Free Radical Biology and Medicine 140 (2019) 206–223

Contents lists available at ScienceDirect

Free Radical Biology and Medicine

journal homepage: www.elsevier.com/locate/freeradbiomed

Cyanobacteria evolution: Insight from the fossil record

Catherine F. Demoulin[a,*,1], Yannick J. Lara[a,1], Luc Cornet[a,b], Camille François[a], Denis Baurain[b], Annick Wilmotte[c], Emmanuelle J. Javaux[a]

[a] Early Life Traces & Evolution - Astrobiology, UR ASTROBIOLOGY, Geology Department, University of Liège, Liège, Belgium
[b] Eukaryotic Phylogenomics, InBioS-PhytoSYSTEMS, University of Liège, Liège, Belgium
[c] BCCM/ULC Cyanobacteria Collection, InBioS-CIP, Centre for Protein Engineering, University of Liège, Liège, Belgium

ARTICLE INFO

Keywords:
Biosignatures
Cyanobacteria
Evolution
Microfossils
Molecular clocks
Precambrian

ABSTRACT

Cyanobacteria played an important role in the evolution of Early Earth and the biosphere. They are responsible for the oxygenation of the atmosphere and oceans since the Great Oxidation Event around 2.4 Ga, debatably earlier. They are also major primary producers in past and present oceans, and the ancestors of the chloroplast. Nevertheless, the identification of cyanobacteria in the early fossil record remains ambiguous because the morphological criteria commonly used are not always reliable for microfossil interpretation. Recently, new biosignatures specific to cyanobacteria were proposed. Here, we review the classic and new cyanobacterial biosignatures. We also assess the reliability of the previously described cyanobacteria fossil record and the challenges of molecular approaches on modern cyanobacteria. Finally, we suggest possible new calibration points for molecular clocks, and strategies to improve our understanding of the timing and pattern of the evolution of cyanobacteria and oxygenic photosynthesis.

1. Introduction

Modern cyanobacteria constitute an ancient and well-diversified bacterial phylum, with unique complex morphologies and cellular differentiation. They play a key role in food webs as primary producers performing oxygenic photosynthesis. Cyanobacteria also played a major role in early biogeochemical fluxes and in Life and Earth evolution. They are the only prokaryotic organisms that perform oxygenic photosynthesis, and are thus generally held responsible for the rise of oxygen in the atmosphere and oceans around 2.4 Ga, during the so-called Great Oxidation Event (GOE [1,2]), facilitated by geological processes [3]. Oxygenic photosynthesis has enabled the oxygenation of oceanic and terrestrial niches, and the diversification of complex life [4]. Indeed, most modern eukaryotes need a minimal concentration of molecular oxygen to synthesize their sterol membranes [5]. They diversified from a last eukaryotic common ancestor (LECA), an aerobe protist with a mitochondrion [6]. Further increased oxygen concentration was required for the metabolic activity of mobile macroscopic metazoans [7]. At least 1.05 Ga ago, oxygenic photosynthesis spread among some eukaryotic clades, giving rise to diverse types of algae and later to plants. This important evolutionary step was due to the primary endosymbiosis of a cyanobacterium within a unicellular eukaryote [8,9], and subsequent higher-order endosymbiotic events [10]. The endosymbiotic theory is well supported by biochemical, ultrastructural, ecological and molecular data [11], although the identity and habitat of the cyanobacterial ancestor of the chloroplast are still debated [12–17].

Despite the importance of cyanobacteria in the early evolution of Earth and life, fundamental questions remain about their origin, the timing and pattern of their diversification, and the origin of oxygenic photosynthesis, ranging from the Archean to the GOE [18]. One crucial problem to solve is the discrepancy between the unambiguous cyanobacterial fossil record, starting at 1.9 Ga, the GOE at 2.4 Ga, and the report of several older geochemical data suggestive of oxygenic photosynthesis ([19]; but see Ref. [20]) [21–25]; and [26,27].

Several types of evidence are used to reconstruct the fossil record of cyanobacteria, but all have their limitations and challenges. Stromatolites are usually associated to cyanobacterial activity. However, although conical stromatolites seem to plead for oxygenic photosynthesis [28], others types of stromatolites and microbially induced sedimentary structures (MISS) [29–31] may have been produced by non-cyanobacterial lineages, such as anoxygenic phototrophs [28,32], or by/in association with methanotrophs [33]. This suggests that stromatolites and MISS are not necessarily indicative of

* Corresponding author.
E-mail address: cdemoulin@uliege.be (C.F. Demoulin).
[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.freeradbiomed.2019.05.007
Received 29 November 2018; Received in revised form 13 March 2019; Accepted 5 May 2019
Available online 09 May 2019

cyanobacteria activity, and perhaps not even of photosynthesis [34]. Biomarkers (fossil molecules) can indicate the presence of metabolisms such as oxygenic photosynthesis, but they are preserved only in well-preserved unmetamorphosed rocks, and contamination is a challenge [35]. Among those, lipids such as 2-methyl-hopanes are produced by cyanobacteria [36] but not only [37], and pigments such as porphyrins with N isotope composition [38]. Other geochemical (redox and isotopic) proxies can also inform on the presence of molecular oxygen in the water column or biologically-induced isotopic fractionation due to oxygenic photosynthesis, but their interpretation is often debated. Finally, microfossils may provide direct evidence for cyanobacteria, but their identification is often ambiguous. At the present time, the cyanobacterial identity of only three fossil taxa is not debated: *Eoentophysalis*, *Eohyella* and *Polybessurus*. *Eoentophysalis belcherensis* is the oldest microfossil interpreted with certainty as a cyanobacterium [39]. This microfossil has been described from 1.89–1.84 Ga silicified stromatolites of the Belcher Supergroup, Hudson Bay, Canada [39].

Microbiology of modern cyanobacteria pairs the geological and paleobiological approaches. The accumulation of modern cyanobacterial genetic data in public databases increasingly allows phylogenetic reconstructions and molecular clock analyses aimed at estimating the origin of the phylum and the origin of oxygenic photosynthesis. However, due to the lack of tree calibrations from the fossil record, contamination of genetic sequences, chosen dataset, and limitations or differences in models, these estimates are quite variable [40]. Thus, discrepancies between the geological and fossil records and molecular phylogenies remain, and the origin and evolution of cyanobacteria, oxygenic photosynthesis, and the chloroplast are still debated.

In this paper, we review classic and new biosignatures of cyanobacteria, critically assess their fossil record, and suggest possible new calibration points for molecular clocks. We also briefly discuss molecular phylogenies, molecular clocks and their discrepancies. We finally make some suggestions for future research, to improve our understanding about the evolution of cyanobacteria and its consequences on Earth and biosphere evolution.

Fundamental and unresolved questions regarding the early evolution of cyanobacteria
What are the timing, pattern, and environment of cyanobacteria origin and evolution?
How to interpret the discrepancies between the fossil record and molecular phylogenies, and how to reconcile these records?
What are the origin and timing of oxygenic photosynthesis?
Which among geochemical redox proxies and stromatolites are reliable indicators of oxygenic photosynthesis?
What is the origin, timing, and environment of chloroplast acquisition by endosymbiosis and evolution of eukaryotic photosynthesis?

2. Identification of cyanobacteria in the fossil record

Paleontologists have to rely on information other than the genomic data and internal cellular organization to identify the biological affinities of early microfossils. In some cases, conventional biosignatures such as morphology, division mode, presence of ornamentation, ultrastructure, and chemistry of carbonaceous cell walls, combined with their distribution pattern within the hosting rocks and the characteristics of their preservational environments may help deciphering their biological affinities [41–43].

Recently, new cyanobacterial signatures, such as intracellular biominerals, molecular fossils of lipids and pigments, and isotopic signatures of carbon and nitrogen, measured on single molecules or whole microfossils, were proposed as tools to better constrain the early evolution of cyanobacteria and their role in early ecosystems. These conventional and new biosignatures of cyanobacteria are discussed below.

2.1. Morphology and division pattern

Cyanobacteria were traditionally described as algae and referred to as 'Cyanophyta' or 'Blue green algae'. Until the end of the 20th century, the nomenclatural system of cyanobacteria followed the International Code of Botanical Nomenclature. In the late seventies, Stanier and colleagues [44] recognized the prokaryotic nature of the cyanobacteria and proposed to follow the International Code of Nomenclature for Bacteria. According to the Bergey's Manual of Systematic Bacteriology, and following the Stanier approach and Rippka et al. (1979) [45] concepts, cyanobacteria were divided into two groups: unicellular and multicellular filamentous cyanobacteria; and five subsections based on morphological criteria, and corresponding to five former cyanobacterial orders: Chroococcales (section I) and Pleurocapsales (section II) harbor unicellular cells, which divide by binary fission in one or multiple plans and are solitary or arranged in colonies. Pleurocapsales can also produce small easily dispersed cells (baeocytes) after division by multiple fissions. Within the multicellular filamentous cyanobacteria, Oscillatoriales (section III) have only vegetative cells arranged in filaments, whereas Nostocales (section IV), and Stigonematales (section V) are capable of producing specialized cells, the heterocytes, which allow N-fixation in an anoxic compartment; or can exhibit environmental stress resistant cells called akinetes. Besides, cyanobacteria from section V are also characterized by their ability to divide in more than one plane and form true branched trichomes [45].

