A Proposal for Formation of Archaean Stromatolites before the Advent of Oxygenic Photosynthesis

John F. Allen *

Research Department of Genetics, Evolution and Environment, University College London, London, UK

Stromatolites are solid, laminar structures of biological origin. Living examples are sparsely distributed and formed by cyanobacteria, which are oxygenic phototrophs. However, stromatolites were abundant between 3.4 and 2.4 Gyr, prior to the advent of cyanobacteria and oxygenic photosynthesis. Here I propose that many Archaean stromatolites were seeded at points of efflux of hydrogen sulfide from hydrothermal fields into shallow water, while their laminar composition arose from alternating modes of strictly anoxygenic photosynthetic metabolism. These changes were a redox regulatory response of gene expression to changing hydrogen sulfide concentration, which fluctuated with intermittent dilution by tidal action or by rainfall into surface waters. The proposed redox switch between modes of metabolism deposited sequential microbial mats. These mats gave rise to alternating carbonate sediments predicted to retain evidence of their origin in differing ratios of isotopes of carbon and sulfur and in organic content. The mats may have arisen either by replacement of microbial populations or by continuous lineages of protocyanobacteria in which a redox genetic switch selected between Types I and II photosynthetic reaction centers, and thus between photolithoautotrophic and photoorganoheterotrophic metabolism. In the latter case, and by 2.4 Gyr at the latest, a mutation had disabled the redox genetic switch to give simultaneous constitutive expression of both Types I and II reaction centers, and thus to the ability to extract electrons from manganese and then water. By this simple step, the first cyanobacterium had the dramatic advantage of emancipation from limiting supplies of inorganic electron donors, produced free molecular oxygen as a waste product, and initiated the Great Oxidation Event in Earth's history at the transition from the Archaean to the Paleoproterozoic.

Keywords: cyanobacteria, redox regulation, Great Oxidation Event, boring billion, proterozoic, protocyanobacterium, redox switch hypothesis, two-component regulatory systems

THE PROBLEM: STROMATOLITES A BILLION YEARS BEFORE THE CYANOBACTERIA THAT MAKE THEM

Stromatolites today are unusual features of shorelines. They grow typically in anoxic, shallow, hypersaline waters (Figure 1) and are constructed by microbial communities whose primary producers are cyanobacteria. In the pre-Cambrian Palaeozoic and Archaean eons, stromatolites were much more abundant than today, took on a wide variety of sizes and morphologies, and built
massive reefs of sediments whose organic and inorganic carbon isotopic signatures suggest large-scale solar energy conversion with primary productivity comparable with that seen today in coral reefs (Bosak et al., 2013).

Archaean stromatolites are an anomaly. If cyanobacteria had yet to appear, what made them? There is clear and multiple, independent lines of evidence that the Earth's oceans and atmosphere were anoxic for roughly half its history, that is, until 2.4 Gyr (Knoll et al., 2016). Oxygen-evolving photosynthesis then emerged from anoxygenic photosynthesis with the advent of cyanobacteria – the only oxygenic phototrophic prokaryotes (Schopf, 2011). Nevertheless stromatolites comprise exposed sediments, notably in South Africa and Western Australia, that are dated unambiguously up to at least a billion years before the start of the rise in atmospheric oxygen concentration (Hofmann et al., 1999; Allwood et al., 2006; Nutman et al., 2016). It has been considered that cyanobacteria may have first emerged during the early or mid-Archaean, giving “whiffs of oxygen” (Holland, 2006; Summons et al., 2006). However, the abundance of Archaean stromatolite coastal reefs (Schopf et al., 2007; Bosak et al., 2013) is likely to reflect abundant photosynthetic microbial activity that could be expected to have created a much earlier Great Oxidation Event if cyanobacteria alone had been responsible.

**HYPOTHESIS: LAMINAR MICROBIAL MATS FROM ALTERNATING MODES OF METABOLISM**

Oxygenic photosynthesis appeared with the first cyanobacterium (Fischer et al., 2016). Photosynthetic oxygen production always requires two, connected photosystems (Nelson and Junge, 2015). Photosystem I uses light energy at its primary photochemical reaction center to oxidize a chlorophyll molecule that donates its electron to a series of iron–sulfur proteins (Fromme et al., 2001; Amunts et al., 2007), and then on to coupled assimilatory metabolism such as the Benson-Calvin cycle of CO$_2$ fixation. In contrast, the oxidized chlorophyll of the photosystem II reaction center passes its electron to a pair of quinone molecules (Nitschke and Rutherford, 1991; Brinkert et al., 2016). The photooxidised chlorophyll of photosystem II is reduced by electrons from water (Umena et al., 2011; Shen, 2015; Ho et al., 2016). Oxidation of two water molecules by transfer of four electrons releases one molecule of oxygen. Photosystem I and photosystem II have homologs in the single, separate photosystems of anoxygenic photosynthetic bacteria, each with either a Type I or a Type II photochemical reaction center (Figure 2), while it is clear that Types I and reaction centers are themselves homologous (Schubert et al., 1998) –

