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WHAT TYPES OF ORGANISMS LEFT THEIR SIGNATURE IN THE MICROBIALITES OF THE NORTH POLE DOME (AUSTRALIA) 3.48 GA AGO?

MICHEL ARAGNO¹ ET BLAISE MULHAUSER²

Résumé

Les plus anciennes traces fossiles avérées d'activité biologique trouvées sur Terre proviennent d'un dépôt vieux de ~3.48 milliards d'années (Ga), la formation de Dresser, située à North Pole Dome, en Australie occidentale. Grâce à la composition des minéraux présents dans ces roches, notamment de la pyrite et de la barite d'origine hydrothermale, mais également des carbonates, il a été démontré que ces activités microbiennes proches des débuts de la vie sur notre planète se sont déroulées dans un complexe de sources d'eau chaude et de geysers situé dans une caldera à activités volcaniques modérées, mais secouée par de fréquents événements sismiques. Quant à la présence de cristaux d'hématite, elle pourrait être liée à la ferro-oxydation réalisée par des organismes phototrophes. Ces informations précieuses nous permettent d'esquisser des hypothèses sur les microorganismes présents dans cet écosystème, au regard des connaissances actuelles en phylogénie microbienne et en paléoécologie.

Les stromatolites sont des structures lamellaires d'origine microbienne, généralement attribuées à la présence de tapis cyanobactériens. Toutefois, sur la base des données les plus récentes de la phylogénie microbienne, la photosynthèse oxygénique et les Cyanobactéries ne seraient pas apparues avant -3.0 Ga, soit environ un demi-milliard d'années après les structures de la Formation de Dresser. Si on admet que ces dernières résultent de la formation de tapis successifs de bactéries photosynthétiques, il est probable que ces dernières étaient des phototrophes anoxygéniques. Toutefois, comme il a été démontré que les représentantes actuelles de ces groupes fonctionnels appartiennent à des lignées contemporaines ou postérieures à l'apparition de la phototrophie oxygénique et des Cyanobactéries, on peut considérer que les phototrophes responsables de la formation de stromatolites il y a 3.48 Ga appartenaient à des lignées aujourd'hui disparues ayant transmis leurs gènes fonctionnels à des lignées plus récentes par transfert horizontal de gènes (THG). L'abondance probable des ions Fe^{2+} solubles dans les eaux de l'Archéen, de même que la présence observée d'oxydes ferriques (hématite) dans les structures de la Formation de Dresser peuvent s'expliquer par la présence de bactéries photoferrotrophes dans ces tapis. En revanche, la présence attestée de bactéries sulfatoreductrices indique qu'une phototrophie sulfureuse anoxygénique est aussi possible.

Une question reste ouverte : les cycles du carbone, du fer ou du soufre étaient-ils opérants dans ces écosystèmes primitifs, ou ces derniers étaient-ils continuellement ou périodiquement alimentés par des flux géothermiques contenant des sulfures et du fer bivalent ?

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Mots-clés: stromatolites, microbialites, microflore archéenne, photosynthèse anoxygénique, photoferrotrophie, tapis microbiens, transfert horizontal de gènes (THG).

Abstract

The oldest certified trace fossils of biological activity found on Earth come from a ~3.48 billion year-old (Giga-annum, Ga) deposit, the Dresser Formation, located in the North Pole Dome in Western Australia. The composition of the minerals in these rocks, including pyrite and baryte of hydrothermal origin, as well as carbonates, shows that microbial activity in the early days of life on our planet took place in a complex of hot springs and geysers located in a caldera that was moderately volcanic but shaken by frequent seismic events. As for the presence of hematite, it could be linked to ferro-oxidation phenomena from phototrophic organisms. This valuable information allows us to draw hypotheses on the microorganisms present in this ecosystem in the light of current knowledge in microbial phylogeny and paleoecology.

Stromatolites are lamellar, biologically induced structures that are generally attributed to the presence of cyanobacterial mats. However, according to recent progress in microbial phylogenetics, oxygenic photosynthesis and Cyanobacteria did not appear before -3.0 Ga, i.e., around 500 Ma after the Dresser Formation structures. Therefore, assuming that these structures were built by phototrophic bacterial mats, it seems probable that the organisms responsible were anoxygenic phototrophs. However, as currently living anoxygenic phototrophs belong to lineages contemporary or posterior to oxygenic phototrophs (Cyanobacteria), it could be considered that the anoxygenic phototrophs responsible for the 3.48 Ga-old stromatolites belonged to extinct lineages having transmitted their functional genes to more recent lineages by multiple horizontal gene transfers (HGTs). The probable abundance of soluble Fe^{2+} in Archean waters, as well as the presence of $Fe(III)$ oxides (hematite) in Dresser Formation structures, would be indicative of the presence of Fe^{2+} -oxidizing photoferrotrophic bacteria in the mats. However, the attested activity of sulfate reducers indicates the possible presence of phototrophic sulfur anoxygenic bacteria.

The question remains, however, if complete iron, sulfur and carbon cycles were operative in those primitive ecosystems, or if the latter were continuously or periodically fed by Fe^{2+} and/or sulfide-containing geothermal flushes.

Keywords: stromatolites, microbialites, Archean microbiota, anoxygenic photosynthesis, photoferrotrophy, microbial mats, horizontal gene transfer (HGT).

Zusammenfassung

Die ältesten zertifizierten fossilen Spuren biologischer Aktivität, die auf der Erde gefunden wurden stammen aus einer etwa 3,48 Milliarden Jahre (Ga) alten Lagerstätte, der Dresser-Formation, die sich im North Pole Dome in Westaustralien befindet. Die Zusammensetzung der Mineralien in dieser Lagerstätte, darunter Pyrit und Baryt hydrothermalen Ursprungs, aber auch Karbonate, weist darauf hin, dass die mikrobielle Aktivität in der Anfangszeit des Lebens auf unserem Planeten in einem Komplex aus heißen Quellen und Geysiren in einer Caldera mit mäßiger vulkanischer Aktivität aber häufigen seismischen Ereignissen stattfand. Das Vorhandensein von Hämatit könnte mit Eisenoxidationsphänomenen durch phototrophe Organismen in Verbindung stehen. Diese wertvollen Informationen ermöglichen es uns, Hypothesen über die in diesem Ökosystem vorhandenen Mikroorganismen im Lichte des aktuellen Wissens in der mikrobiellen Phylogenie und Paläoökologie aufzustellen.

Stromatolithe sind lamellare, biologisch induzierte Strukturen, die im Allgemeinen dem Vorhandensein von Cyanobakterienmatten zugeschrieben werden. Nach jüngsten Erkenntnissen in der mikrobiellen Phylogenie traten die sauerstoffbildende Photosynthese und Cyanobakterien jedoch nicht vor -3,0 Ga auf, dh etwa 500 Ma nach den Strukturen der Dresser-Formation. Unter der Annahme, dass diese Strukturen aus Matten phototroper Bakterien aufgebaut waren, scheint es daher wahrscheinlich, dass die verantwortlichen Organismen nicht-sauerstoffbildende phototrophe Organismen waren. Da jedoch

gegenwärtig lebende nicht-sauerstoffbildende Phototrophen aus derselben Zeit wie die sauerstoffbildenden Phototrophen (Cyanobakterien) stammen, kann man davon ausgehen, dass die für die 3,48 Ga-alten Stromatolithen verantwortlichen, nicht-sauerstoffbildenden Phototrophen zu ausgestorbenen Linien gehörten, die ihre funktionellen Gene durch mehrere horizontale Gentransfers (HGT) an neuere Linien weitergegeben haben. Die wahrscheinliche Fülle an löslichem Fe²⁺ in Gewässern des Archaikums sowie das Vorhandensein von Fe(III)-Oxiden (Hämatit) in Strukturen der Dresser-Formation könnte auf das Vorhandensein von Fe²⁺-oxidierenden photoferrotrophen Bakterien in den Matten hinweisen. Die nachgewiesene Aktivität von Sulfatreduzierern weist jedoch auf das mögliche Vorhandensein, schwefel-oxidierender phototropher Bakterien hin.

Offen bleibt die Frage, ob in diesen primitiven Ökosystemen vollständige Eisen-, Schwefel- und Kohlenstoffkreisläufe funktionierten oder ob letztere kontinuierlich oder periodisch durch Fe²⁺- und/oder sulfidhaltige geothermische Flüsse ernährt wurden.

Stichworte: Stromatolithen, Mikrobialiten, Mikroflora des Archaikums, nicht-sauerstoffbildende Photosynthese, Photoferrotrophie, bakterielle Matten, horizontal Gentransfer (HGT).

INTRODUCTION

The North Pole Dome in the Pilbara Craton in Western Australia (fig. 1) and the Kaapvaal Craton in South Africa are some of the oldest stable continental areas (so called cratons) still existing on our planet. The Pilbara Craton formed during the Archean period at least 3.6 billion years (Ga) ago, and it is there, in the 3.48 Ga old Dresser Formation, where the oldest traces of early life have been discovered. Repeatedly interpreted, the layering of certain rocks represents arguably the oldest evidence of biological activity on Earth (HOFMANN *et al.*, 1999; UENO *et al.*, 2006; ALLWOOD *et al.*, 2007).

GEOLOGY AND MATERIAL

The North Pole Dome

The North Pole Dome is a volcanic terrane located in the centre of the granitic East Pilbara Terrane, near North Shaw in the Pilbara region of Western Australia (fig. 1). A terrane is a piece of the Earth's crust or a tectonic block that has separated from one of

the major tectonic plates before moving and joining another tectonic plate or, in this case, a continental shelf. It should be noted that during the Eoarchean period (4 to 3.6 billion years ago, fig. 5), rock masses were still very unstable, set in motion by episodes of powerful seismic and volcanic activity.

