Sulfur-cycling fossil bacteria from the 1.8-Ga Duck Creek Formation provide promising evidence of evolution’s null hypothesis

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The recent discovery of a deep-water sulfur-cycling microbial biota in the ∼2.3-Ga Western Australian Turee Creek Group opened a new window to life’s early history. We now report a second such subsurface-inhabiting community from the Western Australian ∼1.8-Ga Duck Creek Formation. Permineralized in cherts formed during and soon after the 2.4- to 2.2-Ga “Great Oxidation Event,” these two biotas may evidence an opportunistic response to the mid-Precambrian increase of environmental oxygen that resulted in increased production of metabolically usable sulfate and nitrate. The marked similarity of microbial morphology, habitat, and organization of these fossil communities to their modern counterparts documents exceptionally slow (hypobradytelic) change that, if paralleled by their molecular biology, would evidence extreme evolutionary stasis.

Great Oxidation Event | microbial evolution | null hypothesis | Precambrian microorganisms | sulfur bacteria

We here describe a Paleoproterozoic marine deep-water sediment-inhabiting sulfur-cycling microbial community permineralized in cherts of the ∼1.8-Ga Duck Creek Formation of Western Australia, the second such subsurface biocenose reported from the geological record. Comparable modern communities, well studied in marine mud, are characterized by the presence of large populations of bacteria that metabolically cycle sulfate and by a low content of dissolved oxygen that, in the subsurface parts of the community, is essentially zero. Physically, they typically are composed of two regions: a quiescent subsurface anoxic zone consisting of an interlaced web-like fabric of randomly oriented and commonly exceedingly long filamentous anoxic microbes ≤10 μm in diameter and an overlying, surface-face-to-subsurface zone characterized by the presence of such large-diameter microaerophilic taxa as Thioploca and Beggiaota. Metabolically, sulfur-cycling in such ecosystems is fueled by seawater sulfate that, in the anoxic zone, is bacterially reduced to hydrogen sulfide; such sulfide can then be oxidized to elemental sulfur, either by nitrate-using anaerobes or by microaerophiles, using dissolved oxygen derived from overlying waters, and the sulfur, in turn, can be microbially oxidized to sulfate.

The Duck Creek biota is ∼500 Ma younger than the first such fossil community discovered, a sulfur-cycling microbial biocenose recently described from the Turee Creek Group Kazput Formation, also of northwestern Australia (1). Previously considered to be a cyanobacterium-dominated photic-zone assemblage (2, 3) or a deeper water community using iron-based metabolism (4), our reinterpretation of the Duck Creek biota is consistent with a proliferation of sulfur-cycling biocenoses following the upsurge of biologically available sulfate and nitrate from the ∼2.4- to ∼2.2-Ga Great Oxidation Event, the “GOE” (5). Further, the Duck Creek fossils evidence the “hypo-bradytelic” of early-evolved microbes, an exceptionally low rate of discernable evolutionary change and a term coined (6) to parallel the three other distinct rate distributions in evolution proposed in 1944 by G. G. Simpson (7) on the basis of morphological comparisons of fossil and living taxa. This striking degree of conservatism, documented initially for Proterozoic cyanobacteria (6, 8), is shown here for colorless sulfur bacteria by the marked similarities in habitat, web-like fabric, and organismal morphology and composition of the Duck Creek biota to the ∼2.3-Ga Turee Creek biocenose and modern anaerobic sulfur-cycling biotas known from subsurface sediments off the west coast of South America (9, 10).

The two mid-Precambrian communities, closely similar in all salient characteristics, differ markedly from fossil and modern photoautotroph-dominated stromatolitic/microbially mat-forming microbiotas (refs. 11 and 12, Fig. 1). The fossil filaments are also unlike modern iron-metabolizing microbes, whether Fe3+ oxidizing or Fe2+ reducing. That they are neither aerobic iron oxidizers nor anaerobic photosynthetic iron oxiders is evidenced by their anoxic subsurface habitat, discussed in Geological EVIDENCE AND PLANETARY SCIENCES.

Significance

An ancient deep-sea mud-inhabiting 1,800-million-year-old sulfur-cycling microbial community from Western Australia is essentially identical both to a fossil community 500 million years older and to modern microbial biotas discovered off the coast of South America in 2007. The fossils are interpreted to document the impact of the mid-Precambrian increase of atmospheric oxygen, a world-changing event that altered the history of life. Although the apparent 2-billion-year-long stasis of such sulfur-cycling ecosystems is consistent with the null hypothesis required of Darwinian evolution—if there is no change in the physical-biological environment of a well-adapted ecosystem, its biotic components should similarly remain unchanged—additional evidence will be needed to establish this aspect of evolutionary theory.