**FIGURE 1 | Stromatolites at Hamelin Pool, Western Australia, 4 October 2007.** Photograph kindly provided by Dr. Catherine Colas des Francs-Small.
related by descent from a common ancestor. For the origin of oxygenic photosynthesis, the reaction centers of two independent photosystems must have become connected, electrically in series, to allow two separate light reactions (Hill and Bendall, 1960) to transfer electrons from water to the iron–sulfur acceptors that supply electrons at low redox potentials to assimilatory reactions (Hohmann-Marriott and Blankenship, 2011) (Figure 3).

One proposal for the way in which this close coupling began is that genes for each of the two reaction centers, Types I and II, were present as alternatives in a versatile, anoxygenic photosynthetic bacterium termed the “protocyanobacterium” (Allen, 2005; Allen and Martin, 2007).

Photosynthesis is a light-driven redox reaction that can be supported by any of a variety of electron donors (sources) and acceptors (sinks). Archaean electron donors included hydrogen, ferrous iron, and hydrogen sulfide, each varying in availability with time and location (Bosak et al., 2013). Major Archean electron acceptors were carbon dioxide and nitrogen gas, as today, but not oxygen.

The overall process of photosynthesis as light-driven electron or hydrogen transfer to CO₂ is summarized in the van Niel equation (1) (Van Niel, 1954):

\[ 2H₂A + CO₂ \xrightarrow{\text{light}} CH₂O + H₂O + 2A \]  

Where H₂A is an electron donor, A is its oxidation product, and CH₂O represents sugars, organic products of CO₂ fixation. H₂A can be inorganic, giving photolithotrophy, or organic, giving photoorganotrophy. Oxygenic photosynthesis is the special case of photolithotrophy where H₂A is H₂O and 2A is O₂. Anoxygenic photosynthesis today typically relies either on inorganic donors, as seen in green and purple sulfur bacteria, which are obligate anaerobes, or on organic donors, as seen in green and purple non-sulfur bacteria, which today can often tolerate oxygen, but not while remaining phototrophic.

It should be noted that CO₂ is an assimilatory substrate and not a direct electron acceptor for photosynthesis, and the van Niel equation (1) can be regarded as the sum of two half reactions, (2)
The reduction of ferredoxin drives eventual assimilation of CO$_2$ together with coupled synthesis of ATP. Photosynthetic electron transport is coupled to proton translocation through the cytochrome $b$-$f$ complex. Light-driven transmembrane electron transport is vital for photosynthesis. Photosynthesis can be oxygenic, where oxygen is released, or anoxygenic, where oxygen is not produced.