Seen from above, the North Pole Dome looks like an ovoid dome, 35 km long on the SW-NE axis and 25 km wide on the E-W axis. The landscape is dominated by poorly deformed mafic (iron and magnesium rich) volcanic rocks of the Warrawoona Group (fig. 1), which form a broad dark green belt around a central core occupied by a magmatic intrusion called the North Pole Monzogranite (NPM, fig. 1).

The Dresser Formation is a belt of chert (siliceous sedimentary rock) and barite hills layered over basalt. This formation's outcrops within the North Pole Dome have a diameter of 14 km, between the basalts of the Warrawoona Group and the Coonturunah Subgroup (fig. 1).

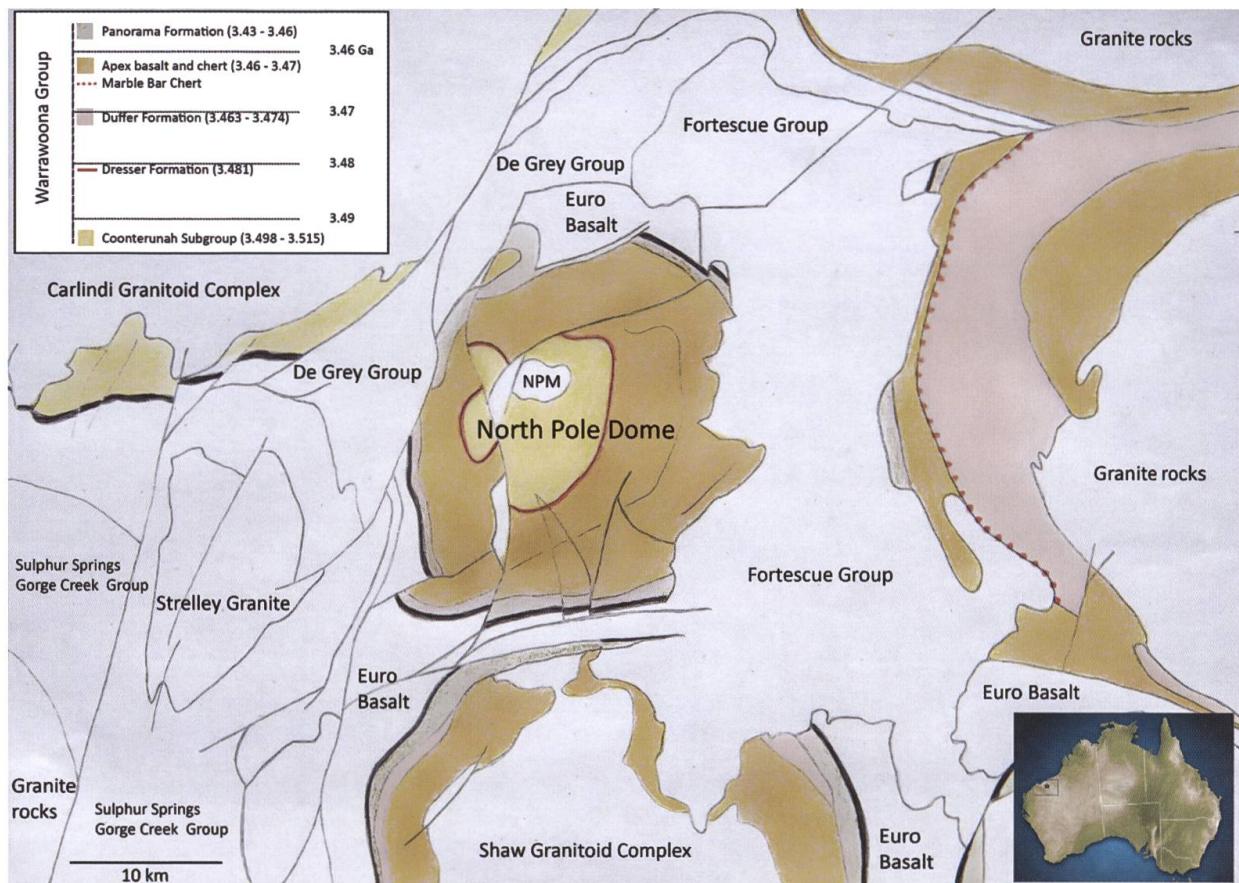


Fig. 1. Simplified geological map of the North Pole Dome area, Pilbara Craton, Western Australia (after VAN KRAENDONK *et al.*, 2008; NOFFKE *et al.*, 2013). The coloured geological layers belong to the Warrawoona Group. The red lines represents the Dresser Formation. Thick black lines represent the Strelley Pool Chert, a 3.43 Ga old geological layer with extensive stromatolite deposits. NPM: North Pole Monzogranite.

The age of the rocks

Numerous radiochronological investigations (including the radio-isotopic Uranium-Lead method in zircons and the isochronous Lead-Lead method in galena) have enabled the various outcrops to be dated. The oldest rocks belong to the Coonturunah Subgroup (ca. 3.515 to 3.498 billion years old; VAN KRAENDONK *et al.*, 2006). Zircons found higher up in the site's stratigraphy are of the same age (BUICK *et al.*, 1995). The North Pole Monzogranite is younger (3.459 ± 0.018 billion years). The Pb-Pb isochron method gave an age of 3.490 billion years for the galena embedded in the Dresser

Formation barite (THORPE *et al.*, 1992), which is supported by more recent analyses of the 3.481 ± 0.0038 -billion-year-old rocks, in which there is evidence of biological activity (VAN KRAENDONK *et al.*, 2006).

Microbialites of the Dresser Formation

Microbialites are organo-sedimentary deposits resulting from the activity of a benthic microbial community trapping and binding detrital sediments or forming a site of mineral precipitation. Fossil stromatolites are microbialites (fig. 2) where thin layers of precipitated minerals with different natures and colours alternate

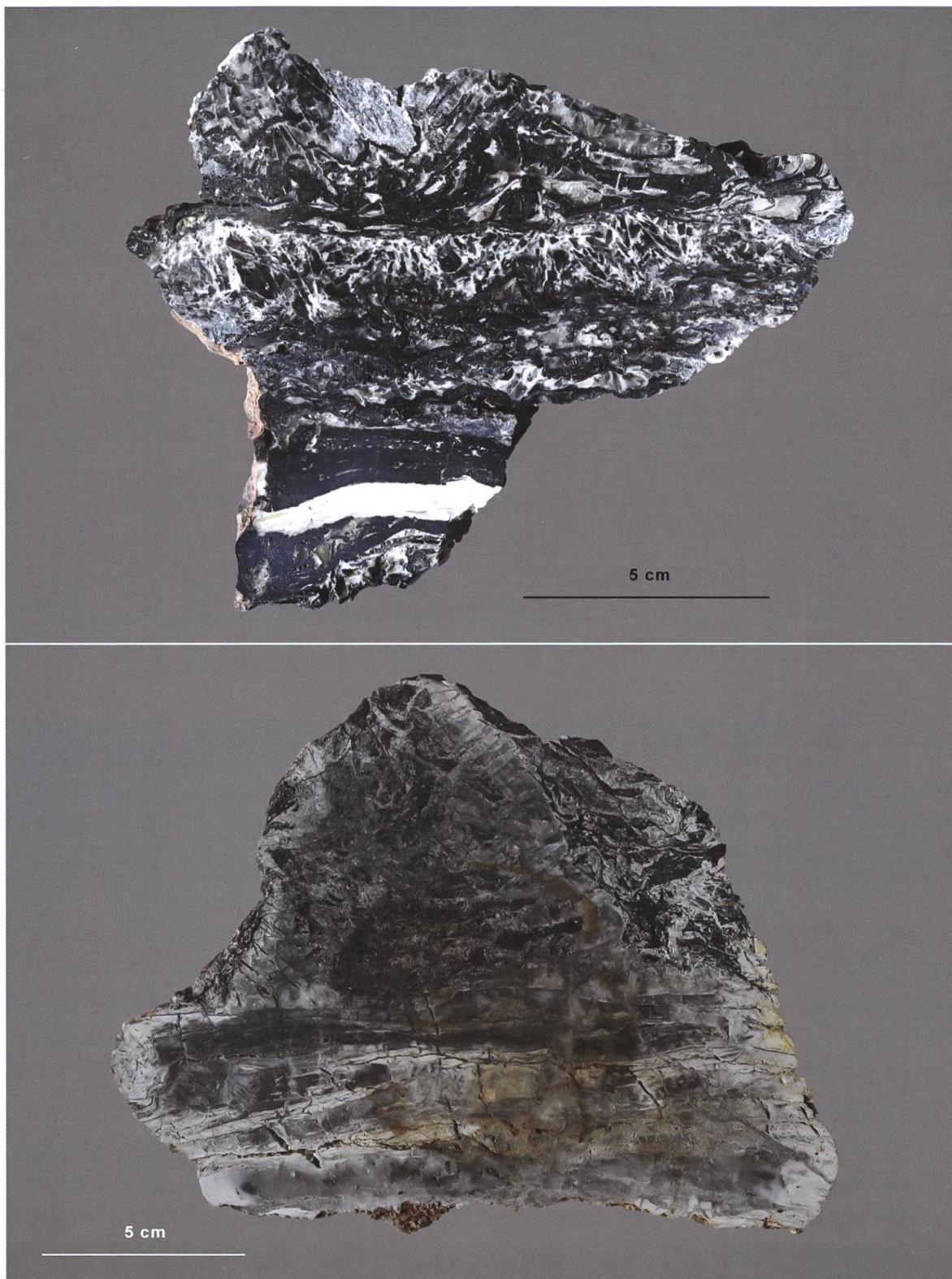


Fig. 2. Two specimens of microbialites with alternating layers of silica (dark) and barite (light); the latter mineral being of hydrothermal origin. Dresser Formation (Palaeoarchean, 3.481 Ga); North Pole Dome, Pilbara Craton, Western Australia. Collection of the Botanical Garden of Neuchâtel, Switzerland. Above: JBN.Pal.0176 / below: JBN.Pal.0175. Photos by the second author.