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The microbial biota reported here, in rocks from Duck Creek Gorge (Fig. S1), occurs in fine-grained black or mottled gray-and-black carbonaceous cherts at two localities from which fossils were first reported in 1983 (19), Precambrian Paleobiology Research Group (PPRG) samples 049–053, collected at Wyloo 1:250,000 map sheet area grid reference 436195 (latitude 22.29.208’S, longitude 116.18.886’E) and 059–062, at grid reference 459195 (lat. 22.29.213’S, long. 116.18.986’E) (20). These fossil-bearing cherts, recollected in 2012 (Fig. S1), are thin (5- to 15-cm-thick) discontinuous lenses enclosed in flat-beded buff to light brown weathered fine-grained ferruginous dolostone (20).

Although peritidal stromatolites occur in this stratigraphically upward-deepening sedimentary succession (4, 20), the cherts and their encompassing carbonates do not contain such shallow-water indicators as stromatolites, interclasts, cross-lamination, ripple marks, mud cracks, or other desiccation features. The position of the fossiliferous strata in the well-documented sequence stratigraphy of the Duck Creek strata (4) substantiates their deposition in a relatively deep-water facies of the marine basin.

Like the fossil-containing cherts of the ~2.3-Ga Turee Creek Group (1), we interpret those of the ~1.8-Ga Duck Creek Formation to have formed beneath storm wave base and likely subphotic zone. The fossil-bearing chert lenses of the two units are similar: In both, they occur in deeper water regions off distally steepened carbonate ramps (1, 4); are dominantly sub-parallel to the bedding of encompassing carbonates but locally pinch, swell, and transgress bedding planes, attributes supporting their subsuelfloor formation; and contain carbonate thrombolites and microcrystalline quartz and microbes preserved before cellular disintegration that indicate the lenses to be early diagenetic replacements of carbonate marls.

Microbial Composition and Physiology. The distinctive, irregular web-like fabric of the Duck Creek biota differs markedly from the layered structure of Precambrian phototroph-(cyanobacterium-) dominated stromatolitic communities (8, 21) but is indistinguishable from that of the ~500-Ma-old Turee Creek Group sulfur-cycling biota (Fig. 1). In both units, random meshworks of microbial filaments enclose ellipsoidal domains of clear quartz interpreted to represent replaced anhydrite (1). Similarly, the dominant microbial components of the two assemblages are essentially identical: relatively large diameter (7-8 to 9-μm-broad) elongate-celled filaments (Fig. 2 B–D and F–H), smaller diameter (~1- to 4-μm-wide) filaments composed of bead-shaped cells (Fig. 2 L–U), and very narrow (≤1-μm-diameter) thread-like cellular filaments (Fig. 3 D–I)—morphotypes that differ from phototrophic cyanobacteria (6, 10, 11) but closely resemble principal components of the anoxic subsuelfloor parts of modern sulfur-cycling communities (9, 10) off the western coast of South America (Figs. 2 and 3), modern communities that exhibit an irregular web-like fabric similar to that of the fossil assemblages (compare Fig. 1 A–F with figure 10 in ref. 10) in which many of the “bead-celled” filaments contain sulfur granules (ref. 10, figures 6 and 7), products of anaerobic sulfide oxidation. Moreover, in all three communities—the Duck Creek, Turee Creek, and modern sulfur-cycling biotas—the randomly interlaced microbial filaments that comprise their web-like fabric (refs. 1, 10, and 15, Fig. 1) can be exceedingly long (Figs. 2 A–D and N–R and 3 D–F), more than a thousand microns in length, lengths not recorded in wave-agitated photic-zone stromatolitic assemblages that further evidence a physically quiescent subsuelfloor environment.

Morphometric comparison of the principal components of the fossil and modern sulfur-cycling communities with oscillatoriae cyanobacteria, the dominant microorganisms of photic-zone stromatolitic/mat-forming assemblages, documents their dissimilarity (11, 12). The broadest of the fossil sulfur bacteria are ~8 μm in diameter, composed of 12- to 15-μm-long cells. Such dimensions are highly unusual for cyanobacteria. Of 436 taxa of modern oscillatoriaeans analyzed, only two (<1%) have similar dimensions (11), and of 94 taxa of septate unbranched...
filaments reported from 69 Proterozoic geological units, only one
(Partitiofilum tungusum), preserved in a photic-zone intertidal
setting unlike that of the fossil sulfur bacteria, is morphometri-
cally comparable (11, 12). Similarly, the ~1- to 4-μm-wide bead-
celled fossil filaments are of appreciably smaller diameter than
Nostoc or other morphologically comparable cyanobacteria and,
unlike many such taxa, are enclosed by a prominent cylindrical
sheath and lack heterocysts and akinetes (Fig. 2 L–U); and the
≤1-μm-diameter and commonly exceedingly long thread-like
fossil bacteria are morphometrically decidedly unlike cyanobac-
teria, both fossil and modern (11, 12).