Since that time, the taxonomic classification of cyanobacteria has been continually reevaluated with the development of electron microscopy and genetic characterization methods [46]. The classification into subsections is practical but does not reflect phylogeny because they are not all monophyletic except for the Nostocales and Stigonematales.

Interpreting microfossils as cyanobacteria is generally based on morphological criteria, and their mode of division. However, the simple shape of many microfossils makes an unambiguous identification very difficult [40]. The size of cyanobacteria cells or filaments may be used as a taxonomic criterion for microfossil biological affinity. However, microfossil size does not correspond exactly to the size of living microorganisms due to modification by taphonomic processes, including diagenesis, collapsing and flattening [47]. Moreover, different fossil and modern groups of bacteria, cyanobacteria and eukaryotic algae have overlapping size ranges. Therefore, microfossil size alone does not constitute a reliable criterion for the interpretation of a microfossil as a cyanobacterium [48] or even as a prokaryote or a eukaryote [49].

Cyanobacteria form spheroidal or rod-shaped cells, filaments or tubes. Some of them occur as spiral filaments (e.g. *Spirulina*, modern counterpart of *Obruchevella* [50]) but this morphology also occurs in other bacteria (*Leptospira* [51]). Cyanobacteria from the Nostocales and Stigonematales orders may present some of the most complex morphologies among prokaryotes, including specialized cells such as larger elongated cells with thicker walls (akinetes) and round cells in or at the end of the filament (heterocytes, fixing nitrogen). The complex multicellular filamentous forms of nostocalean and (uniseriate or multiseriate) stigonematalean cyanobacteria may also display false or true branching. These more complex cyanobacteria may present unique characters allowing to not only identify their fossils as cyanobacteria, but also as specific cyanobacterial clades, more useful as calibrating points.

However, most cyanobacteria have simple morphologies, widespread in the three domains of life. Simple prokaryotic shapes may lead to erroneous interpretations since abiotic processes, such as mineral growth, fluid inclusions, organics migration, or interstitial spaces between grains, can mimic biogenic forms [40,47,52–57]. Once the biogenicity of a microfossil is established, morphological observations need to be combined with other criteria, including the wall ultrastructure and molecular composition, in order to confirm unambiguously its identity [58,59].

The division pattern of fossil cells, when preserved, indicates their

reproduction, and in some cases, may be indicative of particular taxonomic groups [60,61]. Cyanobacteria reproduce asexually by binary or multiple fissions. Multiple fissions may lead to the formation of baeocytes, which are small cells formed within the parental cell [62]. They can also divide in two or three planes of division, such as *Entophysalis* spp., the modern counterpart of *Eoentophysalis*. Moreover, some cyanobacteria occur as colonies either within (e.g. *Gloeocapsa* spp., modern counterpart of *Gloeodiniopsis*) or without (e.g. *Cyanobium* spp., *Synechococcus* spp., and *Synechocystis* spp.) a thick polysaccharide envelope. They can also present more or less organized and dense aggregates (e.g. *Microcystis* spp., modern counterpart of *Eomicrocystis*) and even cells organized as tablets (e.g. *Merismopedia* spp.). Some cyanobacteria can also reproduce with the aid of hormogonia, which are short filaments resulting from break up of longer filaments [63]. Trichomes are ensheathed individual filaments [63].

2.2. Ultrastructure

The wall ultrastructure of modern cyanobacteria consists of a peptidoglycan layer of varying thickness in the periplasmic space between a cytoplasmic and an outer membrane, with generally an external S-layer [64]. In some cases, a transparent or pigmented exopolysaccharidic (EPS) envelope, the so called sheath, may surround cells, filaments or colonies. Cyanobacterial EPS includes two forms, one attached to the cell wall and one released in the environments. They may be composed by up to twelve different monosaccharides, including pentoses, hexoses, and acid hexoses as well as methyl sugars and/or amino sugars (e.g. N-acetyl glucosamine, 2,3-O-methyl rhamnose, 3-O-methyl rhamnose, 4-O-methyl rhamnose, 3-O-methyl glucose, see Ref. [65] for a review). In the fossil record, sheaths of cyanobacteria are very common given that they are more readily fossilized, or less easily degraded, than the unsheathed ones [66]. The association of sheaths with clay minerals is more frequent than with unsheathed cyanobacteria, which helps the preservation of these structures [67,68]. This association would be due to differences in the chemical composition between the EPS and the sheath, and the rapid coating of sheaths [67]. Precipitation of other minerals such as nano-aragonite [68] or silica [69] may also enhance preservation.

As phototrophs, all cyanobacteria but *Gloeobacter* spp [70]. possess internal membranes called thylakoids hosting the photosynthetic apparatus, the two photosystems and their pigments. The arrangement of the thylakoids in cells is well organized and coincide with cyanobacterial lineages taxonomy [71]. For example, in tested strains from Nostocales/Stigonematales thylakoids are coiled and concentrated at the periphery [71]. Since cyanobacteria are the only oxygenic photosynthetic organisms among prokaryotes, the presence of preserved thylakoids in microfossils would be a reliable criterion to confirm that they were able to make this type of photosynthesis [72]. So far, ultralaminae interpreted as thylakoids based on their stacking and thickness, were preserved in microfossils as old as 155 Ma [72]. In acid extraction of 600 Ky microbial mats also revealed the resilience of thylakoids displaying their concentric structure over the hosting cell walls [68]. In both cases, the preservation of thylakoids made of lipids, pigments and proteins was favored by clay minerals ([68,72] and discussion therein). Moreover, although eukaryotes also have thylakoids, they are compartmentalized in chloroplasts and often are arranged differently than in cyanobacteria. Therefore, the distinction between cyanobacterial and eukaryotic thylakoids would be possible in fossils if they are preserved [72].

2.3. Paleoecology and behavior

Geochemical proxies may provide indirect evidence for oxygenation, at the planetary scale, such as the GOE, or at the scale of basins [73–77], and permit the reconstruction of the evolution of paleoredox conditions. However, as mentioned above, their interpretation can be challenging and do not necessarily imply the existence of oxygenic photosynthesis. In the best cases, they represent average values of local conditions over a relatively large time scale compared to the life span and sedimentation of individual taxa within a given microfossil assemblage (which itself also represents a time average, biased by taphonomy). Thus, establishing the paleoecology of fossil assemblages is difficult, although combining micropaleontology and geochemistry at high-resolution along a paleoenvironmental gradient may be informative [54,75], review in Ref. [78]. Hence, examining the consistent trends in distribution of some microfossil taxa in photic zones, in silicified stromatolites or other carbonates, or in microbial mats preserved in siliciclastic rocks, might give a hint to their metabolism and point to (anoxygenic or oxygenic) photosynthesis. Nevertheless, paleontologists and biologists have to keep in mind that the paleoecology of fossil organisms might differ from their modern relatives.

At the microscale, the distribution and the orientation of microfossils within rocks may also provide insights about their ecology [41]. Moreover, their orientation might help to infer the behavior of microfossils, such as phototropism of filaments erected towards the light or chemotropism, rock-boring by endolithic microbes, mat-building benthic microbes, or plankton settling down with no preferential orientation [79,80]. For example, Green et al. [81] and Golubic and Seong-Joo [61] concluded that *Eohyella* was a euendolithic cyanobacterium owing to its orientation in oolithes, by analogy with its modern counterpart, *Hyella* [41]. Euendoliths are rock-inhabiting microorganisms, which dissolve mineralized substrates to penetrate the rock [82], in contrast to other endoliths, e.g. chasmoendoliths, which are endoliths that colonize existing rock fissures [82].

2.4. Molecular fossils

Molecular fossils include complex organic molecules produced only by biology and, in some cases, are indicative of particular metabolisms or lineages [83]. Cyanobacteria produce lipids (2-methyl-hopanes – [83,84] and pigments that can potentially be preserved in the unmetamorphosed geological record [35,36]. So far, the lipids 2-methylhopanes were extracted from bitumen in black shales as old as 1.6 Ga (McArthur basin, Australia) [83,84]. Their oldest record at 2.7 Ga [85] was reassessed as younger contaminants [86,87]. These fossilized lipids were first attributed to cyanobacteria [84], but it is now acknowledged that they might be signatures of other bacterial lineages [37].

Pigments are also used as signatures for (anoxygenic and oxygenic) photosynthesis. More precisely, the presence of ancient chlorophylls can be detected by the preservation of their nitrogen-containing tetrapyrrole (porphyrin) core. Moreover, some fossilized forms of carotenoids, such as okenane and isorenieratane evidence the presence of purple S-bacteria, green S-bacteria and other bacterial lineages (incl. cyanobacteria) [83]. Even if they are not unique to cyanobacteria, their report shows pigment can be preserved in relatively old unmetamorphosed rocks.

The oldest porphyrins reported so far are preserved in shales of the 1.1 Ga Taoudeni basin, Mauritania [38], which also preserves exquisite microfossils, including eukaryotes and cyanobacteria [88]. These fossilized pigments exhibit a specific N isotope fractionation indicating a cyanobacterial source and permit to suggest that cyanobacteria were the dominant primary producers in mid-proterozoic oceans [38].