(fig. 3), often giving them a millefeuille-like appearance (GREY & AWRAMIK, 2020).

In very old deposits altered by volcanic and hydrothermal activity, it is a challenge to distinguish the results of mineralisation processes of biological and/or geochemical origin, even more so if they may be linked. Therefore, the distinction of microfossils present in Archean rocks is still debated (WACEY *et al.*, 2016; LEPOT, 2020).

A comprehensive mineralogical analysis of the Dresser Formation's layers with stromatolite-like layered arrangements indicated that some of the elements resulted from biological activity. The red or black inclusions between the strata consist of pyrite of hydrothermal origin around which carbonate residues are found, which suggests a biological origin for part of the rock (fig. 3). Very fine deposits of micritic carbonates confirm this. Finally, the alteration of tiny hematite crystals in the centre of siderite and dolomite crystals can be interpreted as the result of an increase in pH, probably related to microbial activity (VAN KRANENDONK *et al.*, 2008). An analysis of different present-day sedimentary structures compared to those of the outcropping surfaces of the Dresser Formation supports the hypothesis of the deposition of MISS. These Microbially Induced Sedimentary Structures (fig. 4) are consequent to biofilm and material deposits of bacterial origin (NOFFKE *et al.*, 2013).

Recently, further mineralogical investigations were carried out by high-resolution microscopic mapping of pyrite crystals and sulfur isotope analyses of sulfides in the Dresser Formation's rocks (SHEN *et al.*, 2001; BAUMGARTNER *et al.*, 2019) and the Strelley Pool Formation (BONTOGNALI *et al.*, 2012). The results of the different analyses converge to explain the action of microbiological organic matter, thus leading to the presence of baryte microspherulites (BAUMGARTNER *et al.*, 2020b) and pyrite (BAUMGARTNER *et al.*, 2020a) with digitated or wrinkled textures in the microbialites of the Dresser Formation (BAUMGARTNER *et al.*, 2020c).

Paleoenvironment

Stratigraphic and petrographic analyses carried out at the site have highlighted the importance of regular water flows within an active volcanic caldera. Initially, the preferred scenario was the development of microbial life in a protected lagoon or along a mid-ocean ridge (VAN KRANENDONK *et al.*, 2008). However, the discovery of microbialites in geyserite deposits, a siliceous rock that forms in hydrothermal settings such as hot springs and sinter terraces, has added to our understanding of the system in which the micro-organisms developed (DJOKIC *et al.*, 2017). The microbialites did not thrive in a shallow marine environment as previously thought, but in a hydrothermal setting as active as the ones that can still be found today, for example, in Yellowstone National Park (USA) or in Iceland. This living environment remained very unstable because of frequent volcanic eruptions and earthquakes, which caused the large faults still visible today at the North Pole Dome site.

WHAT KIND OF MICROORGANISMS COULD THESE BE?

1. *The evolution of early life on Earth*

Fossil records of the biological structures and events which occurred during the Archean period (-4 to -2.5 Ga) (NUTMAN *et al.*, 2016; VAN KRANENDONK *et al.*, 2008) are extremely scarce and difficult to interpret with certainty. For example, some Cyanobacteria-like structures were shown to result from coatings of cell-mimicking mineral templates (LEPOT, 2020). Moreover, the microbial cell morphology of fossils is by no means indicative of the functions they had, which may in particular be the case for cyanobacteria-like fossilized cells. Precise information can only be drawn from present-time microorganisms which have functions that were supposed to have been active in ancient life forms. They might

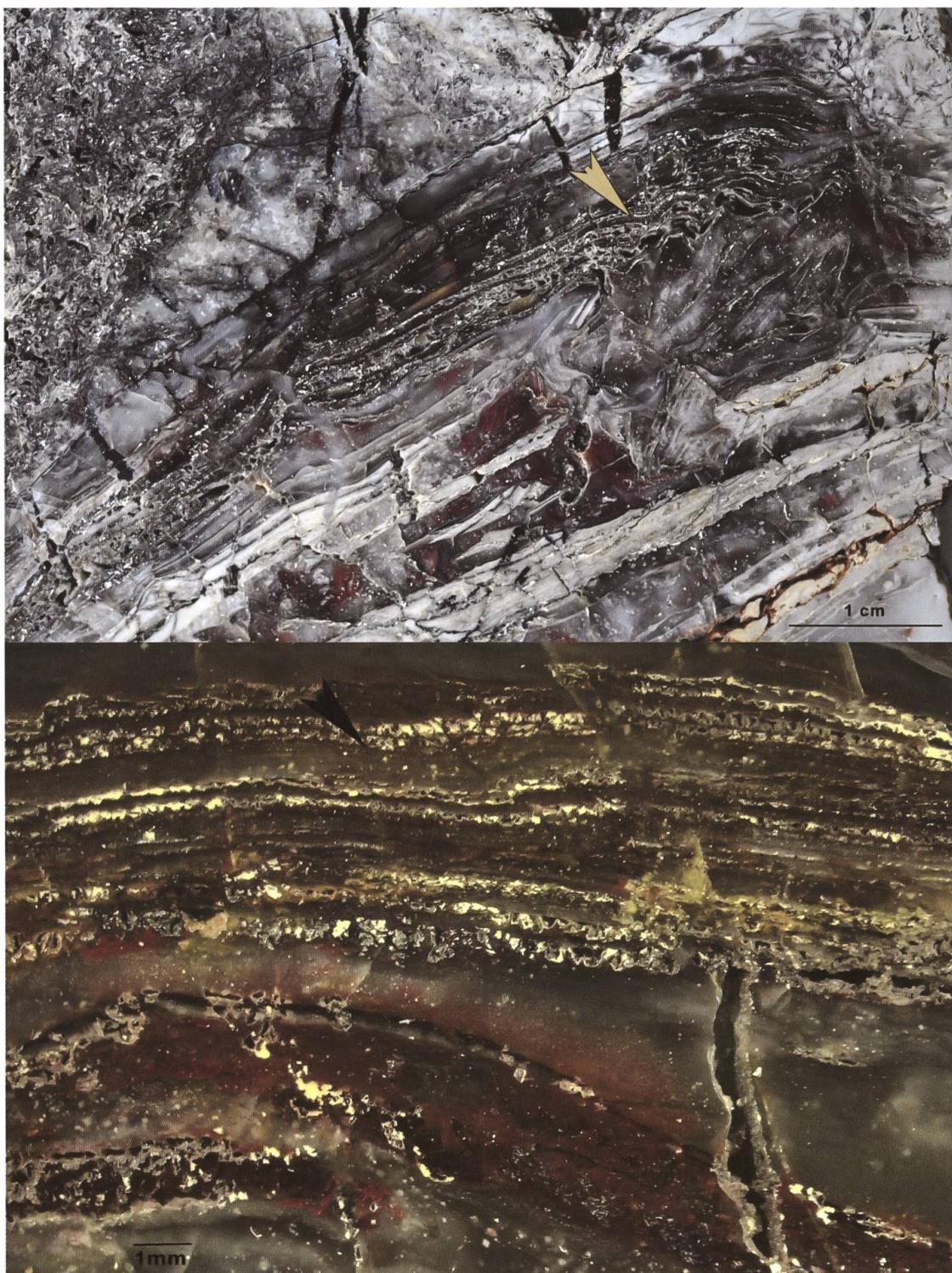


Fig. 3. Detail of two layered stromatolite-like (JBN.Pal.0175) showing alternating layers (arrows) of pyrite (black) and carbonates (white), and jaspilite “veins” in which hematite microcrystals may be present. Dresser Formation (Paleoarchean, -3.481 Ga); North Pole Dome, Pilbara Craton, Western Australia. Collection of the Botanical Garden of Neuchâtel, Switzerland.

Above: JBN.Pal.0175 / below: JBN.Pal.0272.

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Fig. 4. Detail of two parts of Microbially Induced Sedimentary Structures (MISS) which represent potential ancient biofilms (above) or microbial mats (below) (terms according to NOFFKE *et al.*, 2013). Dresser Formation (Paleoarchean, -3.481 Ga), North Pole Dome, Pilbara Craton, Western Australia. Collection of the Botanical Garden of Neuchâtel, Switzerland.

Above and below: JBN.Pal.0271.

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be direct descendants of or descending from more recent cell-lineages that acquired gene packs coding for a given function from other lineages by horizontal gene transfer (HGT). This was shown, for example, for dinitrogen fixation in legume nodulating symbionts, which belong to distinct cell-lines of α - and β -Proteobacteria, and whose close phylogenetical neighbors are non-nodulating. The responsible genes for nodulation and dinitrogen fixation are all located in a distinct genomic “island” with a (G+C) content that is completely different from the main genome; they may be present either on the bacterial chromosome or on megaplasmids (YOUNG *et al.*, 2006). Thus, microbial genomes may be composed of “core components”, genes associated with basic cell processes, for example, ribosomal genes, and “accessory components” comprising, for example, metabolic genes which could have been acquired secondarily by horizontal gene transfer. Such a path might have enabled extinct phyla to transmit functional genes to younger and still existing phyla.

The following considerations are therefore putative: “functional evolution could likely have occurred through such a path”. Or not.

A primary question is concerned with the origin of life itself. Did it evolve from prebiotic material on Earth itself, or was it brought from space by a comet or meteorite which could have contained previously evolved communities of microorganisms? Such a question could only be answered seriously by discovering presently living extra-terrestrial organisms, thus allowing us to verify if they are related to life on Earth, having DNA, RNA, ribosomes, proteins, a similar genetic code, etc., or not. One thing is clear: all living things on Earth exhibit numerous common properties that rule out the co-existence of unrelated life forms. Life on Earth is monophyletic. A theoretical organism sharing all these properties (about one hundred, including DNA, RNA, proteins, a genetic code,

ATP, NAD(P)H), was nick-named LUCA, for Last Universal Common Ancestor, and precedes the separation of the first lineages, bacteria, and archaea.