### Table 1: Characteristics of oxygenic and anoxygenic photosynthesis.

| Oxygenic photosynthesis | Anoxygenic photosynthesis |
|-------------------------|---------------------------|
| Light-driven transmembrane electron transfer | Light-driven transmembrane electron transfer |
| Coupled to proton translocation | Coupled to proton translocation |
| Including a proton-motive Q-cycle through a cytochrome $b$-$f$ complex | Including a proton-motive Q-cycle through a cytochrome $b$-$c_1$ complex |
| Two photosystems or “light reactions”: Type I (PS I) and Type II (PS II) | One photosystem or “light reaction” of either Type I or Type II. |
| Includes non-cyclic electron transport pathway with H$_2$O as the initial electron donor | Non-cyclic electron transport pathway with inorganic electron donors (e.g., H$_2$S, Fe$^{2+}$, H$_2$O, or organic electron donors) |
| Special case of the van Niel equation | Other special cases of the van Niel equation |
| Carbon dioxide fixation by the Benson–Calvin pathway (a.k.a. reductive pentose phosphate pathway) | Carbon dioxide fixation by the Benson–Calvin pathway (a.k.a. reductive pentose phosphate pathway) OR by other pathways such as the “reverse” (i.e., reductive) TriCarboxylic Acid cycle |
| Makes oxygen | Inhibited by oxygen |
| In cyanobacteria and chloroplasts | In purple and green photosynthetic bacteria, and heliobacteria |
| Resulted in the Great Oxidation Event; oxygen-rich atmosphere and eventually oceans; aerobic respiration; ozone layer and life on land; end of MIFS and BIFS from Fe$^{3+}$→Fe$^{2+}$; N as nitrite/nitrate; S as sulfide/sulfate; eukaryotes; multicellularity | Resulted in increased biomass in coastal microbial mats and stromatolites as free energy input from sunlight added to geochemical sources. |
| Appeared at the Archaean to (paleo)proterozoic boundary (~2.5 Gyr) or earlier if “whiffs of O$_2$” are real and a signature | Appeared early in the Archaean eon from 3.8 Gyrs |
was lower, and facultative Type I–Type II photosynthesis can be envisaged as an optimal growth strategy where supplies of an inorganic electron donor varied. One reason for this variation may have been the cyclic depletion of Fe²⁺ when insoluble Fe³⁺ salts were formed, thus giving rise to the banded iron formations seen throughout the Archaean and well into the Proterozoic. Fe²⁺ depletion could also have arisen where H₂S was in excess of Fe, giving FeS and FeS₂ (pyrite). However, when Fe³⁺ ran out, and, in any case, in shallow waters above hydrothermal fields, hydrogen sulfide derived ultimately from magma would have been introduced at specific points, and along fissures, in the bedrock, and would have been available an electron donor both by sulfur bacteria and by the protocyanobacteria. The competitive advantage of the protocyanobacteria would have been maintenance of populations of cells with their core metabolisms and genetic systems always in place. It is thus possible that protocyanobacteria contributed to the massive stromatolite and microbialite reefs laid down before, after, and across the Archaean-Proterozoic boundary.

Observations on the Strelley Pool formation of the Pilbara Craton in Eastern Australia shows that stromatolites were abundant at 3.4 Gyr (Wacey, 2010), and their distribution coincides spatially with hydrothermal venting as judged by lithography and with the presence of sulfur isotopes in both organic (kerogen) and inorganic (carbonate) stromatolite composition (Sugitani et al., 2015). The proposed process of stromatolite building as H₂S supply fluctuated is outlined schematically in Figure 5. Figure 6 provides a context for hydrothermally derived columnar stromatolites built by influx of H₂S.

PREDICTIONS OF THE HYPOTHESIS

1. Location of Stromatolites
In contrast to the first bacteria and archaea, and to microbiota growing in the vicinity of submarine hydrothermal vents, all of which were chemoautotrophic, by the Archaean extensive microbial growth had become dependent on photosynthesis, and required sunlight. Depending on solutes and turbidity, water transmits light only to limited depths at wavelengths and flux densities that can be used by photosynthesis (Falkowski and Raven, 2007). Thus stromatolites grew in shallow water, and became abundant where large surface areas were exposed to sunlight, typically adjacent to shorelines or in river estuaries.

2. Coincidence of Individual Stromatolites with Hydrothermal Outlets
Where H₂S was the photosynthetic electron donor, photolithoautotrophic growth would have been favored at precise locations where H₂S flux gave rise to optimal steady-state concentrations, that is, in the vicinity of sources of H₂S from hydrothermal activity. Such coastal hydrothermal fields supported microbial communities and stromatolite formation at 3.4 Gya as seen in the Strelley Pool Formation, Pilbara Craton, Western Australia (Sugitani et al., 2015). Fractured rock in hydrothermal fields is predicted to have given a specific spatial pattern of seeding or initiation of stromatolite growth, corresponding to the pattern of entry to dissolved H₂S into the water. It is therefore proposed that each individual Archaean stromatolite column can be assigned to an individual channel or fissure in the field’s bedrock.
3. Delta $^{13}$C Variation with the Frequency of Stromatolite Laminae

Enzyme-catalyzed reactions discriminate in favor of lighter isotopes of elements in substrates. $^{13}$C is about one percent of total carbon on Earth, the rest being $^{12}$C. Photoautotrophic growth thus preferentially assimilates $^{12}$CO$_2$ into organic products. The greater the number of enzymatic steps involved, the greater the depletion of $^{13}$C in the photosynthate, as illustrated today by the differing isotopic compositions of C$_3$ and C$_4$ crop plants (von Caemmerer et al., 2014). If stromatolite laminae were formed by alternating phases of autotrophic and heterotrophic growth, then the delta-$^{13}$C composition of the organic material should fluctuate and be expected to be lowest in the heterotrophic layers, reliant on metabolic reactions additional to those of the preceding, primary carboxylation step of CO$_2$ assimilation. Photoautotrophically obtained carbon in alternate laminae will show a lower delta-$^{13}$C than that of the surrounding environment. A clear pattern is also to be expected of increased $^{13}$C in carbonates precipitated from the surrounding medium. These would be richest in $^{13}$C where they had selectively been depleted of $^{12}$C by CO$_2$ assimilation, while showing evidence of re-enrichment with $^{12}$C from the environment during the heterotrophic phase of growth.
4. Delta $^{34}$S Variation with the Frequency of Stromatolite Laminae