Other UV-protective (sunscreen) pigments may be used as signature for bacterial life, such as the mycosporin-like amino acids (MAAs), and two colored molecules specific of cyanobacteria: scytonemin and gloeocapsin. For instance, the combined analyses of modern cultures and fossil (4500 years BP) microbial mats of cyanobacteria from Antarctica revealed that cells and pigmented filamentous sheaths can withstand acetolysis (used to isolate them from the mineral matrix) and retain their molecular signature identified by FTIR microspectroscopy [68]. They are also preserved in siliciclastic sediments by precipitation of nano-aragonite and clay minerals [68]. FTIR microspectroscopy of

microfossils enables the non-destructive analysis of the biopolymer composition of cell walls or sheaths. Comparison with taxonomically informative polymers unique to particular modern clades permit to identify the microfossils, in combination with the morphology and wall ultrastructure [58]. However, the scarce knowledge of the composition of pigments, preservable cells, cysts and other structures produced by modern microorganisms, and of their transformation and alteration through fossilization, limits this approach. Moreover, high temperature and pressure (metamorphism) after burial can alter even more or erase original biological properties [89]. Raman microspectroscopy enables estimating the temperature at which the organic material has been submitted (e.g. Ref. [90]), which is necessary to interpret properly the spectra obtained by FTIR microspectroscopy [89]. Raman spectroscopy also permits to characterize molecules in modern organisms, including cyanobacteria [68,91–94]. Scytonemin is a molecule consisting of phenolic and indolic subunits [95]. Today it is notably biosynthesized in benthic filaments of *Calothrix* sp. [68], and in the endolithic cyanobacteria *Hyella* sp. and *Solentia* sp., from coastal carbonates [93]. It may be a promising signature of cyanobacteria given that it can be fossilized [68,96]. In older deposits from Antarctica, derivatives of scytonemin and carotenoids can be extracted from 125000 years BP sediments [97]. However, the preservation potential of scytonemin in older rocks is not known. Artificial taphonomic experiments of decaying cyanobacterial cultures showed the recalcitrance of filamentous polysaccharide sheaths, possibly helped by the presence of pigments [66]. However, in lake sediments from Antarctica, both brown (scytonemin-rich) and transparent (scytonemin-poor) filamentous sheaths were well preserved; hence, scytonemin probably was not the factor driving their preservation [68].

Gloeocapsin, an enigmatic pigment detected in the thick sheath enveloping colonies of the cyanobacterial genus *Gloeocapsa* growing on carbonate surfaces [93] and in lichens (with cyanobacterial symbionts), might also become a useful indicator, but its molecular composition remains to be characterized and its preservation potential is currently unknown [93].

2.5. Isotopic fractionation

Carbon isotopes fractionation do not permit to discriminate oxygenic photosynthesis from other metabolisms that have overlapping range of fractionation, except for methanogenesis [98,99]. At the microscale, C and N isotopic composition can be measured on single microfossils with undisputed biogenicity [100–102] and might reveal some information on inferred paleobiology and metabolism, but only when combined with their morphology, ultrastructure, molecular composition, paleoecology and behavior.

Analyses of N isotopic fractionation measured on molecular fossils can also indicate metabolism and cyanobacterial affinity. Phototrophic organisms have a specific nitrogen isotopic offset between total biomass and chloropigments [38]. Based on laboratory experiments, this offset is independent of the nitrogen source (NH_4^+, N_2, or NO_3^-) and its isotopic composition and from redox conditions during cell growth. The N isotopic offset remains relatively constant within different phototrophic organisms such as cyanobacteria, bacteria, red or green algae or plants, and thus may help identify the source organisms. This offset was notably measured on in 1.1 Ga porphyrins, permitting to relate them to cyanobacteria [38].

2.6. Intracellular biomineralization

Passive biomineralization leads to precipitation of minerals on filaments, sheaths, or cells and enhance their preservation potential but is not specific of particular microorganisms [103,104]. Active biomineralization is controlled by the cell or the organism and might be indicative of its metabolism and taxonomic identity. In modern oceans and alkaline lakes, some cyanobacteria have the capacity to form beads of intracellular Ca-carbonates [57,105], but their preservation potential is unknown. Some extant cyanobacteria also have the capacity to produce intracellular ferric phosphates [106]. In the 1.88 Ga Gunflint Formation, Canada, specific microfossil taxa preserved in silicified stromatolites contain internal Fe-silicate and Fe-carbonate nanocrystals, absent from the external wall surfaces. This feature and its distribution pattern are consistent with intracellular biomineralization, with subsequent recrystallization, and not with known patterns of diagenesis. Thus, the combination of large size, morphology and intracellular Fe biominerals is consistent with a cyanobacterial affinity, and not with other known Fe-mineralizing microorganisms [107]. High-resolution observations, as illustrated in Ref. [107], might possibly reveal new cyanobacteria signatures at the nano-scale, in the rock record.

3. The fossil record

Microfossils interpreted as cyanobacteria have been reported in rocks as old as the early Archean, but their biogenicity and interpretation is highly debated. The necessity of reliable criteria for the study of microfossils is well illustrated with the famous controversy surrounding the “microfossils” from the 3.45 Ga Apex Chert, Australia [108]. These traces interpreted as fossil cyanobacteria based on their morphology and the geological context [108] were subsequently reassessed either as pseudofossils [109–111], contaminants [48], mineral artefacts [53], or microfossils [112–114] and the geological context was revised [110].

In this section, we discuss a selection of (1) unambiguous cyanobacteria microfossils for which morphological features and habitats coincide strikingly with modern lineages, (2) probable and possible cyanobacteria microfossils that share morphological similarities both with a taxon belonging to the cyanobacterial phylum and with other lineages belonging to another phylum or domain of life. The limited number of preservable characters, along with their taphonomic alteration, and possible morphological convergence, limits the interpretation of the fossil record. Therefore, additional signatures would strengthen the confidence in the identification of fossil cyanobacteria. Table 1 summarizes the morphology, dimensions, habitats, and geological occurrences of the fossil taxa discussed below and their possible modern counterparts. Supplementary Table 1 summarizes the geochronological information dating these fossil occurrences.

3.1. Unambiguous microfossils of cyanobacteria

Although microfossils attributed to cyanobacteria are abundant during the Proterozoic, many of them are identified with some ambiguities. Knoll and Golubic [41] determined a confidence range for these microfossils, since most of them are identified based on morphology, sometimes coupled with their occurrence in the photic zone, despite the possibility of morphological convergence. So far, only three taxa are unambiguously identified as cyanobacteria: *Eoentophysalis, Polybessurus* and *Eohyella,* because they also present distinctive modes of division.

3.1.1. Eoentophysalis

The cyanobacteria fossil record starts around 1.9 billion years ago with the most emblematic Proterozoic microfossil identified so far with certainty as a cyanobacterium, *Eoentophysalis belcherensis* (Fig. 1A). *E. belcherensis* was first described in the 1.89–1.84 Ga Belcher Supergroup, Hudson Bay, Canada, where this colonial microorganism formed mats in silicified stromatolites [39,115].

The identification of *E. belcherensis* is based on comparison with the modern cyanobacterium genus, *Entophysalis* [115]. Based on morphology, *Entophysalis* belongs to the order Chroococcales [116] and consists of coccoidal unicells forming characteristic pustular palmelloid colonies. The morphology of *Entophysalis* colonies is due to its mode of cell division by binary fission in three perpendicular planes. Modern

Table 1
Summary of microfossil morphological features, habitat, occurrences and their modern analogues.