For extant prokaryotes, phylogenetic relations and physiolog-
ical characteristics can be determined by molecular biology
backed by growth experiments. For fossil communities, however,
the biomolecules required (DNA, rRNA, enzymes, etc.) have
been lost during preservation. Thus, analyses of fossil commu-
nities such as those described here must rely on evidence pro-
vided by proxies—the morphometrics of the preserved fossils
backed by studies of their regional and local geological setting
and their paleoecology and community fabric.

On the basis of such proxies and the notable similarities in
habitat, fabric, and microbial composition of the fossilized bio-
coenos of the ~1.8-Ga Duck Creek and ~2.3-Ga Turee Creek
to the anoxic zone of modern sulfur-cycling communities, we
interpret the Duck Creek fossils to represent an anoxic sediment-
inhabiting sulfur bacterial bioeno like that of their modern
counterparts in which marine sulfate is microbially reduced to
H₂S that, by use of nitrate, is then anaerobically oxidized to el-
emental sulfur and subsequently to sulfate (9, 10, 22).

This interpretation is supported by δ³⁴S (~ Vienna Canyon Diablo Troilite, VCDT) values determined by secondary ion mass spectroscopy (SIMS) analyses of Duck Creek pyritized filaments and associated py-
rite, 66 measurements that span a range of >50‰, from ~9.4
to +43.4‰ (Fig. S2 and Dataset S1). Of these, values mea-
sured on individual Duck Creek pyritized fossils are typically
~40‰ (Fig. 4). The most plausible explanation for the broad
range and virtually uniformly positive δ³⁴S values of the Duck
Creek pyrite (Dataset S1) is the precipitation of pyrite by sul-
fate-reducing bacteria in an environment exhibiting very low
seawater sulfate concentrations, like that indicated for other
Proterozoic units of comparable age (23), in a relatively closed
subseafloor system where microbial sulfur cycling would have
been prevalent and/or at a rate similar to that of the diffusion of
marine sulfate into the zone of its reduction. Under such con-
ditions, the microbially precipitated pyrite would have the same
or similar δ³⁴S as the metabolized seawater sulfate, indicating that
the maximum value measured (43.4‰; Fig. 4 and Dataset S1)
Fig. 4. Sulfur isotopic SIMS δ34S values analyses of Duck Creek pyrite. Back-scattered electron images of pyritic filaments (A–C) and framboidal pyrite (D) (M.R.W. collection 12.06.18.2, compare PRPG samples 049–053). The insets in A–C, acquired by combined transmitted and reflected light, show filaments plugging beneath the thin section surface; arrows point to SIMS analytical pits.

approximates the δ34S of mid-Precambrian oceanic sulfate (see SI Text, Fig. S2, and Dataset S1).

Paleooecology. Although data summarized above indicate that both the ~1.8-Ga Duck Creek and ~2.3-Ga Turee Creek fossiliferous cherts are benthic and subseafloor, evidently formed beneath storm wave base and likely subphotic zone, there is no reliable geologic index to establish quantitatively their bathymetric setting. Nevertheless, their formation in such an environment is consistent with and supported by both positive and negative evidence.

Positive evidence indicating the fossil assemblages to be subseafloor include the following: Regional geology, sequence stratigraphy, local geology, disposition of the fossil-bearing beds, paleoecologic setting, fabric of the fossiliferous cherts, morphology of the fossils, sulfur isotope data showing the prevalence of strictly anaerobic sulfate reducers in a restricted environment, and the community composition and one-to-one comparison of the morphology of the fossil microbes to principal components of extant anaerobic subseafloor sulfur-cycling communities.

Negative evidence indicating the fossil assemblages not to be shallow-water photrophic include the following: Regional and local geology (namely, sequence stratigraphy, lack of shallow-water indicators, and the fine-grained petrology of associated carbonates and their lack of clastics), morphometrics of the fossils documenting their dissimilarity from coeval shallow-water photic-zone phototrophs, and sulfur isotope data establishing the prevalence of anaerobic sulfate reducers.