The same logic applies to predicted sulfur isotopic signatures, where negative relative values of the ratio $^{34}$S/$^{32}$S are taken to indicate a biological origin. Large negative $^{34}$S/$^{32}$S values are reported for bulk barite (barium sulfate) deposits in chert of the Dresser formation (Philippot et al., 2007). These values could be predicted to have arisen from an H$_2$S-oxidizing, Type I photosynthesis, where the initial enzyme-catalyzed reaction is that of sulfide-quinone oxidoreductase (Arieli et al., 1994). If the biological mass fractionation of sulfur isotopes arose from alternating photolithotrophy and photoautotrophy, giving stromatolite laminae by a process as depicted in Figures 5 and 6, then, given sufficient spatial resolution, negative delta $^{34}$S excursions in products of lithotrophic growth should be coincident with negative delta $^{12}$C excursions reporting autotrophy.

For both predictions 3 and 4, above, mass spectroscopy of Archaean stromatolite laminae nanometer-scale resolution (Lepot et al., 2008) may be required. Laminae can be as thin as a millimeter (Bosak et al., 2009), arguing for relatively transient deposition of sequential layers of microbial biomass.

THE HYPOTHESIS EXTENDED TO PROTOCYANOBACTERIA AND THE REDOX SWITCH HYPOTHESIS FOR THE ORIGIN OF OXYGENIC PHOTOSYNTHESIS

Each of the predicted observations 1–4, above, might be explained by cyclical replacement of anoxygenic microbial mats each composed of either sulfur (Type I) or non-sulfur (Type II) photosynthetic bacteria. However, another possibility is that one type of protocyanobacterium predominated and left signatures of alternating modes of metabolism supported by one genome containing genes for both Types I and II reaction centers. The advantage of this special case of the hypothesis is that it allows us to envisage simple steps from anoxygenic to oxygenic photosynthesis, a profound evolutionary transition otherwise lacking clear explanation supported by observation. The late Archaean abundance of the protocyanobacterium and its proposed role in the onset of the GOE makes further predictions 5–7, as follows.

5. Manganese Oxidation and Deposition As Precondition to the Emergence of the First Water-Splitting Enzyme Liberating Oxygen and Feeding Electrons to Photosystem II

Photosystem II abstracts four electrons from two water molecules, yielding one oxygen molecule. It does this by accumulating four positive changes in an inorganic prosthetic group of four manganese atoms, one calcium, and five oxygen atoms (Umena et al., 2011). A Type II reaction center oxidizing manganese seems likely to have been a precursor of the oxygen-evolving photosystem II reaction center (Khorobrykh et al., 2013) and might itself have evolved from a Type II reaction center capable of oxidizing chlorophyll $a$ to chlorophyll $f$ (Ho et al., 2016). A sequence of manganese carbonate from the Koegas Subgroup, Kaapvaal Craton, South Africa is reported at 2.41 Gyr, when free oxygen is reported to have been absent (Johnson et al., 2013). The bacterium that deposited manganese may have done so as a result of the first coupling of Types II and I reaction centers, and only later could higher oxidation states of manganese become re-reduced by water (Allen, 2014; Fischer et al., 2016). When this happened, environmental manganese would have ceased to be a substrate for lithotrophy, and manganese became obligatory as a catalyst of water oxidation, to be sequestered and conserved. It is possible that minerals such as hollandite with a unit cell resembling the water-oxidizing cluster of photosystem II accumulated from such biological concentration and deposition (Russell et al., 2008).