Microfossil	Morphology	Dimensions (μm) (length x width)	Habitat	Occurrences Formation/Group, (age in Ga), country	Modern analogue
Anhuithrix magna	Uniserial, straight, curved, bent or twisted filament. Presence of globose cells (akinetes) in or at the end of the filament. In aggregates, filaments are in a common mucilaginous matrix. If isolated, trichomes may be enveloped by an extracellular sheath (thin and non-lamillated).	Filament: up to 2 cm x 141-615 Cells: 56–425 × 113-614 Globose cells: 364-800	Transitional to offshore zones. Benthic organism.	Liulaobei Fm (0.84), North China [128]	Nostocales and Stigonematales
Archaeoellipsoides	Ellispoidal vesicle with a smooth or ribbed wall. With rounded, flat or slightly depressed ends, Solitary or in groups	50–100 × 15-25	Peritidal platform	Francevillian Group (2.1–2.04), Gabon [135]; McArthur Group (1.653–1.647), Australia [136]; Salkhan Limestone (1.6), India [173]; Gaoyuzhuang Fm Jixian section (~1.58), China [144]; Kotuikan Fm & Yusmastakh Fm (1.5), Siberia [133]; Wumishan Fm (1.425), China [174]; Dismal Lake Group (1.4), Canada [175]; Debengda Fm (1.265–1.04), Siberia [176]; Shorikha Fm (1), Siberia [177]; Kirgitey & Lopatinskaya Fm (0.8), Siberia [178]; Chichkan Fm (0.65), South Kazakhstan [179]	*Anabaena* (akinetes) Possible Nostocales or Stigonematales
Eoentophysalis belcherensis	Spheroidal to ellipsoidal cells arranged in dyads, tetrads, octets or in loose or palmelloid colonies (spherical, hemispherical or mushroom-like shape), Division by binary fission in three perpendicular planes. The outer layers of colonies are pigmented.	2,5-9	Intertidal, mudflats and shallow sub- and supratidal zone	Belcher Supergroup (1.89–1.84), Canada [39]; Amelia Dolomite (McArthur Group – 1.653–1.647), Australia [180]; Kotuikan Fm & Yumastakh Fm & Avzyan Fm (1.5), Ural Mountains [133]; Kheinjua Fm (1.5–1), India [181]; Balbirini Fm (1.483), Australia [182]; Gaoyuzhuang Fm & Wumishan Fm (Changcheng Group – 1.425), China [139]; Sukhaya Tunguska Fm (1), Siberia [154]; Bitter Springs Fm (0.81–0.79), Australia [140]; Deoban Limestone & Jammu Limestone Fm (1–0.967), India [183]; Jiudingshan Fm (0.8), China [184]; Min'Yar Fm (0.79–0.68), Southern Ural Mountains [185]; Svanbergfjellet Fm (0.75–0.7), Spitsbergen [171]; Narssârssuk Fm (0.688), Greenland [186]; Ediacaran Shuurgat Fm (0.635), Mongolia [187]	*Entophysalis* Chrooccocales
Eohyella	Uni-, bi- or multiseriate pseudofilament which penetrates the substrate. Branched or unbranched.	4–21 × 8,5- < 50	Euendolithic in silicified ooids, intertidal and subtidal environments	Dahongyu Fm (Changcheng Group – 1.63), China [126]; Koldaha Shale Fm (1.5–1), India [188]; Backlundtoppen Fm (0.8–0.7), Spitsbergen [189]; Eleonore Bay Group (0.95–0.68), Greenland [81]; Red Pine Shale unit (Uinta Mountains Group – ~0.75), USA [190]; Nagod Limestone Fm (0.625 or 0.75–0.65), Central India [191]	*Hyella* Pleurocapsales
Eomicrocystis	Subspheroidal colonies, or packets, of spheroidal to ellipsoidal vesicles with a single layered wall.	0,8–6,5 or 15-17	Subtidal to intertidal environment	Kotuikan Fm (1.48–1.47), Siberia [138]; Widely distributed in Meso-Neoproterozoic	*Microcystis* Chroococcales
Gloeodiniopsis	Spheroidal vesicles, sometimes solitary but commonly in colonies. Vesicles are usually with multilayered envelope.	0,8-8	Intertidal environment	Bitter Springs Fm (0.81–0.79), Australia [140]; widely distributed in Meso-Neoproterozoic	*Gloeocapsa* or *Chroococcus* Chroococcales
Obruchevella	Tightly or loosely coiled empty tube with loose or regular cylindrical spirals.	Width: 0,8-8; 11–25; 27-55	Intertidal to supratidal; in open shelf; in tidal flats	Gaoyuzhuang Fm (~1.58), China [144]; Kamo Group (1.5–1.05), Russia [192]; Thule Supergroup (1.3–1.2), Greenland [193]; Avadh Fm (1.25–1.15), India [194]; Atar/El Mreïti Group (1.1), Mauritania [75]; Mbuji-Mayi Supergroup (1.03–0.95), DRC [165]; Bylot Supergroup (1.092 ± 59 Ma), Canada [163]; Burgess Shale (0.5), Canada [147];	*Spirulina* for narrower diameter, and *Arthrospira* for larger forms, Oscillatoriales, or eukaryotes

(*continued on next page*)

Table 1 (*continued*)

Microfossil	Morphology	Dimensions (μm) (length x width)	Habitat	Occurrences Formation/Group, (age in Ga), country	Modern analogue
Oscillatoriopsis	Uniseriate and unbranched trichome, without sheath, formed by discoidal to cylindrical cells whose length is less or equal their diameter. Apices may sometimes be tapered. Solitary or in mat-like mass.	Cell length: 1,8-12 Trichome width: 1-11; 25; 63	Shallow water marine environments, subtidal shelf environments, peritidal flat and pluvial lakes	Bitter Springs Fm (0.81–0.79), Australia [140]; widely distributed in Proterozoic	*Oscillatoria*, Oscillatoriales or other bacteria
Palaeolyngbya	Uniseriate unbranched trichome formed by discoidal to cylindrical cells. Trichome surrounded by an uni- or multilayered smooth sheath.	2–8 x 8-85	Peritidal flat, restricted tidal flat or open shelf	Bitter Springs Fm (0.81–0.79), Australia [140]; Widely distributed in Proterozoic	*Lyngbya* Oscillatoriales, or other bacteria
Polybessurus	Multilamellated cylindrical stalk with concave and regularly spaced layers and with funnel-like shape. The top of the stalk is open or is ended by preserved cells.	Cell: 25–85 × 20-60 Stalk: 20–600 × 15-150	Intertidal to subtidal environments	Avzyan Fm (1.35–1.01), Russia [123]; Society Cliffs Fm (1.2), North America [169]; Hunting Fm (1.2), North America [195]; Sukhaya Tunguska Fm (1), Siberia [196]; Seryi Klyuch Fm (1.1–0.85), Siberia [197]; Skillogalee Dolomite (0.77), Australia [198]; Svanbergfjellet Fm (0.75–0.7), Spitsbergen [171]; Eleonore Bay Group (0.95–0.68), Greenland [121]	*Cyanostylon* -like, Pleurocapsales
Polysphaeroides filiformis	Spheroidal vesicles arranged in a filamentous aggregate surrounded by a common sheath closed at both ends. Cells are dispersed or arranged in pairs, tetrads, octets or in colonies. Colonies sometimes arranged in pairs forming pseudobranched filament.	Sheath: 300–500 x 7–13,5 Cell width: 3,5-8	Shallow subtidal shelf	Ust'-Il'ya Fm & Kotuikan Fm (1.48–1.46), Siberia [199]; Mbuji-Mayi Supergroup (1.03–0.95), DRC [165]; Miroedikha Fm (0.85), Siberia [162]; Vychegda Fm (0.635–0.55), East European Platform [200]	*Stigonema robustum*, Stigonematales, or green and red algae
Siphonophycus	Cylindrical empty tube, unbranched with non-septate. Solitary or generally arranged in mass.	≤120 x 1–3,7	Subtidal environments	Bitter Springs Fm (0.81–0.79), Australia [140]; Widely distributed in Proterozoic	*Oscillatoria* –like, Oscillatoriales, Or other bacteria

Entophysalis produce highly hydrated exopolymer envelopes that expand during cell division. With this expansion, the older exopolymer envelopes are moved outward. Another particularity of *Entophysalis* colonies is the presence in the outer layers of the colonies of a yellow-brown UV-protecting pigment, scytonemin, that is produced by the most external cells for protection against intense solar radiation [117]. *Entophysalis* cells grow in the form of mats in the intertidal range of shallow marine basins [115,117]. This cyanobacterial genus may also precipitate micrite in stromatolites such as those in the shallow hypersaline Hamelin Pool, Shark Bay (Western Australia), in association with other cyanobacteria but also other Bacteria, and halophilic and methanogenic Archaea [34,117–119]. *Entophysalis* is dominant in pustular mats, but also in smooth and colloform coccoidal mats and precipitate micrite, playing a key role in lithifying the stromatolites compared to filamentous forms [34]. They are also reported to enable the stabilization of loose sandy substrate and contribute to the formation of stromatolites by passively trapping sediment particles on the mat's surface between its irregularities [115,117].

The microfossils *Eoentophysalis belcherensis* were discovered in silicified stromatolites from the Kasegalik and McLeary formations of the Paleoproterozoic Belcher Supergroup (1.89–1.84 Ga). The geological context of these two formations corresponds to intertidal mudflats as well as shallow subtidal and supratidal zones [39,120]. These paleoenvironments are thus comparable to the modern ecological niches occupied by *Entophysalis*. In addition, *E. belcherensis* and *Entophysalis* have similar morphological attributes and, both consist of coccoidal cells showing the same size range (Table 1). They both reproduce by binary fission in three perpendicular planes with a high production of exopolymeric envelopes. Finally, both fossil and modern colonies present the same characteristic warty (pustular) mamillate shape and darkened external layers [115]. However, the nature of this dark outer layer in the fossil colonies remains to be elucidated, as it could be simply due to desiccation instead of specific pigments [59,115]. The morphology of those cells and colonies occurs exclusively in Chroococcales [41]. Therefore, the combination of those criteria (morphology, development, environment and colony pigmentation) enabled the unambiguous identification of this microfossil.

3.1.2. *Polybessurus*

Polybessurus is another Proterozoic microfossil unambiguously identified as a cyanobacterium [121]. *Polybessurus* was formally described from silicified carbonates of the ca. 950-680 Ma Eleonore Bay Group (East Greenland) [121], following Fairchild, who was the first who described *Polybessurus* in his unpublished PhD thesis [122]. Its oldest occurrence is in the ca. 1.35–1.01 Ga Avzyan Formation, Russia [123].