1.1 Life in the primordial soup

The first evidence of the presence of life dates to 4 – 3.85 Ga (fig. 5), while the occurrence of life before 4 Ga is still controversial. The first forms of life (pre-LUCA), for example, the RNA-world (NEVEU *et al.*, 2013) would have been very fragile. Compared to DNA, RNA is a much more unstable structure, so life invented the more stable DNA molecule, a far more efficient structure for conserving genomic information, which is carried by nucleotide sequences. This was the **first “plateau”** of evolution, i.e., the appearance of relatively genetically stable life forms.

Progressively, more and more efficient genome repair mechanisms would have developed, slowing down the frequency of conserved mutations, and consequently the rate of functional evolution. Therefore, it is conceivable that early functional evolution was faster, including numerous horizontal gene transfers (GOLDMAN & KACAR, 2022), thus allowing innovations to occur within relatively short time periods. Hence, an evolution that includes diverse and efficient life forms could have occurred during the first few millions of years of its existence.

At its very beginning, life could only be sustained by the presence of abiotically synthesized organic matter which could have accumulated during prebiotic times, and/or been brought by meteorites. This so-called “prebiotic or primordial soup” would have provided both energy and building molecules (mainly organic carbon, N, P, S, Fe). A small portion of this “soup” could have served as an energy source through exergonic reactions similar to primitive fermentations. Although the amount of harvested energy would have been very

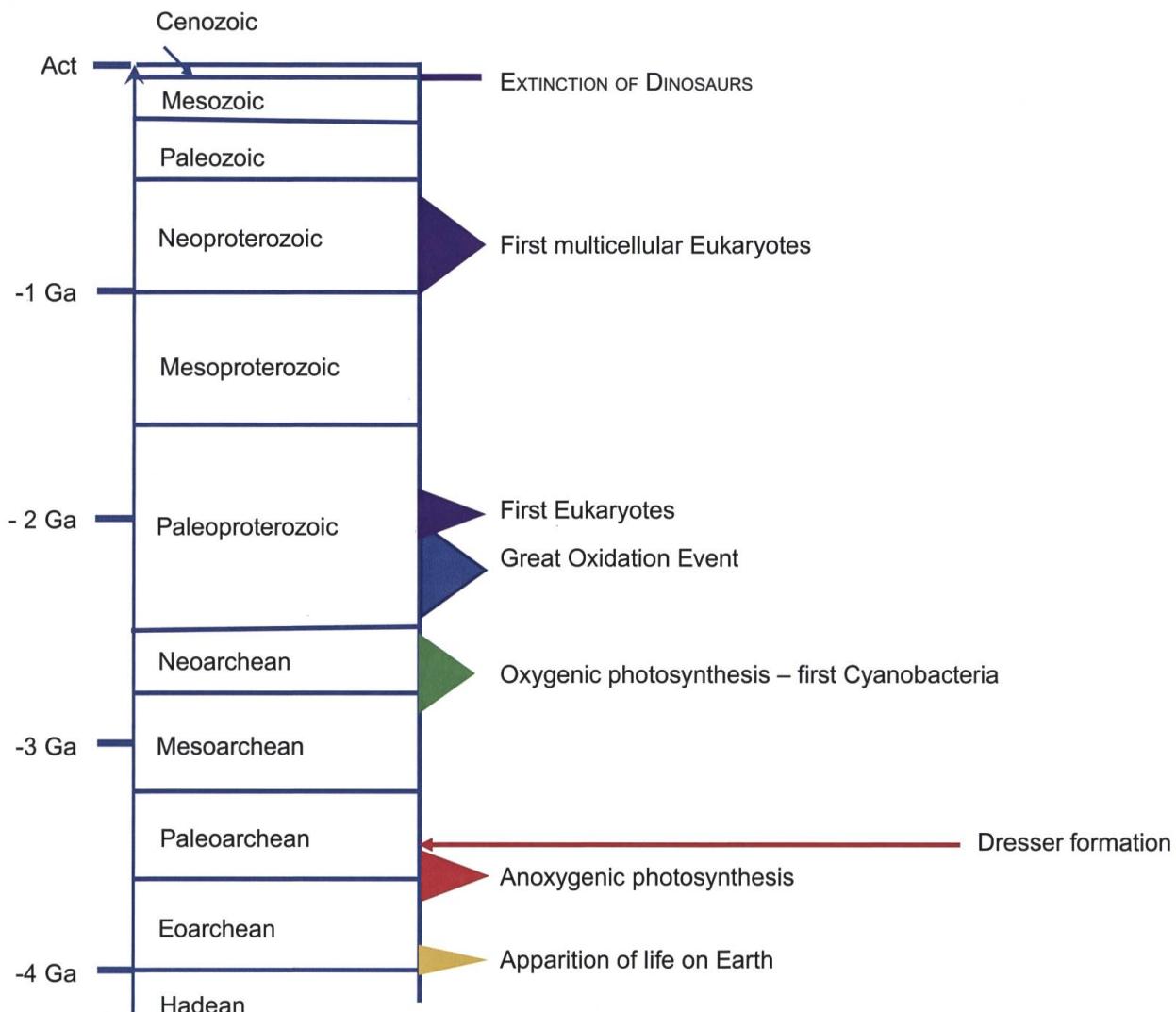


Fig. 5. Approximative age of the main life events on Earth.

small, another energy evolutionary path rapidly evolved: the use of highly reducing compounds, principally H_2 ($E_0' = -420$ mV), and possibly CO , as low-potential electron donors in an anaerobic respiratory system, all by using higher potential electron acceptors (around 0 V) to provide sufficient energy. These acceptors include CO_2 (reduced to CH_4 through methanogenesis), S^0 (reduced to H_2S through sulfur respiration), and $Fe(III)$ (reduced to Fe^{2+} through iron respiration). This was the emergence of **lithotrophy**, i.e., respiration with an inorganic electron donor, H_2 in this case.

1.2 From the invention of autotrophy to the phototrophy revolution

After overcoming energy-limitation, life encountered carbon-limitation due to the scarcity of assimilable organic carbon sources in the “soup”. **Autotrophy**, that is, the synthesis of its own biomass carbon from CO_2 and electrons derived from a low potential reducing electron source, essentially H_2 , was the next step in metabolic evolution. Together with lithotrophy, it achieved a “sustainable” way of life. The evolution of life then reached a

second “plateau”, although it was geographically limited to sites with significant H_2 concentrations (for example, in the micromolar range). Since H_2 diffuses rapidly to reach concentrations below the threshold necessary for an energetically favorable uptake (CONRAD *et al.*, 1983), exploitable concentrations were presumably only encountered in close vicinity to geothermal vents. Such environments were probably more abundant during the Eoarchean, but they still exist as terrestrial and submarine vents and seeps. The organisms encountered there are mainly hyperthermophilic Archaea, many of which are autotrophic, hydrogenotrophic methanogens, sulfur- and Fe(III)-reducers (STETTER, 2006). These organisms form the lowest branches on the “tree of life” (STETTER, 2006) and might well be direct descendants of the first sustainable life-forms. At this stage, a carbon cycle was realized, whereas sulfide, Fe^{2+} , and CH_4 were the end-products that accumulated in the environment (fig. 6). Autotrophic activity has been observed in 3.8 to 3.7 Ga-old sediments through ^{13}C -depletion in carbon particles (SCHILDOWSKI, 1988; ROSING, 1999).

To escape the H_2 -dependance of living ecosystems, a wider colonization of Earth required a source of energy other than telluric. Life activation requires relatively high energy quanta, which can be provided by exergonic chemical reactions (chemotrophy), or by the use of photons in the visible or near infrared light spectrum (phototrophy). Thanks to sunlight, photons were universally available in practically unlimited amounts. The invention of mechanisms that allowed photons’ electromagnetic energy to be converted to cellular biochemical energy (in the form of trans-membrane proton gradients and low potential electrons), i.e., **phototrophy**, enabled life to reach a **third evolutionary “plateau”** and to increase its geographical distribution considerably, along with the amount of biomass in the biosphere.

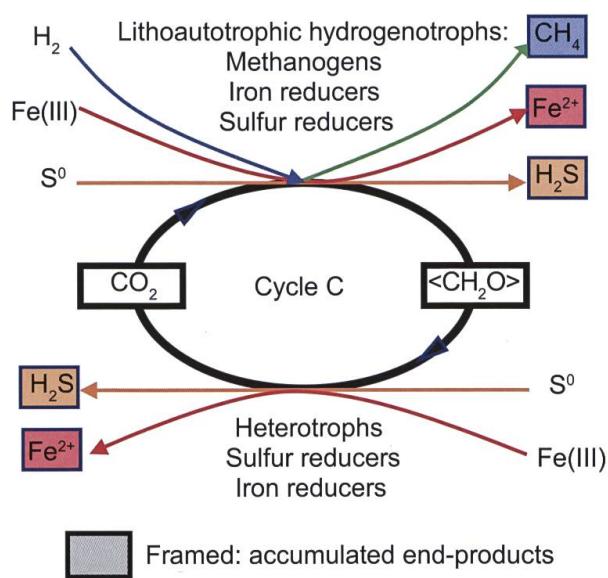


Fig. 6. Acyclic management of iron, sulfur and methane by microorganisms before the advent of phototrophy.

There are two types of phototrophy coupled to autotrophy. Both use chlorophyll complexes at the core of light harvesting systems (photosystems):

- o anoxygenic phototrophy, with medium (Fe^{2+} , H_2S) to low (H_2) redox potential electron donors;
- o oxygenic phototrophy, with a high potential electron donor, H_2O .

