chains of three cells (Figs. 2G and 2H). The compression is consistent with compaction of the sediments prior to lithification, as indicated by the draping of laminations around the microstructures viewed in sections cut perpendicular to bedding (Figs. 2L–2N; Fig. DR2). Some of the compressed structures also display the presence of adpressed walls (Figs. 2O and 2P). See the Data Repository for three-dimensional animations of selected microstructures that illustrate the compressed morphology.

Raman spectra of the microstructures and particulate organic matter in the surrounding chert matrix are dominated by features at ~1600 and ~1360 cm^{-1} (Fig. 4), characteristic first-order bands of disordered macromolecular aromatic organic matter (kerogen) that are distinct from graphite (e.g., Schopf et al., 2005). These Raman spectra are essentially indistinguishable from each other (Fig. 4) and have Raman index of preservation (RIP) values of ~4.0 on a unitless scale of 1–9 (Schopf et al., 2005; Table DR2 in the Data Repository).

[1]GSA Data Repository item 2016332, supplemental figures, text, and movie files, is available online at www.geosociety.org/pubs/ft2016.htm or on request from editing@geosociety.org.

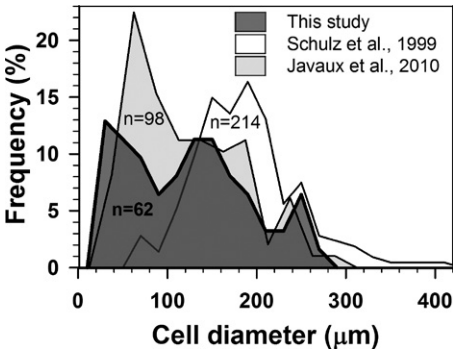

Figure 3. Size distribution of Gamohaan Formation (South Africa) microfossils compared with other coccoidal microbes. Distribution of maximum cell diameters of well-preserved microfossils from this study imaged in plan view (dark gray area) compared with modern *Thiomargarita namibiensis* cells (white area; Schulz et al., 1999) and fossils reported from the 3.2 Ga Moodies Group of South Africa (light gray area; Javaux et al., 2010).

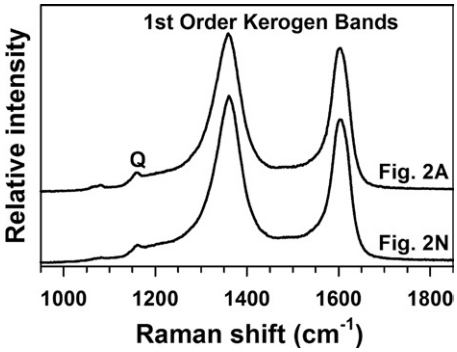

Figure 4. Representative Raman spectra of kerogen within fossiliferous Gamohaan Formation (South Africa) black chert. The Raman bands at ~1360 cm^{-1} and ~1600 cm^{-1} are characteristic of kerogen. Upper spectrum is from coccoidal microfossil pictured in Figure 2A. Lower spectrum is from kerogen-rich lamina near microfossil in Figure 2N. Feature labeled Q at ~1160 cm^{-1} is minor peak of quartz from chert matrix.

DISCUSSION AND CONCLUSIONS

The Gamohaan Formation microstructures are most plausibly interpreted as the remains of coccoidal microorganisms, based on accepted criteria for identifying microfossils from the Archean including age and provenance (see Materials and Methods), indigenousness, syngeneity, and biogenicity (e.g., Buick, 1990; Schopf et al., 2005). The microstructures were located within thick sections of black chert, establishing that they are indigenous features. The fossils are also syngenetic with the primary layering and are not found in veins or other secondary structures. Additionally, the similarity of all of the Raman spectra measured from the fossils and matrix (e.g., Fig. 4) indicates that all of the kerogen has had a shared thermal history (see the Data Repository for further discussion, and Table DR2).

The biogenicity of the fossils is established based on both morphological and geochemical evidence. The fossils show clear indications of having an originally coccoidal shape, including a round to oval outline in their compressed forms (Fig. 2), lanceolate fold structures, wrinkles, and adpressed walls (Figs. 2O and 2P) typical of compressed large, smooth-walled, and flexible coccoids (e.g., Javaux et al., 2010). The compression and folding of the fossils is likely a result of the compaction noted above (Figs. 2L–2N) as well as loss of turgor pressure within the microorganism upon death. The possibility that these specimens were produced by concentration of organic carbon along the boundaries of pore-filling cements can be discounted by the lack of such cement textures and the presence of microcrystalline chert surrounding these specimens (as revealed by plane-polarized light microscopy; Fig. 2M; Fig. DR3). Although the flattened shape of many of the fossils is more oval than round, it is difficult to determine with confidence if they had a spherical or ovoid shape in life is because of the variability in the measured aspect ratios (Fig. DR4) and ambiguities of taphonomic alteration. The kerogenous nature of the fossils is typical of Precambrian organic-walled microfossils, and their RIP values are consistent with a level of thermal alteration attained by unquestioned fossils (Schopf et al., 2005).

The large size and originally coccoidal morphology of the fossils indicate an affinity with one of five microbial groups: soil-dwelling myxobacteria, *Epulopiscium* (a genus of obligate gut microbes in tropical fish), single-celled eukaryotic photoautotrophs, cyanobacteria, or large sulfur-oxidizing bacteria. One caveat to consider is that assigning a taxonomic placement for such ancient organisms based on morphological comparison with modern or even with fossil specimens younger than themselves can be difficult because of the incompleteness of the ancient fossil record. Membership in the first two groups can be discounted, however, because those groups do not occupy the same ecological setting as the fossil organisms described here (cf. Javaux et al., 2010). Thus, we are left with the possibilities that the Gamohaan Formation fossils were planktonic eukaryotes or cyanobacteria that settled into the deep basin, or that they were sulfur-oxidizing bacteria that were buried in place.