Polybessurus is a fossil of a coccoidal unicellular microorganism with a very particular morphology unique to cyanobacteria (Fig. 1B). This microfossil is composed of a cylindrical stalk produced by means of asymmetric and unidirectional secretion of extracellular mucopolysaccharide envelopes, growing from within the sediments upward. Ellipsoidal cells, surrounded by multiple envelopes, are present at the higher end of the stalk. The primordial role of this stalk is to maintain the cells at the sediment-water interface [124]. The morphology of *Polybessurus* resembles a stack of cup shaped envelopes.

This particular morphology with cells jetted upward by the stalk is similar to the modern cyanobacterium *Cyanostylon* belonging to the order Chroococcales (Fig. 1C). However, *Polybessurus* reproduced by the formation of baeocytes (smaller cells) which is characteristic of the order Pleurocapsales, but is unlike the modern *Cyanostylon* [121]. Indeed, the reproduction mode of *Polybessurus* was inferred from preserved clusters of narrow tubes radiating from the same point. This particularity allows to suggest that those narrow tubes were produced by small cells [121]. Thus, the modern counterpart of *Polybessurus* is a not yet described Pleurocapsales *Cyanostylon*-like cyanobacterium discovered in peritidal environments of the Bahama Banks, environments

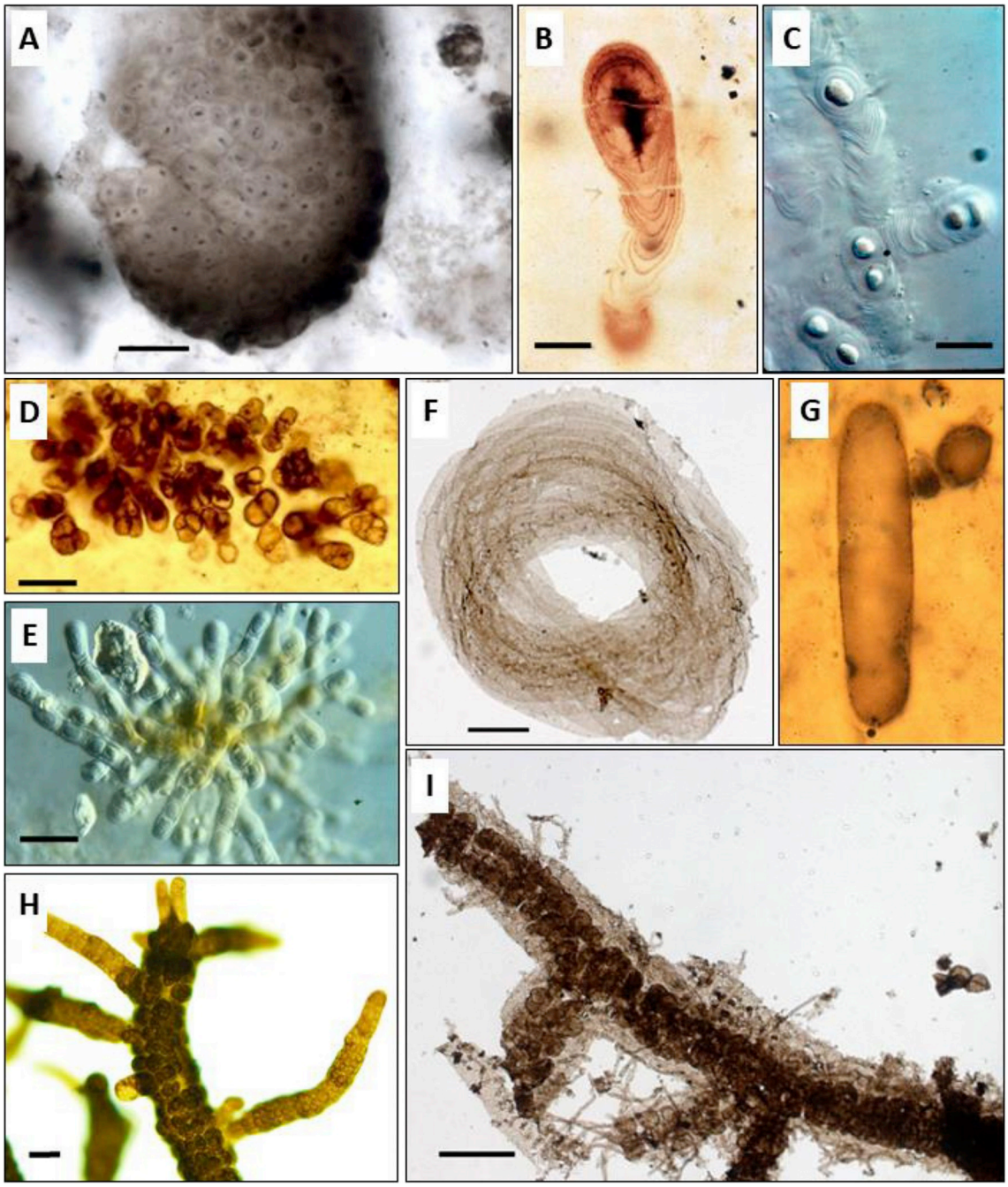

Fig. 1. Microphotographs of fossils with some of their modern analogues. A) *Eoentophysalis belcherensis* from the 1.89–1.84 Ga Kasegalik Formation, Belcher Supergroup, Canada; B) *Polybessurus* from the 800-750 Ma Draken Formation, Svalbard, photo courtesy of A. H. Knoll; C) *Cyanostylon*, the modern analogue of *Polybessurus*, photo courtesy of A. H. Knoll; D) *Eohyella*, the euendolithic cyanobacterium from the 950-680 Ma Eleonore Bay Group, central East Greenland, photo courtesy of A. H. Knoll; E) *Hyella*, the modern analogue of *Eohyella*, photo courtesy of A. H. Knoll; F) *Obruchevella* from the 1.03–0.95 Ga Mbuji-Mayi Supergroup, Democratic Republic of the Congo, photo courtesy of B. K. Baludikay; G) *Archaeoellipsoides* from the 1.48–1.3 Ga Billyakh Group, Siberia, photo courtesy of A. H. Knoll; H) *Stigonema robustum*, the modern analogue of *Polysphaeroides filiformis*, photo courtesy of T. Hauer; I) *Polysphaeroides filiformis* of the 1.03–0.95 Ga Mbuji-Mayi Supergroup, Democratic Republic of the Congo, photo courtesy of B. K. Baludikay. Scale bars = 20 μm in A, B, E, F, G and H; = 10 μm in C; = 100 μm in D; = 50 μm in I.

similar to the paleoenvironment of *Polybessurus* [79]. Actually, it is the discovery of the fossil *Polybessurus* that permitted to predict the environment where to look for its modern counterpart [121,124]. Taken together, the particular morphology of *Polybessurus*, its mode of reproduction and ecology enable its affiliation to cyanobacteria, probably within the Pleurocapsales.

3.1.3. Eohyella

The Limestone-Dolomite series of the ca. 950-680 Ma Eleonore Bay Group (central East Greenland) also preserve a group of particular microfossils showing a distinct endolithic behavior [81]. Among them, *Eohyella* is a coccoidal microfossil forming pseudofilaments (where juxtaposed cells do not share a common wall), sometimes branching depending on the microfossil species, by the juxtaposition of several cells surrounded by extracellular envelopes (Fig. 1D). *Eohyella* was

qualified as an euendolith cyanobacterium because of its orientation within the substrate: they crosscut the substrate laminae [81,125]. *Eohyella* microfossils occur in oolites and pisolites of shallow peritidal environment. Within the euendolithic cyanobacteria group of the Limestone-Dolomite series, *Eohyella* was the most abundant genus. So far, its oldest occurrence was found in the 1.63 Ga Dahongyu Formation, China [126].

The morphology, behavior and paleoenvironment of *Eohyella* are similar to those of the modern genus *Hyella* (Fig. 1E), which enabled the identification of this microfossil as a cyanobacterium, of the order of Pleurocapsales. In the present day, *Hyella* is an euendolithic cyanobacterial taxon present in ooids of the shallow subtidal environment in the Bahamas Banks [81].

3.2. Probable and possible cyanobacteria microfossils

Other microfossils are identified with less confidence but still considered as probable or possible cyanobacteria, depending on the authors. They are discussed below in alphabetical order. While analyses of fossil porphyrins suggest that cyanobacteria were the dominant primary producers in mid-proterozoic oceans [38], it is still unknown whether they were planktonic or benthic, and mostly small and coccoidal or filamentous, or both. The geological record seems to preserve mostly benthic cyanobacteria in the form of microbial mats or endoliths, although some microfossils, such as *Eomicrocystis*, are possible planktonic cyanobacteria. Modern *Microcystis* colonies overwinter on lake sediment after summer blooms and reinvade the water column in the spring [127]. This alternance of benthic and planktonic stage of life may have evolved early in cyanobacteria.