Reduced chlorophyll becomes highly reductive after light absorption, enabling it to transfer electrons both to an electron transport chain, whose final acceptor is the oxidized chlorophyll centre (fig. 7), and to a low potential electron transfer co-enzyme, such as ferredoxin (in type I reaction centres) or a quinone (in type II reaction centres), which in turn provides electrons, for example, through the coenzyme $NAD(P)^+$ / $NAD(P)H$, to a cytoplasmic CO_2 -fixation pathway, thus realizing autotrophy. Phototrophy coupled to autotrophy is termed **photosynthesis**.

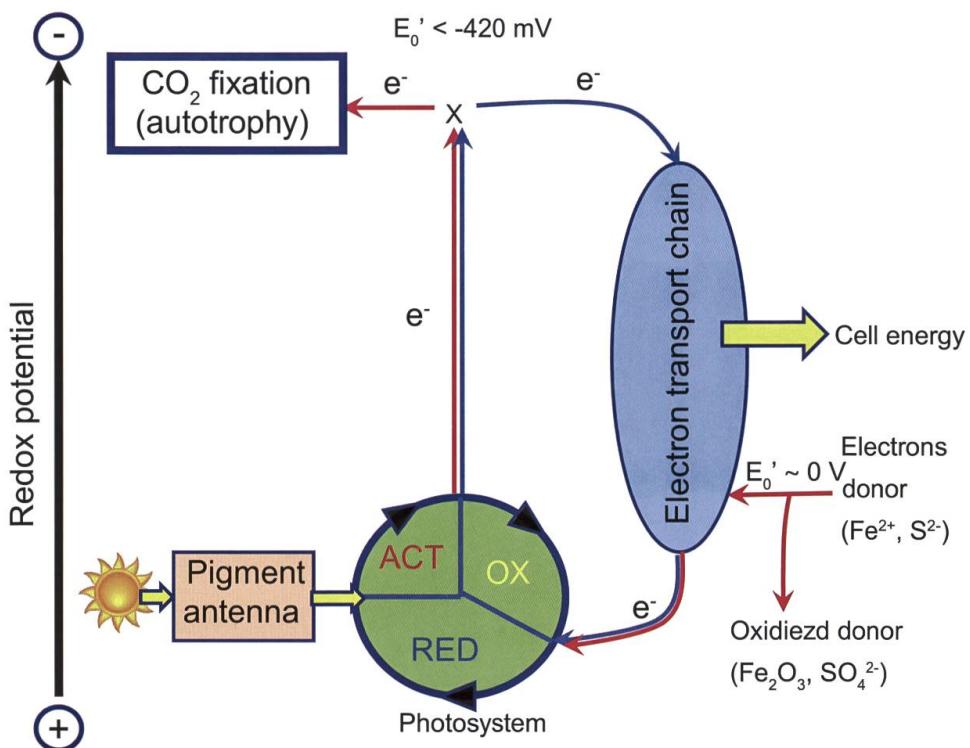


Fig. 7. General principle of anoxygenic phototrophy (photosynthesis if coupled with autotrophic CO_2 fixation).

The activation of electrons from a medium redox potential donor requires only one light quantum and, therefore, one photosystem (PS), transferring electrons from donors to a low potential intermediate electron transporter (fig. 7). This system is called **anoxygenic phototrophy**, because the oxidation products from the donors are not oxygen. These photosynthetic organisms encounter a new limitation in their development due to the limited availability of appropriate inorganic electron donors, sulfides, Fe^{2+} , and H_2 (WARD *et al.*, 2019).

1.3 Oxygenic phototrophy, a decisive corner in the evolution of life

There is another much more widespread potential donor: water. However, the redox potential of the couple $\text{H}_2\text{O} \longleftrightarrow 2 \text{H} + \frac{1}{2} \text{O}_2$ is high ($E_0' = +815 \text{ mV}$), and the overall

potential difference (1235 mV between $\text{O}_2/\text{H}_2\text{O}$ and NAD^+/NADH) cannot be overcome by one photon only. Therefore, water activation requires the successive absorption of two photons, which is achieved through two different photosystems. Photosystem 2 brings electrons from water to an intermediate potential, thus allowing the chlorophyll centers in photosystem 1 to be reduced (fig. 8). This system is called **oxygenic phototrophy**. The by-product of water oxidation is O_2 , whose formation was of enormous importance for the chemical evolution of the biosphere. Molecular oxygen, as an electron acceptor of **aerobic respiration**, allows a much higher energetic yield, and therefore a higher growth potential for heterotrophs. With aerobic respiration, the **fourth evolutionary plateau** was reached, which paved the way for the further

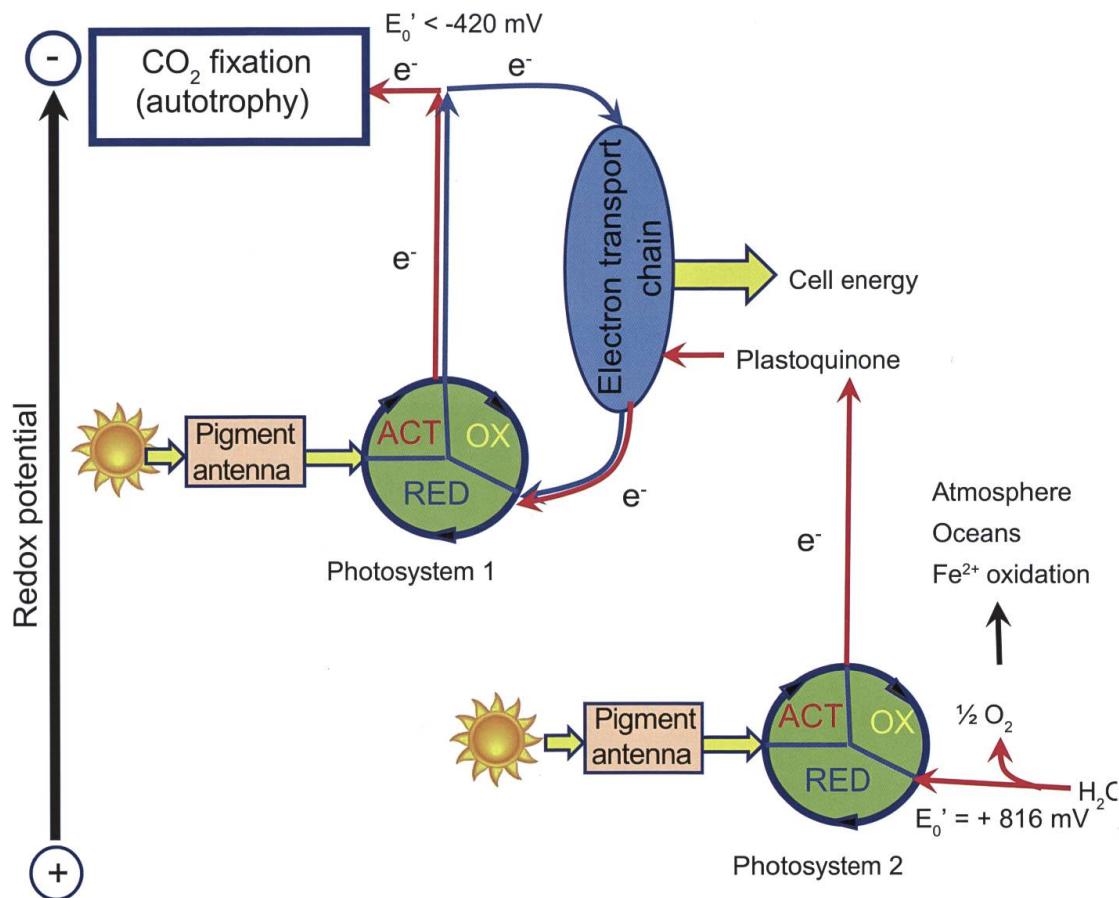


Fig. 8. General principle of oxygenic phototrophy / photosynthesis.

evolution of Eukaryotes, including multicellular organisms such as plants, fungi, and animals. In the present-day biosphere, oxygenic photosynthesis is strictly confined to a phylogenetic group comprising exclusively Cyanobacteria. The latter gave rise, through endosymbiosis with a primitive Archaeal cell, to the chloroplasts of all photosynthetic Eukaryotes (MOORE *et al.*, 2019). It is generally considered that oxygenic photosynthesis was the only significant process that allowed the evolution of O_2 in the biosphere. Then, O_2 could only accumulate as a counterpart to the fossilization of produced organic matter.

Photosystem 1 in Cyanobacteria and chloroplasts is a type I reaction centre, whereas Photosystem 2 is a type II reaction center.