Other lines of evidence further support interpretation of the Duck Creek biota as a sulfur-cycling mud-inhabiting community of anaerobic microbes: (i) Global models suggest that subsurface water masses of the latest Paleoproterozoic were essentially anoxic and in some regions sulfidic, evidenced in the rock record by pyritic shales (23–25). (ii) The fossiliferous Duck Creek chert locally contains copious authigenic pyrite, some encrusting microbial filaments, and a firm indicator of local anoxic conditions (Fig. S3). (iii) The Duck Creek biota, like others of similar age (1, 26–29), contains the asteroﬁrm microbe Eosaurus (Figs. S4 and S5) that closely resembles modern Metallogenium, a planktonic microaerophile that inhabits the hypolimnion, where it

precipitates MnO2, Fe2O3, and TiO2 in a dysoxic environment (30), encrustations like those of Duck Creek specimens (Fig. S4). (iv) Present also in the Duck Creek (Fig. S4) and other Paleoproterozoic biotas (1, 26–29, 31, 32) are Huroniospora-like unicells morphologically comparable (33) to the free-swimming (34) modern microaerophilic sulfur bacterium Thiouvalum that, like Metallogenium, the modern counterpart of Eosaurus, inhabits the oxic–anoxic interface and, as previously interpreted (26), a planktonic microbe evidently deposited from overlying waters. (v) The Duck Creek assemblage, like that of the older Turee Creek biocoenose (1), lacks large-diameter filamentous microbes morphologically comparable to microaerophilic “megabacteria” such as Beggiatoa, present in modern sulfur-cycling biota at the sediment–water interface, and Thioploca, an extensive sulfur cyclers that commonly penetrates into underlying anoxic mud (22, 35, 36). The single large-celled partial filament reported from the Duck Creek chert is regarded as possibly cyanobacterial and allochthonous (3), an interpretation suggesting that sulfur-cycling megabacteria may have been of later origin.

Discussion

In the aftermath of the ~2.4- to ~2.2-Ga GOE, it is likely that surface waters of the Duck Creek basin were at least weakly oxic (37–40). The increase of atmospheric oxygen at the GOE would have increased the abundance not only of seawater sulfate (5, 25)—precursor of the bacterially generated H2S that, despite competition for reaction with dissolved ferrous ion, would have produced local sulfidic regions (38, 39) that may have promoted the spread of sulfur-cycling communities—but also of nitrate, “oxygen” oxidized of the upper parts of the oceans almost certainly [being] accompanied by a shift in the marine chemistry of nitrogen from NH4+–dominated to NO3−–dominated (ref. 5, pages 3820–3821) with “a complete nitrogen biogeochemical cycle [being] established by about 2.0 Ga” (41, p. 349). Such nitrate, diffusing from overlying waters into subseafloor sediments, would have served to fuel anaerobic oxidative phosphorylation in the anoxic zone of sulfur-cycling communities. The GOE-spurred increase of H2S may also have affected photic-zone communities where it would have been consumed by associated sulfur cyclers, by anoxicogenic photosynthetic bacteria, and by cyanobacteria capable of facultative (anoxicogenic or oxygenic) photosynthesis (42).

Thus, we interpret the microbial biotas of the Turee Creek and Duck Creek cherts to reflect an opportunistic response to the GOE, an interpretation consistent with the metabolic and biosynthetic pathways of modern microbes as well as fossil evidence suggesting the immediately post-GOE appearance of oxygen-protective mechanisms in nostocalean cyanobacteria and the advent of obligately aerobic eukaryotes (43).

How could the seemingly identical sulfur-cycling anoxic sediment-inhabiting biotas of the ~1.8-Ga Duck Creek and ~2.3-Ga Turee Creek cherts, like those of Proterozoic stromatolitic cyanobacteria (6, 8), have evidently remained fundamentally unchanged over billions of years?

We suggest differing answers for these two early-evolved hypobradietic lifestyles:

i) For cyanobacteria, the answer evidently lies in a genetically encoded ecological flexibility derived from their early adaptation to geologically exceedingly slow changes of the photic-zone environment (e.g., of solar luminosity, UV flux, day length, and CO2, O2, and usable sulfur and nitrogen). Because of their large population sizes, global dispersal by ocean currents and hurricanes, and capability to generate oxygen toxic to anaerobic competitors for photosynthetic space, these ecologic generalists adapted to and survived in a wide range of habitats (6).

ii) Once subseafloor sulfur-cycling microbial communities had become established, however, there appears to have been little
or no stimulus for them to adapt to changing conditions. In their morphology and community structure, such colorless sulfur bacteria—inhabitants of relatively cold physically quiescent anoxic sediments devoid of light-derived diel signals and a setting that has persisted since early in Earth history—have exhibited an exceedingly long-term lack of discernable change consistent with their asexual reproduction (6).