This review does not illustrate all the Proterozoic microfossils interpreted as cyanobacteria, often displaying simple colonial morphologies also encountered in other bacterial clades. Sergeev et al. [50] list additional taxa such as *Eosynechococcus*, *Leiosphaeridia*, *Myxococcoides* in their extensive review about all the Proterozoic microfossils currently interpreted as cyanobacteria. Here, we discuss those we consider the most relevant, common or distinctive taxa that could be used directly, or after further characterization, as new possible calibration points.

3.2.1. Anhuithrix

Pang et al. [128] described a new mat-forming filamentous microfossil, *Anhuithrix magna*, from the Tonian Liulaobei Formation (0.84 Ga), North China. They interpreted this fossil as a heterocytous N-fixing cyanobacterium of subsections IV or V (Nostocales or Stigonematales), based on the occurrence of large globose cells, observed between smaller vegetative cells within a filament, or at filament ends. These large cells were interpreted as probable akinetes according to their dimensions (364–800 µm in diameter) and their location in filaments. This microfossil reproduced by the production of hormogonia and grew by binary fission. However, the preservation of those microfossils as carbonaceous compressions might lead to cell deformation, making difficult the interpretation based on size and simple morphology.

This new fossil genus is, as *Archaeoellipsoides* (discussed below), a promising calibration point for molecular clocks to provide a minimum age of the Nostocales or Stigonematales. Therefore, this probable interpretation should be strengthened by microanalyses (ultrastructure, chemistry) of extracted microfossils to confirm its identity.

3.2.2. Archaeoellipsoides

Nostocales and Stigonematales are modern cyanobacterial orders that, as mentioned above, have evolved specialized cells, the heterocytes [129], and in some cases akinetes [130]. Akinetes, formed from vegetative cells, differ from those by their larger size, a thicker cell wall and absence of cell division. Modern akinetes, in all known species of akinete-bearing cyanobacteria, have an ellipsoidal to cylindrical morphology and range from 2 to 450 µm in length and to 1.8–30 µm in width [128,131]. The microfossils *Archaeoellipsoides* are cylindrical cells that include several species differing by their size [50] (Fig. 1G). Golubic et al. [132] hypothesized that *Archaeoellipsoides* from the 1.48–1.3 Ga Billyakh Group (Siberia) were fossil akinetes, based on morphological characteristics (size, elongated shape, and absence of cell division), by comparison with the akinetes of the extant analogue *Anabaena*. *Anabaena*, a nostocacean cyanobacterium, produces akinetes ranging from 7 to 90 µm in length and to 1.8–25 µm in width [128,131]. Moreover, *Archaeoellipsoides* are associated, in the Billyakh assemblage, with short trichomes. Those trichomes were interpreted as possible products of akinete germination [133], but the relationship between the akinetes and the co-occurring trichomes is discussed [134]. Older occurrences include poorly preserved microfossils in the 2.1–2.04 Ga Francevillian Supergroup, Gabon [135] and better preserved specimens in the 1.65 Ga McArthur Supergroup, Australia [136].

However, the simple morphology of *Archaeoellipsoides* might also occur among other microorganisms, such as some giant Firmicutes, e.g. the parasitic *Epulopiscium* [137] or green algae, such as *Spirotaenia* or *Stichococcus* [134]. Therefore, the identity of *Archaeoellipsoides* remains to be confirmed by other evidence than morphology alone.

3.2.3. Eomicrocystis

Eomicrocystis is a microfossil genus described in 1984 by Golovenok and Belova [138], and interpreted as a cyanobacteria. It was named according to its possible modern analogue, *Microcystis,* a planktonic coccoid cyanobacterium that forms colonies in freshwater lakes and ponds [133,138]. *Eomicrocystis* also formed colonies composed of small spheroidal to ellipsoidal cells (Fig. 2A), but preserved in marine environments. It may dominate assemblages and occur as blooms in specific levels of the 1.1 Ga El Mreiti Group, Mauritania [88]. Sergeev et al. [133] suggested that *Eomicrocystis* was a junior synonym of the genus *Coniunctiophycus* that Zhang [139] had also described and interpreted as the fossil analogue of the extant *Microcystis*. *Eomicrocystis'* oldest occurrence is in the 1.48–1.46 Ga Kotuikan Formation, Siberia [133]. However, the simple morphology of this microfossil does not enable a confident interpretation as a cyanobacterium. Indeed, this morphology is also encountered among eukaryotic algae (e.g. *Nannochloropsis*) [63] and other bacteria.

3.2.4. Gloeodiniopsis

Gloeodiniopsis is also another possible fossil of a benthic chroococcacean cyanobacterium [140]. Its stratigraphic range starts with the ~1.58 Ga Gaoyuzhuang Formation, China, and the 1.55 Ga Satka Formation, the Southern Ural Mountains [139,141].

Gloeodiniopsis consists of several spheroidal to ellipsoidal vesicles surrounded by a multilayered envelope. They are generally grouped in colonies but they may also occur occasionally as isolated cells. This morphology resembles that of modern *Gloeocapsa* or *Chroococcus*. These two possible modern analogues show both a similar morphology but differ slightly by the presence (*Gloeocapsa*) or the absence (*Chroococcus*) of a colored sheath and the thickness of this sheath. The distinction between these two modern cyanobacteria is still debated because some consider this difference between *Gloeocapsa* and *Chroococcus* as minor [50], and moreover, molecular analyzes show that they both are polyphyletic groups [45,142].

Although the morphology of *Gloeodiniopsis* is very similar to *Gloeocapsa*, some green algae may also present a similar morphology, e.g. *Volvox* [143], *Sphaerocystis* or *Eudorina* [63]. Again here, new analyzes of ultrastructure and chemistry, including the presence of unique pigments [93] in microfossils and modern specimens might help the discrimination.

3.2.5. Obruchevella

Obruchevella is a microfossil that consists of an empty helically coiled tube (Fig. 1F). This fossil genus includes several species differing

by their tube and spiral diameters. The stratigraphic range of *Obruchevella* starts in the third member of the ~1.58 Ga Gaoyuzhuang Formation, China [144]. When preserved as carbonaceous compressions in shale, the helicoidal filaments are compressed into more or less tight spirals. When preserved in 3D in chert, they occur as screw-like coiled filaments [145].

Reitlinger [146] first described *Obruchevella* specimens as foraminifera. Its biological affinity was however reassessed as cyanobacteria with *Spirulina* as modern counterpart, a cyanobacterium belonging to the Oscillatoriales [147,148]. The interpretation of *Obruchevella* was essentially based on its helically coiled morphology and its ecology, both similar to *Spirulina*, a planktonic helically coiled cyanobacterium. However, this morphology is also known in other cyanobacteria (*Arthrospira*) [149], and other bacteria, e.g. the parasitic but also free-living helicoidal species of *Leptospira* [51], *Pararhodospirillum* [150,151] and in some eukaryotic algae (e.g. *Ophiocytium*, a Tribophycean alga [63]). Some species of Leptospirales are associated with marine stromatolites [34]. *Leptospira* has a much thinner diameter (0.1 µm) and does not overlap with the thinnest *Obruchevella* (0.8 µm). Some *Obruchevella* microfossils present dimensions similar to *Spirulina* (tube diameter 0.5–3 µm, see in Ref. [149]), while most other species have sizes close to *Arthrospira* dimensions (tube diameter 2.5–16 µm, see in Ref. [149]. A few other *Obruchevella* species have a tube diameter wider than 20 µm, broader than *Arthrospira* and *Spirulina,* and may perhaps be closer to eukaryotic organisms. Other organisms in the fossil record also have spiral morphology with a larger size and a eukaryotic interpretation. The Mesoproterozoic specimens of *Grypania spiralis*, a coiled filamentous fossil, reach macroscopic size and have been interpreted as a eukaryotic organism based on its size, preserved septae and external sheath, and cell length and size suggesting a coenocytic organization. The older 1.9 Ga *Grypania* are smaller, thinner and do not preserve internal structure, and resemble more ripped-up microbial mat fragments (see review in Ref. [59]).

Thus, although *Obruchevella* is a probable cyanobacteria, these hypotheses are only based on morphology and size, and would be strengthened by ultrastructure and chemical analyzes.

3.2.6. *Oscillatoriopsis*

Oscillatoriacean cyanobacteria are reported as the most represented group of cyanobacteria in the fossil record [152]. One of those is *Oscillatoriopsis,* an unsheathed cellular filament with more or less isodiametric cells (Length:Width ≤ 1) [140,153,154] (Fig. 2D). *Oscillatoriopsis* microfossils are slightly constricted at intercellular septa [153].

Oscillatoriopsis microfossils are commonly found in shallow water marine environments but they also may be found in lacustrine deposits or pluvial lakes [50,140,155]. The stratigraphic record of this genus starts with the ca. 2.2–1.8 Ga silicified carbonates from the Duck Creek Dolomite Formation, Australia [155].

The interpretation is only based on morphology, similar to modern *Oscillatoria*. However, this type of simple morphology is also found among other prokaryotes such as *Beggiatoa*, a sulfide-oxidizing proteobacterium [41,50,155,156] or among eukaryotes such as *Ulothrix*, a green alga [157]. Oscillatoriacean cyanobacteria often reproduce by the formation of hormogonia. The fossil occurrence of such short filamentous microfossils interpreted as *Oscillatoriopsis* could support its identificationas hormogonia of oscillatoriacean cyanobacteria [141]. However, other bacteria, again including *Beggiatoa*, may also produce hormogonia. Therefore, the interpretation of *Oscillatoriopsis* as an oscillatoriacean cyanobacterium, albeit plausible, is still debated [41].