2. Geological records of early life

The period when free oxygen began to accumulate in the upper oceans and atmosphere is called the “Great Oxidation Event” (GOE, TRENDALL, 2002). The scientific community agrees that the GOE took place between 2.43 and 2.1 Ga (BEKKER *et al.*, 2014; GUMSLEY *et al.*, 2017). With the early development of Cyanobacteria, the highly oxidizing O_2 molecules would obviously have spontaneously reacted with the reduced metal ions, in particular Fe^{2+} , Mn^{2+} , sulfides, or organic compounds, which may have been present in the early anoxic ocean of the Archean. However, the duration of the latency period between the first phototrophic O_2 production and its liberation into the atmosphere is still controversial (DAVID *et al.*, 2011; LYONS *et al.*, 2014). The deposition of $Fe(III)$ oxides

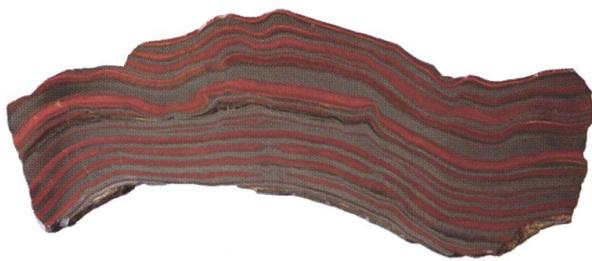


Fig. 9. Specimen of Cleaverville Banded Iron Formation (BIF), North Pilbara Craton, Western Australia (~3.1 Ga). Collection of the Botanical Garden of Neuchâtel, Switzerland: JBN.Pal.0282. Photo by the second author.



during the GOE gave rise to important banded iron formations (BIFs, fig. 9) (GUMSLEY *et al.*, 2017). Reduced iron (Fe^{2+}) is very soluble, in contrast to its oxidation products, i.e., $\text{Fe}(\text{III})$ oxides and (oxy)hydroxides, which are almost insoluble. Before the GOE, much fainter BIFs were formed. Are they earliest indicators of the first occurrence of O_2 -evolving phototrophs? This is not necessarily the case, because other mechanisms, mainly the activity of anoxygenic photoferrotrophs, result in Fe^{+2} oxidation and $\text{Fe}(\text{III})$ deposition in the complete absence of O_2 (WIDDEL *et al.*, 1993; KAPPLER *et al.*, 2005; CANFIELD *et al.*, 2006; WALTER, 2011; WALTER *et al.*, 2014; KONHAUSER *et al.*, 2017; CAMACHO *et al.*, 2017; WARD & SHIH, 2021; HEARD *et al.*, 2022).

Fossilized stromatolites were observed within the ancient sediments of the late Archean and, more frequently, of the Proterozoic eras. The hypothesis that they resulted from abiotic stratification phenomena has generally been ruled out, and early microbial mats are considered to be of photosynthetic origin (TICE & LOWE, 2004), with the possible exception of Greenland's 3.7 Ga-old formations, which are rather considered to be “dubiofossils” (LEPOT, 2020).

Modern representatives of ancient stromatolites can still be observed today, although

Fig. 10. Contemporary stromatolites at Shark Bay (Western Australia).

Above: General view in shallow waters.

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Below: Transversal section.

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at rare sites such as Hamelin Pool (Shark Bay, Western Australia) (fig. 10). They are mainly structured by successive cyanobacterial mats through the secretion of exopolymeric substances (EPS) and the deposition of carbonates. Ancient stromatolites were often considered to have been structured by similar cyanobacterial mats (POPALL *et al.*, 2020).

Presently-living cyanobacteria constitute a single, homogenous phylum in the bacterial phylogeny (fig. 14). Other non-phototrophic organisms branch next to the basis of this phylum (SHIH *et al.*, 2017a; MOORE *et al.*, 2019). It is not clear whether oxygenic phototrophy emerged as a new trait at this particular point in evolution, or whether it could have been acquired by horizontal transfer from ancient lineages of organisms that have successively disappeared. Accordingly, the issue remains of whether to date the appearance of oxygenic phototrophy along with the appearance of Cyanobacteria or before them. Recent phylogenetic studies place this origin between -2.8 (MAGNOBOSCO *et al.*, 2018) and -2.6 (SHIH *et al.*, 2017a; WARD & SHIH, 2021) Ga as the upper limit (fig. 5), about 700 – 900 Ma after the age of the Dresser formation during the Paleoarchean era. Archean stromatolites structured by mats of anoxygenic photosynthetic bacteria are, so far, the most probable hypothesis (BOSAK *et al.*, 2013).

3. The Dresser Formation

With regard to the microbial communities present in Dresser formation microbialites, it is possible at this point to formulate several hypotheses.

3.1 Geochemical characteristics

We will consider it highly probable that these stromatolites were structured by the development of mats comprising photosynthetic bacteria (TICE & LOWE, 2004). It is arguable that the layered structure and the presence of carbonates (FeCO_3 – siderite, and CaCO_3 - calcite) were a possible consequence of autotrophic activity.

Anoxygenic phototrophs are able to oxidize two anaerobic respiration products, Fe^{2+} and sulfides, thus bringing two new element cycles into the biosphere: a sulfur cycle and an iron cycle (fig. 11).

The presence of pyrite (Fe(II)-bisulfide) and hematite (Fe(III)-oxide) has been

documented in Dresser formation microbialites (VAN KRANENDONK *et al.*, 2008). It is often admitted that Fe^{2+} was much more abundant than S^{2-} in Archean waters (CAMACHO *et al.*, 2017). This demonstrates the possible activity of a biological iron cycle controlled by photoferrotrophic bacteria and Fe(III)-respiring bacteria. However, the occurrence of a biological, mesophilic sulfate-reduction activity was attested by isotopic fractionation in pyrites (SHEN *et al.*, 2001). Hence, the occurrence of both S and Fe cycles is possible here.

3.2 Photosynthetic microbial mats

Microbial mats formed by anoxygenic phototrophs are well known. Mats of filamentous *Chloroflexus* bacteria are regularly observed in the outflows of thermal springs, and mats of purple sulfur phototrophs grow in the outflows of sulfur springs (fig. 12). Spectacular, thick, and complex mats, consisting of superposed layers of cyanobacteria, purple sulfur bacteria, and sulfate-reducing bacteria have been observed in alpine ponds in the Piora Valley (Ticino Canton, Switzerland) (fig. 13, WALTER *et al.*, 2007). Experimentally, mats based on H_2 and Fe^{2+} anoxygenic phototrophs resist scour and shear forces as much as oxygenic ones (BOSAK *et al.*, 2013).

Anoxygenic phototrophs include several unrelated clades (fig. 14, IMHOFF *et al.*, 2019). The earliest appearance in the phylogeny of Bacteria are *Chloroflexaceae*, including moderately thermophilic, gliding filamentous bacteria. However, they are facultatively aerobic, facultatively autotrophic, and facultative phototrophs. They possess a type II phototrophic reaction center with a distinct CO_2 -fixation pathway (the hydroxy-propionate pathway, HERTER *et al.*, 2002) now considered to be of relatively recent origin (SHIH *et al.*, 2017b). They possess an a-type bacteriochlorophyll. *Chloroflexi* would therefore not represent an ancient lineage in terms of phototrophy but would have acquired these capabilities

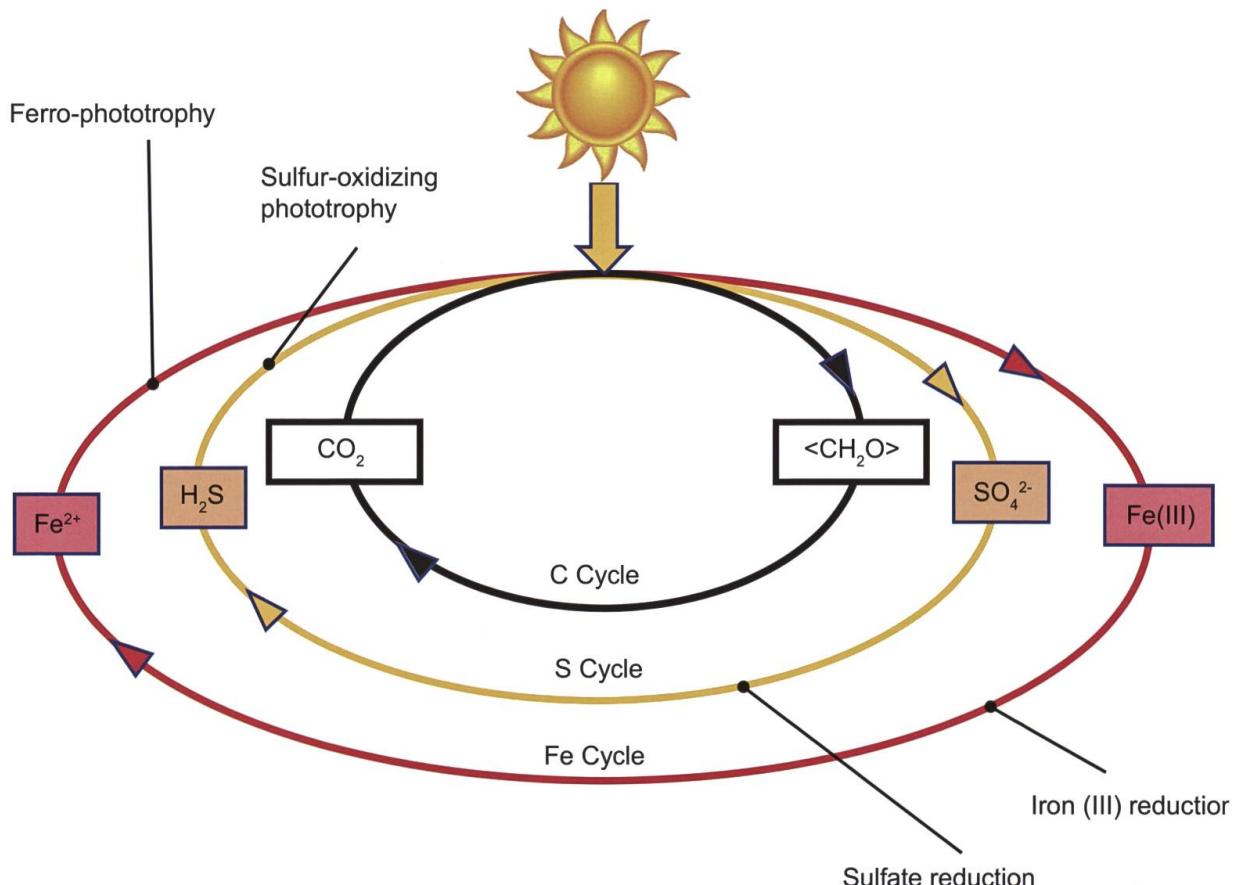


Fig. 11. Cyclic management of sulfur and iron in the presence of anoxygenic photosynthetic organisms.

secondarily through horizontal gene transfer (SHIH *et al.*, 2017b; WARD *et al.*, 2018).