6. Persistence of Living Protocyanobacteria with Genes for Types I and II Reactions Centers

The redox switch hypothesis (Allen, 2005) rests on the assumption of an anoxygenic phototroph as an immediate precursor of the first true two-light reaction phototroph, whether the latter oxidized environmental manganese directly, or water by means of a derived manganese catalyst (Allen and Martin, 2007; Russell et al., 2008). It could be argued that the protocyanobacterium was out-competed and displaced by the cyanobacteria to which it gave rise, and eventually became extinct. There are, however, specialized environments today where a fluctuating supply of hydrogen sulfide into an anoxic, photic water column would confer a selective advantage upon growth by means of a single photosystem, where the quantum yield is twice that of growth requiring two light reactions. Facultatively oxygenic Oscillatoria species, including Oscillatoria limnetica, are today oxygenic in the absence of H$_2$S but switch in the presence of H$_2$S to a Type I-only photosynthesis (Oren and Padan, 1978). If an Oscillatoria species were to retain the capacity for photoheterotrophic growth using a photosystem II depleted of water-oxidizing complex then its quantum requirement (of four) would be lower in both of its modes metabolism than a that (of eight) of a regular cyanobacterium. The protocyanobacterium would be better adapted than cyanobacteria to growth at low light intensity. It seems worth looking for Type I–Type II versatile phototrophs in anoxic, low-light environments with variable concentration of dissolved H$_2$S. Stromatolite formation by anoxygenic photosynthesis may have continued through the Proterozoic (Johnston et al., 2009), gradually becoming displaced by facultative, oxygenic photosynthesis in cyanobacteria resembling extant Oscillatoria species.
7. Persistence of Living Protocyanobacteria with a Recognizable Redox Genetic Switch

Cyanobacteria (Ashby and Houmard, 2006) and bacteria in general (Stock et al., 2000) respond to environmental change by means of two-component regulatory systems. These systems consist of a histidine sensor kinase that transfers a phosphoryl group to a response regulator if, and only if, a specific environmental change occurs. The response regulator controls gene expression, usually though not exclusively at the level of transcription, in such a way as to bring about a change that better adapts the organism to its changed environment. Redox state of electron carriers responds rapidly to relevant environmental changes, and redox sensor kinases (Allen, 1993) are known to regulate photosynthetic gene transcription in cyanobacteria (Li and Sherman, 2000) and chloroplasts (Puthiyaveetil et al., 2008). A two-component redox genetic switch has been characterized that selects between transcription of photosystems I and II reaction center apoproteins in both chloroplasts (Pfannschmidt et al., 1999) and cyanobacteria (Ibrahim et al., 2016a). A protocyanobacterial version of this system, centered on the conserved Histidine Kinase 2 (Ibrahim et al., 2016b), could govern transcription of Types I and II reaction center genes and underlie the metabolic adaptability of the proposed protocyanobacterium. A simple mutation that impairs the switch could have been the beginning to two photosystems functioning simultaneously and in series (Allen, 2005, 2014).

DISCUSSION

Throughout Earth’s history, its crust, lithosphere, hydrosphere and atmosphere have undergone immense changes in overall composition (Nisbet and Sleep, 2001), while environments for life have been dynamic on a wide range of time scales (Allen, 1998). Life’s capacity to adapt is one of its defining features (Allen, 2010) making regulation at the boundary of internal and external environments coincident with mechanisms of nutrient exchange and energy transduction; a requirement for life’s origin (Mitchell, 1957; Sousa et al., 2013). By the Archaean the planet’s surface had separated into solid, liquid, and gaseous phases – into land and sea sharing a turbulent atmosphere. Tidal action, evaporation and precipitation would have created varying concentrations of solutes, notably at shore-lines and in rock pools, lakes, and rivers. When photosynthesis began to supply an input of free energy, itself varying diurnally and seasonally, then shallow waters, the euphotic zones, are most likely to have become locations of the greatest biological activity and primary productivity.

Here I suggest that alternating Types I and type II photosynthesis is a plausible mechanism for the seeding (Figure 5) and growth (Figure 6) of stromatolites, such as those recorded in Archaean stratigraphy, in the absence of cyanobacteria. It is further suggested that this type of versatile phototrophic growth occurred in single lineages of a protocyanobacterium that was a natural precursor of the first oxygenic cyanobacteria. The single step from Type I-OR-Type II photosynthesis to Type I-AND-Type II photosynthesis gave rise to two-light reactions, water-oxidizing, oxygenic photosynthesis (Allen, 2005; Allen and Martin, 2007; Russell et al., 2008), proliferation of genes for oxidation-reduction enzymes (Baymann et al., 2003; David and Alm, 2011), and to emancipation of biology from fleeting and potentially rate-limiting supplies of inorganic electron donors. The evolutionary success of this transition at 2.4 Gyr was the basis of the Great Oxidation Event, one of the greatest transitions in the evolution of life on our planet (Lyons et al., 2014).

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

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