3.2.7. *Palaeolyngbya*

Palaeolyngbya is interpreted as a hormogonian oscillatoriocean cyanobacterium microfossil found first in the 0.81–0.79 Ga Bitter Springs Formation, Central Australia [140,158], but its oldest occurrence is in the 1.60 Ga Gaoyuzhuang Formation, China [159], and in 1.48–1.46 Ga Kotuikan Formation, Siberia [160]. It is a sheathed filament with a

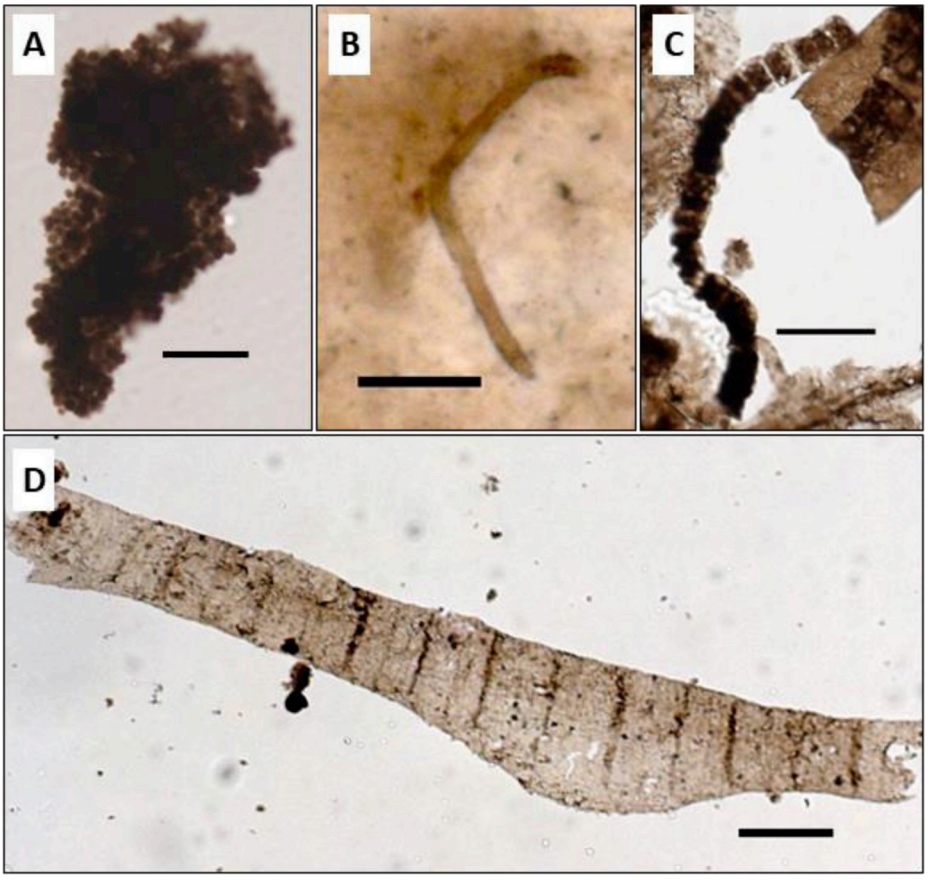

Fig. 2. Microphotographs of fossils considered as probable or possible cyanobacteria. A) *Eomicrocystis* from the 1.1 Ga Atar/El Mreïti Group, Taoudeni Basin, Mauritania. B) *Siphonophycus* from the 1.48–1.3 Ga Billyakh Group, Siberia; C) *Palaeolyngbya* from the 1.03–0.95 Ga Mbuji-Mayi Supergroup, Democratic Republic of the Congo, photo courtesy of B. K. Baludikay; D) *Tortunema* from the 1.03–0.95 Ga Mbuji-Mayi Supergroup, Democratic Republic of the Congo, photo courtesy of B. K. Baludikay. Scale bars = 20 µm.

smooth wall (Fig. 2C). Regular and uniseriate discoidal cells are arranged inside the single sheath [153].

As several other possible cyanobacteria microfossils, *Palaeolyngbya* has been interpreted as such based only on its morphology [140,161] and therefore is debatable.

3.2.8. Polysphaeroides filiformis

Polysphaeroides is a fossil genus described by Hermann [162], which included several fossil species, until 1994, when Hofmann and Jackson [163] moved nearly all of the species of *Polysphaeroides* to the genus *Chlorogloeaopsis*, because of their similar morphology. Only one species remained, *Polysphaeroides filiformis* [164]. *Polysphaeroides filiformis* consists of spheroidal cells arranged in a loose multiseriate filamentous aggregate and surrounded by a common envelope with closed ends (Fig. 1I). The colonies formed by the spheroidal cells may branch. The 1.48–1.46 Ga Kotuikan Formation, Siberia, is the oldest formation in which *Polysphaeroides filiformis* was recorded so far [164].

Polysphaeroides is compared to modern stigonemataleans [164,165], although some authors suggested a possible affinity to eukaryotic algae, either green or red [166], for example the red algae *Polysiphonia* (Figs. 16–42 in Ref. [63]). However, the morphology of *Polysphaeroides filiformis,* characterized by a thick sheath surrounding multiseriate filament arrangement and occasional branching, fits the description of the recently re-evaluated modern genus *Stigonema* [167]. For instance, *Polysphaeroides filiformis* from the 1.03–0.95 Ga Mbuji-Mayi Supergroup, DRC [165], displays cell shape, arrangement, and diameters, as well as the presence of the thick sheath and the occurrence of branching (Fig. 1I) that are strikingly similar to the modern multiseriate species, *Stigonema robustum* (Fig. 1H). We consider that this fossil cyanobacterium may represent a good alternative calibration for future molecular clock analyses as modern taxa belonging to this genus form a monophyletic clade. Modern multiseriate *Stigonema* species including the recently described *S. informe,* and *S. robustum*, are generally epilithic [167] while *Polysphaeroides filiformis* from Mbuji-Mayi Supergroup was associated with intertidal or subtidal environments [165].

3.2.9. Siphonophycus

Siphonophycus is one of the most common filamentous microfossils in the Proterozoic. It is commonly found in shallow water deposits in Proterozoic mat assemblages [41,168], preserved *in situ* in chert [41,80,124,140,169] or as bundles ripped off mats in shales [54], or as the main stromatolite builders [50]. *Siphonophycus* is an unbranched, non-septate and empty smooth-walled filamentous sheath [140] (Fig. 2B). Several species are distinguished based on the diameter range of the filamentous sheath [153]. Broad (15–25 μm) filaments of *Siphonophycus transvaalensis* reported in the latest Archean 2.52 Ga Gamohaan Formation of South Africa were interpreted as non-heterocytous cyanobacteria similar to modern Oscillatoriales [170]. Similar Oscillatoriales-like microfossils occur through all the Proterozoic.

Siphonophycus specimens are generally interpreted as sheaths of oscillatoriacean cyanobacteria. Schopf [140] occasionally observed transverse thickenings that were placed along *Siphonophycus* filamentous sheaths. Therefore, he suggested that modern counterparts of *Siphonophycus* microfossils would be LPP-like cyanobacteria (*Lyngbya*, *Phormidium* and *Plectonema*) [140,141,171]. Nevertheless, this simple morphology is also encountered in other bacteria. For example, minute *Siphonophycus* sheaths may be comparable to *Chloroflexi*-like photosynthetic bacteria [41,168]. Large *Siphonophycus* microfossils might also be the remains of filamentous eukaryotic algae [50]. Some *Siphonophycus* may present a sheath with a thickness of around 2 μm. Thick sheaths are generally common among cyanobacteria and not among other bacterial phyla [172]. They may thus be a criterion of a cyanobacterial affinity for those *Siphonophycus* specimens, in addition to alternating vertical and horizontal disposition in mats, which may indicate phototropism or chemotropism, a behavior not unique to cyanobacteria [41,134].

4. Molecular dating

The understanding of cyanobacterial phylum evolution has progressed significantly with the emergence of molecular biology techniques and new sequencing technologies. Since the late 90's a myriad of phylogenetic studies based on single loci (i.e., 16S rRNA or some protein) have been published (e.g. Refs. [9,201]). Even if the five major sections of Cyanobacteria were not yet represented in genomic databases, the first studies to use a phylogenomic (*i.e.* multilocus) dataset were the works of Rodriguez-Ezpeleta et al. (2005) [202] and then of Criscuolo and Gribaldo (2011) [203]. In 2013, the large CyanoGEBA (Genomic Encyclopedia of Bacteria and Archaea) sequencing project led to an improvement in terms of genomic coverage of cyanobacterial taxa, notably by sequencing genomes belonging to sections II and V [201]. Since then, the number of publicly available cyanobacterial genomes has dramatically increased. Yet, their quality, especially contamination of cyanobacterial assemblies by non-cyanobacterial DNA, has gone worse in parallel, which is a problem for phylogenetic analyses [204]. Moreover, the real biodiversity of cyanobacteria is still under-represented in genomic databases, mainly because of a biased sampling in the sequencing effort [205,206]. Nevertheless, since Shih et al. (2013) [201], many authors have taken advantage of these new genomes to carry out phylogenomic analyses [13,15,207–213]. Most of these studies focussed on integrating new genomic data to the same set of 100–200 hundreds loci (but see Ref. [15]). By doing so, few tried to handle the methodological difficulties associated with the use of large-scale data to resolve the phylogeny of old groups such as Cyanobacteria, whether during dataset assembly (e.g., contamination, horizontal gene transfer, hidden paralogy) or phylogenetic inference (e.g., substitutional saturation, compositional bias, heterogeneous evolutionary rate) [214–217], except [203]. Consequently, among the ten phylogenomic studies cited above, only three are in agreement on the cyanobacterial backbone [13,201,210].