The other phototrophs branch at different points in the pluriphyletic “crown” of the Bacteria phylogeny (fig. 14). They include mainly :

- green phototrophs, e.g., *Chlorobium* spp. and related species, which form a distinct clade. They are obligately phototrophic, sulfide, H₂, or Fe(II)-oxidizers, which produce extracellular sulfur granules as an intermediate oxidation product between sulfur and sulfate. Their unique light harvesting system includes chlorosomes, vesicles attached to the inner face of the cell membrane. These allow a much greater affinity for light, enabling them to grow

at lower light intensities than other phototrophs. They possess a type-I phototrophic reaction center;

- anoxygenic purple phototrophs. They are widespread in the Proteobacteria phylum and their lineages are mixed with non-phototrophic lineages. For this reason, Proteobacteria were first named “purple bacteria phylum”, based on the hypothesis that this phylum originated from a purple bacterium and further evolved while losing phototrophic ability in most clades. This hypothesis is no longer considered valid and horizontal gene transfer is now seen as the most probable cause of the polyphyletic distribution within purple phototrophs. They include sulfur-oxidizers, for example, *Chromatiaceae* and



Bacterial mat formed by sulfur-oxidizing, anoxygenic and anaerobic phototrophs (*Chromatiaceae*).

Bundles of *Thiothrix* filaments, sulfur-oxidizing, aerobic chemolithoautotrophic bacteria, living in proximity of the surface.

Fig. 12. View from above of an anoxygenic, sulfur oxidizing phototrophic bacterial mat in the laminar flow at the outlet of a sulfur spring. Location: Vallée des Ponts-de-Martel, Canton of Neuchâtel, Switzerland. Photo by the first author.

Ectothiorhodospira spp., and non-sulfur phototrophs, for example, *Rhodospirillum* spp., using H₂ or organic compounds as electron donors. Both groups include some photoferrotrophs. All proteobacterial phototrophs rely on a type II phototrophic reaction center.

Phylogenetic studies have developed significantly during the last 20 years due to spectacular progress in sequencing technology, bioinformatics, metagenomics, and whole

genome phylogeny. Thus, quite recent studies (for example, WARD & SHIH, 2021) have shed completely new light on the evolution of phototrophy.

As stated above, there is solid evidence that horizontal gene transfer (HGT) was a fundamental mechanism in the evolution of phototrophs. A recent hypothesis states that chlorophyll would have preceded bacteriochlorophyll during evolution (WARD & SHIH, 2021), having therefore existed in a hypothetical ancestor of all phototrophs, the

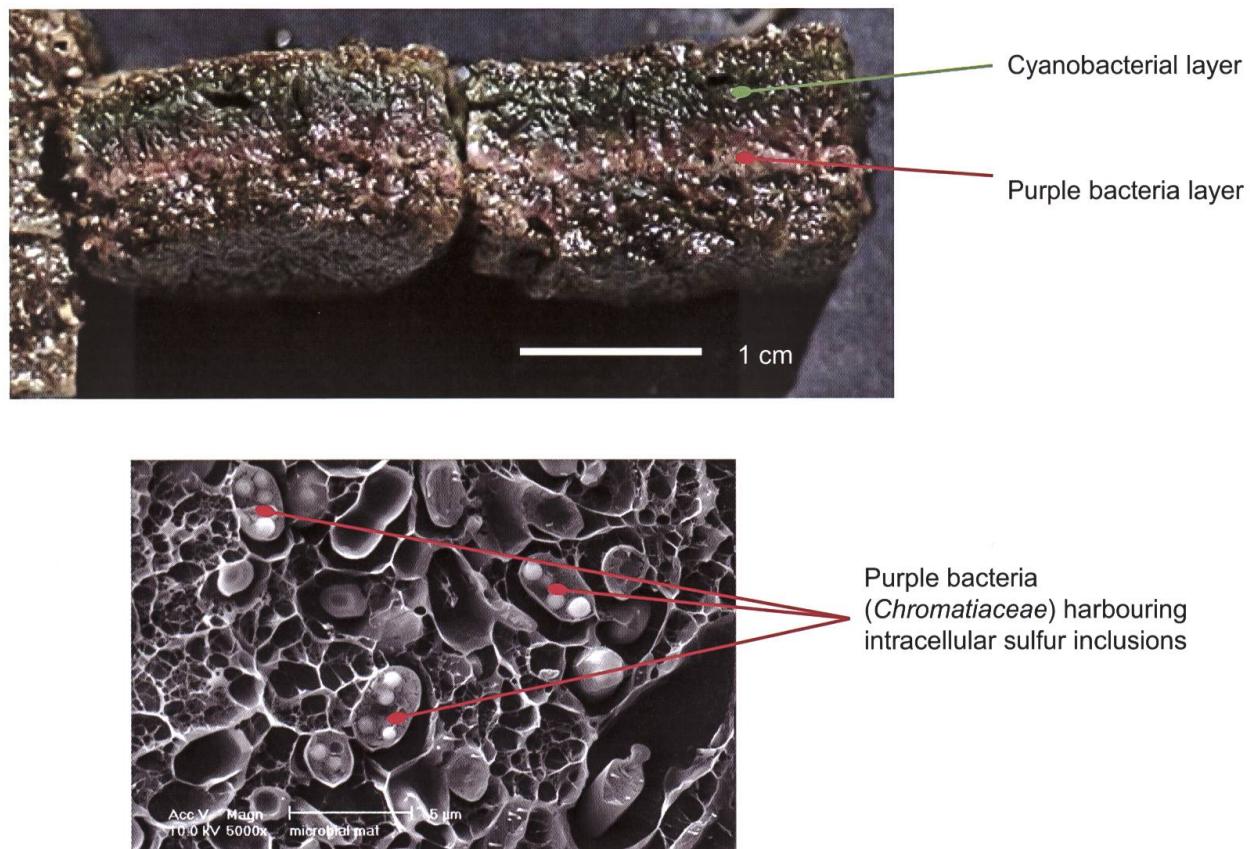


Fig. 13. Cross section of a photosynthetic complex microbial mat. Location: Cadagno, Alpe di Piora, Canton of Ticino, Switzerland (WALTER *et al.*, 2007). Courtesy of X. A. WALTER.

“ur-phototroph”. Indeed, chlorophylls have a lower affinity for light than bacteriochlorophylls, needing greater light intensities to function. Light intensity is not limiting for phototrophs exposed to direct sunlight. However, the appearance of oxygenic phototrophs was an ecological catastrophe, first and foremost because of the molecular oxygen emissions, which were toxic to the un-adapted anaerobic organisms. Before the GOE, reductants such as Fe^{2+} and sulfide buffered this toxicity, giving organisms time to develop protective mechanisms against the activated forms of oxygen, such as superoxide dismutase (converting superoxide radicals to peroxides), catalase (converting peroxides to water and O_2), and carotenoids (catalysing the return of toxic singlet oxygen to its normal triplet

form). These organisms then became aero-tolerant. Strict anaerobes, among which the anoxygenic phototrophs, were consequently restricted to environments devoid of oxygen and therefore of light! As they were in the shadow of the oxygenic phototrophs, they had to develop bacteriochlorophylls and other light capturing antenna pigments with greater affinity for low light intensities and different light-absorbing spectra. This situation is well illustrated in the complex mat in fig. 13, where a layer of anoxygenic, sulfur-oxidizing photosynthetic bacteria is lying below a cyanobacterial layer. The evolution of chlorophylls into bacteriochlorophylls would then have occurred during or after the GOE.

Therefore, it is considered that the contemporary groups of anoxygenic phototrophs