The Gamohaan Formation fossils are unlikely to be the remains of planktonic unicellular eukaryotes. The fossils are morphologically very similar to large, smooth-walled acritarchs in the form genus *Leiosphaeridia* that have been reported from the Phanerozoic and Proterozoic back to 1.8 Ga (e.g., Moczydłowska et al., 2011) and are probably eukaryotes, although acritarchs are by definition of uncertain taxonomic placement. A eukaryotic interpretation is only supported, however, when fossils possess characters that link them to crown-group eukaryotes, namely if they possess three attributes: a large size (>60 μm), surface ornamentation, and a preservable cell wall with a complex ultrastructure (Javaux et al., 2004; Knoll et al., 2006). The majority of the fossils described here, like the large organic-walled microfossils from the 3.2 Ga Moodies Group (Javaux et al., 2010), are much larger than 60 μm (Fig. 3) and have preservable cell walls, but are smooth-walled without surface ornamentation and have no discernable cell wall ultrastructure.

A cyanobacterial classification for the Gamohaan Formation fossils is possible, based on gross morphology, but unlikely. Many large, smooth-walled coccoidal cyanobacteria exist, but the largest modern forms are ≤60 μm in diameter (Desikachary, 1959), much smaller than the fossils reported here. It is conceivable, however, that stem-group cyanobacteria in the Archean grew to larger sizes and filled the niche now occupied by single-celled eukaryotic phytoplankton, but have no modern descendants.

We interpret the Gamohaan Formation fossils to be the remains of sulfur-oxidizing bacteria based on their environment of deposition, morphologies and sizes, and sulfur isotope geochemistry. Sulfur-oxidizing bacteria typically inhabit deep shelf and slope environments in anoxic and sulfidic sediments called sulfureta (e.g., Schulz et al., 1999; Kalanetra et al., 2005). Examples of fossil filamentous sulfur-oxidizing bacteria, interpreted as probable *Beggiatoa* of Miocene age (Williams and Reimers, 1983; Bailey et al., 2013) or other narrow filamentous forms of Paleoproterozoic age (Schopf et al., 2015), have been reported. The fossils described here are more similar to members of the genus *Thiomargarita*. This taxon consists of sulfur-oxidizing bacteria that grow up to 750 μm in diameter, but are typically 100 to 300 μm, and occur as either solitary cells or as a variety of colonial forms, including unconnected chains surrounded by a mucilaginous sheath (Figs. 2J and 2K; Schulz et al., 1999; Kalanetra et al., 2005; Salman et al., 2013). Both types were found amongst the Gamohaan Formation fossils, although only smaller specimens (~20–30 μm) were found in chains (Figs. 2G and 2H). Modern populations of *Thiomargarita* can include a wide range of cell sizes and morphologies as well as multiple taxa (J. Bailey, 2016, personal commun.). Measured sizes of the Gamohaan Formation fossils suggest that there could be two or more fossil taxa in the population, one <~80 μm in diameter and one >~80 μm (see Fig. 3).

Multiple-sulfur-isotope data from Gamohaan Formation pyrites collected from drill core and stratigraphically near the chert studied here support the interpretation of a thriving sulfur-cycling microbiota in the deep water of the paleobasin. Nonzero $\Delta^{33}S$ values indicate sulfur mass-independent fractionation (S-MIF) most likely caused by UV photolysis, and variable $\delta^{34}S$

values indicate redox reactions between sulfur species. Kaufman et al. (2007) reported arrays of positively correlated positive $\Delta^{33}S$ and $\delta^{34}S$ values (their samples 217.2 and 219), suggesting that sulfur-reducing bacteria converted elemental sulfur, having a positive S-MIF signal, to sulfide, which subsequently became sequestered in pyrite. Kamber and Whitehouse (2007) measured a similar array (their sample SrKu34), but with a nonzero intercept, which suggests that sulfide produced by sulfate-reducing bacteria (with significantly negative $\Delta^{33}S$ and $\delta^{34}S$ values) was re-oxidized and mixed with elemental sulfur that had positive $\Delta^{33}S$ and $\delta^{34}S$ values to produce the observed mixing trend. This scenario would require sulfide oxidizers that likely would have utilized nitrate as an oxidant, such as *Thiomargarita*, which store nitrate in a central vacuole (e.g., Kalanetra et al., 2005). Nitrogen isotope analyses of kerogen from the Gamohaan Formation suggest that biological nitrification was occurring at this time (Godfrey and Falkowski, 2009), consistent with an increasing number of studies documenting evidence of oxygen production prior to the GOE at ca. 2.4 Ga (e.g., Lyons et al., 2014). These interpretations overall suggest a complex ecosystem in place at 2.5 Ga involving multiple redox steps and multiple taxa of microorganisms, similar to sulfureta on the modern Earth and in the Paleoproterozoic. The small size (a few microns) and simple morphologies of sulfate- and sulfur-reducing bacteria make their preservation difficult, and no such objects were detected.

The fossils described here are amongst the largest fossils reported from the Archean and represent the oldest sulfur-oxidizing bacteria yet reported, which could have provided the source of sulfate for sulfate-reducing bacteria prior to significant oxygen in the atmosphere and oceans. Additional studies, including those that combine micropaleontology with in situ analyses of geochemical and isotopic proxies for microbial metabolisms, will help to further broaden our knowledge of the diversity of life on the ancient Earth. Because of the linkage between the biosphere and the composition of the atmosphere-hydrosphere, such studies can also help constrain the evolution of Earth's surface conditions by providing a test for models of atmospheric evolution, of particular importance at the Archean-Proterozoic transition and the GOE.

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