Given these observations, it might be tempting to interpret such sulfur-cycling communities as evidencing the “negative” null hypothesis of Darwinian evolution—if there is no change in the physical-biological environment of a well-adapted ecosystem, there should be no speciation, no evolution of the form, function, or metabolic requirements of its biotic components—a confirmation of Darwin’s theory that seems likely to be provided only by ecosystems fossilized in an environment that has remained essentially unaltered over many hundreds of millions of years.

Although logically required, this aspect of evolutionary theory has yet to be established. Unlike stromatolitic cyanobacteria-dominated biocoenoses, for which evolutionary conservatism has been documented by comparison of more than 120 fossil species and some 24 modern genera in scores of deposits investigated by many workers (6), comparison of fossil sulfur-cycling communities with the anaerobic components of their modern analogs is based only on the two fossil assemblages described here and the subseafood microbes of modern communities off the west coast of South America (9, 10), none of which has received detailed morphometric, taxonomic, and systemic evaluation.

Moreover, and although, like Simpson’s classic rate distributions of evolution (7), the morphology-based “concept of hypobradytely does not necessarily imply genomic, biochemical, or physiological identity between modern and fossil taxa” (6, page 6736), a claim of extreme evolutionary stasis—a lack of speculation over billions of years—would be strengthened not only by discovery of additional fossil communities but by firm evidence of their molecular biology. Although speculation-based evolution occurs at the phenotypic rather than genotypic level of biologic—environmental interaction, the biomolecules underlying such change are not preserved in the rock record in which such assessment can be based only on indirect proxies and inferences of physiology based on isotopic analyses.

For cyanobacterial communities, such problems have been overcome by nearly 50 y of studies that have documented their evolutionary conservatism in many deposits and scores of taxa belonging to diverse cyanobacterial families. In addition, their hypobradytic evolution is evidenced by numerous proxies—not only the habitat, community fabric, cellular morphology, and isotopic composition of preserved microbes but also their taphonomy, patterns of cell division, modes of colony and filament formation, inferred behavior, and the structure and form of the distinctively layered millimetric to decimetric photic-zone stromatolites and bioherms they produce (e.g., refs. 6, 19–21, 26–31, and 44). A comparable array of data are not available for sulfur-cycling bacteria.

Finally, unlike cyanobacteria for which “essentially all of the salient morphological features used in the taxonomic classification of living cyanobacteria can be observed in well-preserved fossils” (45, page 453), sulfur-cycling bacteria are classified primarily on the basis of their (geologically unpreservable) genomic composition. Moreover, large-diameter (“giant”) sulfur bacteria of differing phylogenetic lineages can exhibit similar morphologies and patterns of behavior suggesting convergent evolution of morphologic “look-alikes” adapted to a same or similar function (46, 47).

Although it remains to be established whether such morphological “mimicry” is exhibited also by the more narrow ≤10-μm-diameter sulfur bacteria described here—the two modern sulfur bacterial taxa of similar dimensions being aerobes (ref. 46, table 2) rather than anaerobes like the Duck Creek and Turee Creek fossils—it remains conceivable that the marked similarities between the two mid-Precambrian communities and their modern counterparts could be an example of the so-called Volkswagen Syndrome, a lack of change in organismal form that masks the evolution of internal biochemical machinery (6).

We regard it likely that ancient subseafood microbial biocoenoses will be discovered to fill the gap between the mid-Precambrian and the present and that these communities will be fundamentally similar in their form, function, and metabolic requirements to those of the Duck Creek and Turee Creek cherts. Such findings may eventually be regarded as having confirmed the null hypothesis required of Darwinian evolution, but such an assessment would be, at present, premature.

Methods

Optical Microscopy and Raman Spectroscopy. Optical studies of all specimens, embedded in petrographic thin sections, were performed using standard techniques. Raman analyses of these specimens were acquired by use of a triple-stage laser-Raman system that has macro-Raman and confocal micro-Raman capabilities (for details, see SI Methods and ref. 48).

Secondary Ion Mass Spectroscopy. Pyritic specimens were analyzed in petrographic thin sections using newly developed sample holders that provide high precision and accuracy for targets within 8 mm (in comparison with 5 mm for standard sample holders) of the center of the specimen-containing discs (see SI Methods for details).

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10. Gallardo VA, Espinoza C (2007) Large multicellular filamentous bacteria under the basis of their (geologically unpreservable) genomic composition. Moreover, large-diameter (“giant”) sulfur bacteria of differing phylogenetic lineages can exhibit similar morphologies and patterns of behavior suggesting convergent evolution of morphologic “look-alikes” adapted to a same or similar function (46, 47).