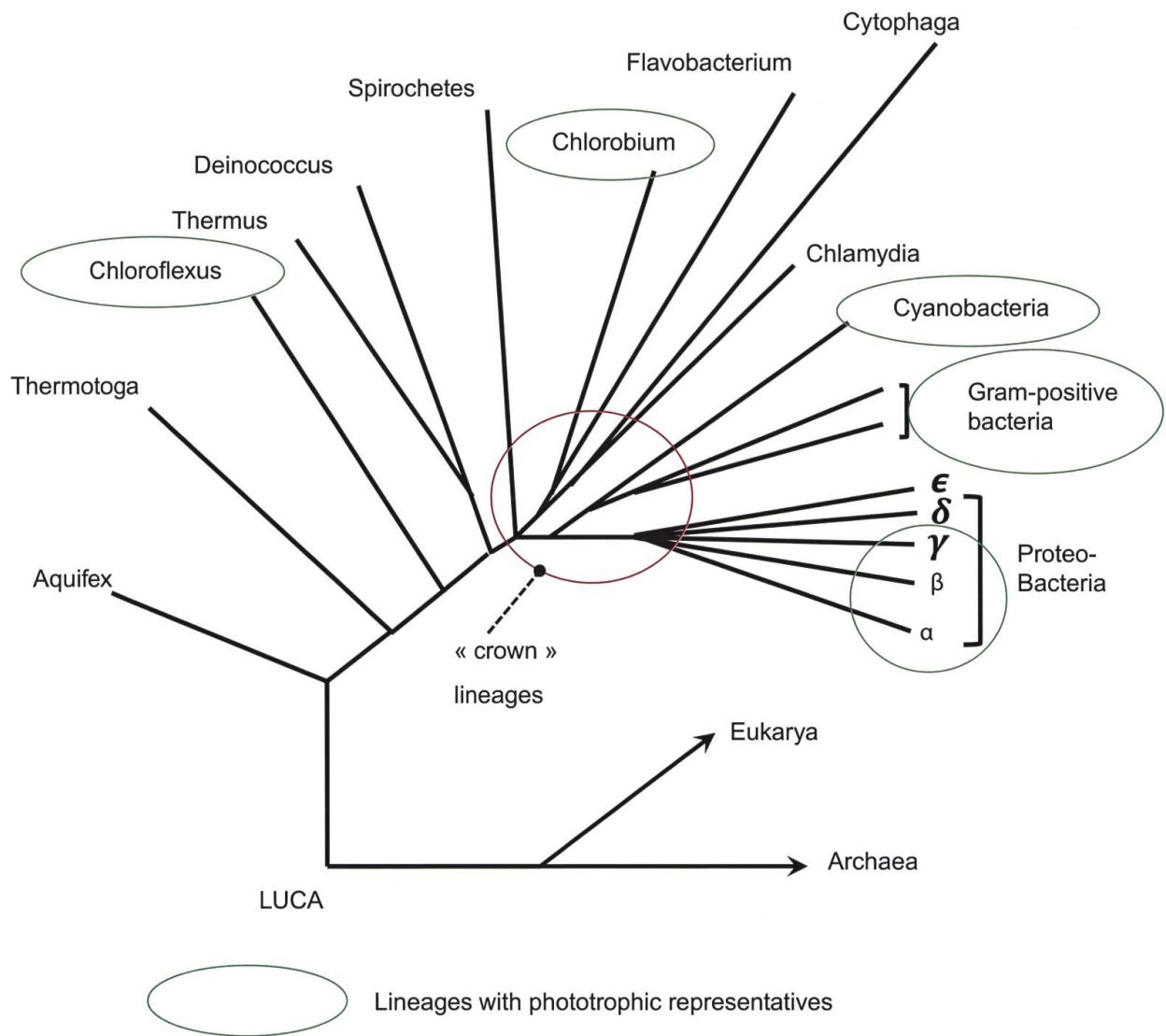


Fig. 14. Global representation of the phylogeny of the Bacteria domain, drawn from ribosomal sequences comparison. Adapted from MADIGAN & MARTINKO (2006).

have differentiated posteriorly to cyanobacterial settlement. Ancient phototrophs would then belong to “ghost” groups, having transferred their photosynthetic abilities through multiple HGTs to “crown” prokaryotes before their extinction. In general, it is estimated that most of the bacterial lineages ever to have inhabited this planet have become extinct.

3.3 Microbial communities in Dresser formation stromatolites

So, how can we imagine the inhabitants of bacterial mats / stromatolites to have existed in Dresser formation microbialites and other similar structures in Paleoarchean times?

Looking at the present-time mat in fig. 13, except the cyanobacterial layer, anoxygenic phototrophs of the ur-phototroph type, with chlorophyll-like pigments in their light-converting

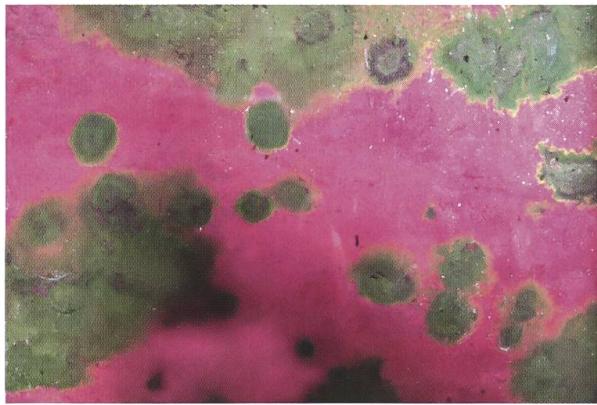


Fig. 15. A detail of a Winogradsky column in the Botanical Garden of Neuchâtel, showing the development of green and purple anoxygenic phototrophs. This ecosystem was constructed 20 years before the picture was taken and was hermetically closed from the beginning. Laboratory of Microbiology, Institute of Biology, Neuchâtel University. Photo by the second author.

photosystem, would have been the basic structuring agents. They would have produced extracellular polymeric substances (EPS) resistant to degradation by methanogenic communities (BOSAK *et al.*, 2013), which could also have had a catalytic effect favoring carbonates and Fe(III) precipitation. Their reductive, heterotrophic counterparts should have been present, i.e., elemental sulfur- / sulfate-reducers or Fe(III) reducers, to complete either the S or Fe cycles, thus allowing a cyclic management of the energy transfer elements linked to their respective metabolisms (fig. 11). A carbon cycle would have been realized through the intermediary of fermenting bacteria, which would have fed on primary metabolites such as biopolymers, sugars, and amino acids, secreted or issued from the decaying biomass of phototrophs. The production of intermediate metabolites from their activity such as alcohols and organic acids would have, in turn, fed sulfate or Fe(III) reducers that would have produced HCO_3^- , as a carbon source for the photoautotrophs. This cycle is realized in the Winogradsky columns (figs. 15 and 16). An unanswered question is protection

against UV radiation in the absence of the ozone shield, which only appeared after the GOE. This could have been achieved if the mats had been formed in shallow water, for example, in lagunas. Another possibility is the development of a protective layer (like in fig. 13) above the phototrophic mat, possibly formed by highly radio-resistant bacteria similar to *Deinococci*, which show a considerably greater resistance to radiation than common bacteria.

Another possibility, particularly in the supposed conditions of the Dresser formation (VAN KRANENDONK *et al.*, 2006) would be the presence of geothermal waters that contained HCO_3^- and H_2 , H_2S , or Fe^{2+} flowing across surfaces exposed to light and allowing continuous feeding of anoxygenic phototrophs without the need for the cyclic management of these elements, like the sulfur spring mats in fig. 12. A combination of both cyclic and acyclic ecosystems could also have been possible.

CONCLUSION

The anoxygenic phototrophs that were active 3.48 Ga ago most probably belonged to ghost lineages, having transferred through multiple HGTs to present-time lineages, descendants of those old metabolic functions (SHIH *et al.*, 2017a; WARD & SHIH, 2021), as well as the ability to form mats through the secretion of EPS, thus giving rise to MISS (microbially induced sedimentary structures, NOFFKE *et al.*, 2013) among which there were stromatolites. Dissimilatory Fe(III) and SO_4^{2-} reductions were present in both the Archaea and Bacteria domains with related enzyme sequences (WAGNER *et al.*, 1998; DONG *et al.*, 2021), indicating a probable very ancient, pre-LUCA origin, or post-LUCA HGT between both domains. Thus, the actors in a complete photo-anaerobic ecosystem, as shown in fig. 11 and realized with present-time bacterial communities in Winogradsky columns (figs. 15 and 16), were most probably present

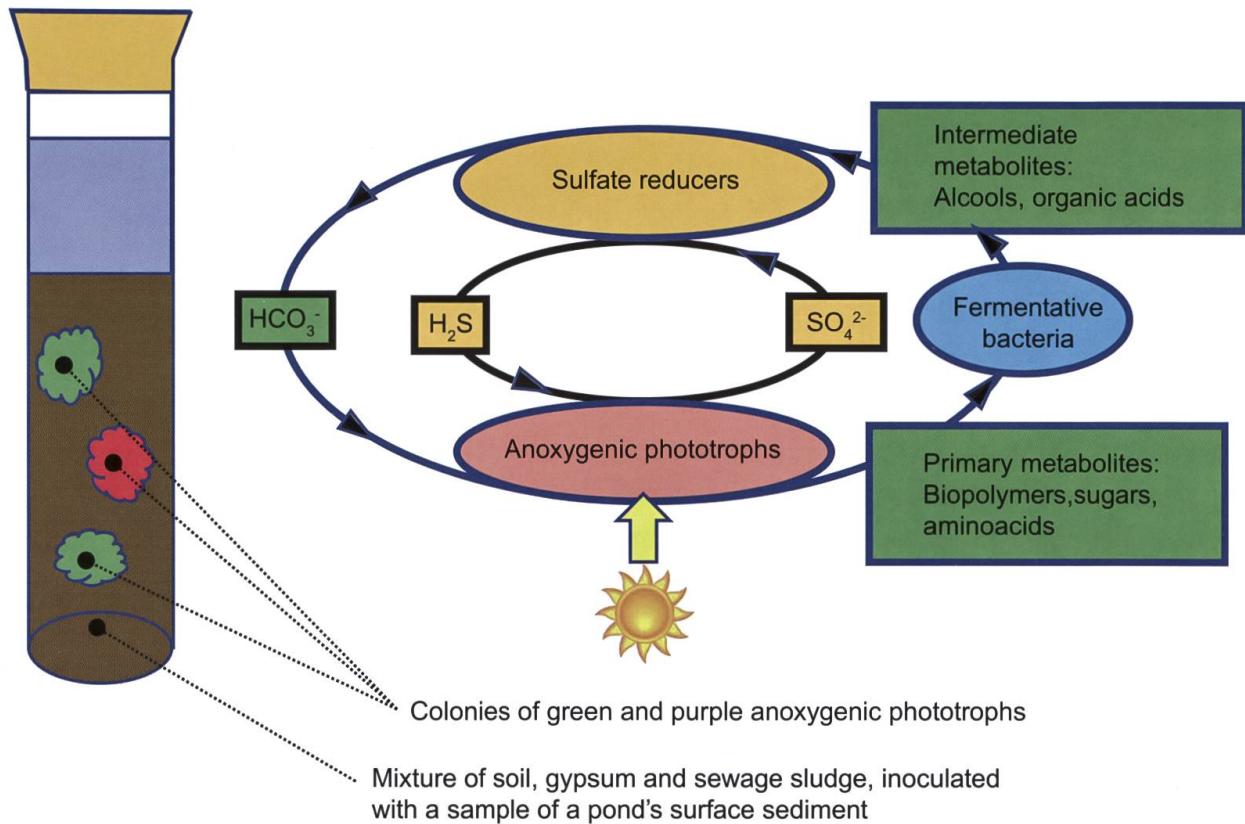


Fig. 16. Combined carbon and sulfur cycling in a Winogradski column.

during the time when “Dresser formation” microbes were active.

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