4.1. Calibration, models, and datasets

For molecular clock reconstructions, microfossils of cyanobacteria are needed as a source of calibration of the molecular phylogenies. However, only few calibration points are available to date oxygenic photosynthesis, the endosymbiotic event having given rise to the chloroplast, as well as the origin of cyanobacteria. For the latter, estimates range from the early Archean to the GOE, in the Paleoproterozoic (Fig. 3). Beyond the lack of congruence of the phylogenomic studies and the polyphyletic nature of many cyanobacterial groups (including well-known genera such as *Synechoccocus* and *Leptolyngbya*), the issue is complicated by the absence in genomic databases of modern counterparts (*Entophysalis*, *Hyella* or *Cyanostylon*-like) of the unambiguous cyanobacteria microfossils (*Eoentophysalis*, *Eohyella* and *Polybessurus*). As we have no reliable indication of the phylogenetic position of these important modern taxa, researchers often use flimsy affiliations as calibration points. Usually, only few cyanobacterial fossils are used as constraints for molecular clock analyses. They include *Archaeoellipsoides* for monophyletic Nostocales and Stigonematales lineages, and *Eohyella* for Pleurocapsales lineages, despite the absence of a genetic characterization of the modern counterpart *Hyella* (e.g. Refs. [210,218]). The occurrence of fossil diatoms is often used for the advent of the endosymbiont *Rivularia intracellularis,* and the fossil red algae *Bangiomorpha* for the minimum age of the primary endosymbiosis. Moreover, some authors have chosen not to use cyanobacteria microfossils in their analysis, but instead fossils from eukaryotic lineages such as plants [219], or the occurrence of horizontal gene transfer [213], or the GOE to set a lower bound on Cyanobacteria as a phylum [220]. In a non-exhaustive survey, we observed more than 89 different approaches used to estimate the evolution of cyanobacterial phylum. This diversity of phylogenies, and calibration points, but also of clock models and dating software packages, has led to a large

variety of age estimates.

So far, all the attempts to date the evolutionary events of the cyanobacterial phylum used a fixed-node approach, where researchers manually select nodes to place calibration points. This strategy has the disadvantage of inducing an unmeasurable uncertainty on the inferred node ages, due to errors in taxonomic affiliation and/or specified geological ages. The affiliation error is often due to misleading morphological similarities between unrelated extant organisms and (ambiguous) microfossils. Moreover, polyphyletic groups make impossible to specify node calibrations, except by reporting their origin to a (much) older common ancestor far back in the tree. This problem could be even worse if some scarcely sampled extant organisms used for calibration are actually polyphyletic. Regarding ages, they are specified as prior distributions partly based on the minimum age (lower bound or oldest occurrence) of a given microfossil in the paleontological record. However, owing to issues due to taphonomy and extinction of stem groups, this may introduce an unmeasurable divergence between the ages specified for the fossil and the real geological span of the organism. Ultimately, inferred node ages are thus highly dependent on the completeness of the paleontological record [221].

Because of these limitations, an alternative strategy, termed tip-dating, would be more suitable for dating the evolution of Cyanobacteria. In such an approach, the placement of the microfossils within the tree is guided by a morphological matrix and supported by statistical values, the posterior probabilities [222]. The consequence of this “automatic” placement is that tip-dating enables the use of a wider range of microfossils, not only the unambiguous ones, but also the numerous ambiguous microfossils. Further, by explicitly modeling stem groups within the tree [221], tip-dating is able to test (and thus either confirm or reject) the affiliation of microfossils to extant organisms, which is usually taken for granted in the paleontological literature and many molecular dating studies building upon it.

4.2. Origin of cyanobacteria and oxygenic photosynthesis

In most cyanobacterial phylogenetic analyses that are using a non-cyanobacterial outgroup to root the tree, the reference strain *Gloeobacter violaceus* PCC7421 has a basal position [9,223–225]. Consequently, the phylogenetic node bearing *Gloeobacter* and the rest of modern cyanobacterial lineages serves as calibration for the origin of cyanobacteria in several studies [226–228]. In these studies, the authors have set different root limit ages, so that the maximum root age may vary between the earliest estimate of abiogenesis around 4.2 Ga [226], the end of the Late Heavy Bombardment at 3.85 Ga [228], or the GOE at 2.4 Ga [229].

Recently, two newly discovered lineages were proposed as sister groups of the cyanobacterial phylum, the Melainabacteria [230] and the Sericytochromatia [231]. Of note, these lineages (mostly known as metagenomics assemblies) do not contain genes required for photosynthesis nor carbon fixation [231]. The integration of genetic data from Melainabacteria and Sericytochromatia as outgroups for molecular clock analyses suggested that cyanobacteria evolved just before the GOE [213,219]. Taken together, this suggests that oxygenic photosynthesis has evolved after the separation of cyanobacteria from Melainabacteria [213,219]. However, the loss of photosynthetic capability in the ancestor of the three lineages before or at the time of GOE has been suggested as an alternative hypothesis that cannot be ruled out [232].

Among bacterial phototrophs (cyanobacteria, green S-bacteria, green non sulfur bacteria, purple bacteria, heliobacteria, some acidobacteria and gemmatimonadetes), Cyanobacteria is the only lineage that possesses two photosynthetic reaction centers of the Fe–S type (RCI) and Quinone type (RCII), whereas anoxygenic bacteria possess either the Fe–S or Quinone type. So far, three hypotheses were proposed to explain the presence of both types of RC in modern cyanobacteria. Two of these hypotheses suggest that both RCs would have been present in an anoxygenic phototrophic ancestor. In a first hypothesis, RCs evolved within the common ancestor of (all) bacterial phototrophs. Both of them were kept in the cyanobacterial lineage whereas there was a selective loss of one type of each in the modern anoxygenic lineage ancestors [233,234]. In the second hypothesis, the RCI and RCII would have emerged in the protocyanobacterial ancestor by duplication of a unique ancestral RC. This was followed by lateral transfer of a different RC type to the ancestors of the modern anoxygenic phototrophs [235]. The existence of an anoxygenic cyanobacterial ancestor may be supported by the occurrence of several genes involved in anoxygenic photosynthesis in modern cyanobacterial genomes [236], and the co-occurrence of both anoxygenic and oxygenic photosynthesis in several lineages of modern cyanobacteria clades [237,238]. A third hypothesis rather suggests the independent evolution of the two RCs in separate lineages of anoxygenic phototrophs and their lateral transfer into a protocyanobacterial ancestor, the so-called fusion hypothesis [239,240]. At least in purple bacteria, the genes for RCII are clustered in an ensemble of operons, the photosynthesis gene cluster (PGC), some organisms even harboring the PGC on large plasmids. This observation makes the transfer of full photosystems highly plausible, and recent events of such kind have been convincingly inferred in Rhodobacteraceae [241].

In order to test the likelihood of the ancient transfer of photosystems between the bacterial phototrophic lineages, Magnabosco and colleagues [213] added horizontal gene transfer events information of two genes (encoding for Mg-chelatase and S-adenosyl-L-homocysteine hydrolase) as additional constraints to their models to estimate the stem age of the bacterial phototrophs (Cyanobacteria, green S-bacteria and green non-sulfur bacteria). These authors assumed that such estimates would allow them to investigate the feasibility and timing of the RC transfer events between phototrophic lineages. Their results excluded the possibility of a RC transfer from the green sulfur bacteria to cyanobacteria, and thus, invalidated the fusion hypothesis. However, they were not able to choose between the two hypotheses suggesting that both RCs emerged from a common ancestor [213].

First, the reaction centers RCI and RCII would operate separately and asynchronously in the same ancestral anoxygenic phototroph organism. The RCI would catalyze H_2S oxidation as in green S-bacteria, while the RCII would act as a light-dependent electron transporter as in purple bacteria [242]. A water-splitting RCII could also have evolved from an ancestral RCII type already capable of photosynthesis and manganese oxidation [243]. However, the evolution of these processes, and the early or late evolution of oxygenic photosynthesis, are still debated e.g. Refs. [99,244].

4.3. Diversification

Several studies suggested that ancestral cyanobacteria first inhabited freshwater ecosystems [13,15,17,210,218,226], but see e.g. Ref. [16] for a marine origin. Nevertheless, these estimates are based on comparison with the modern ecology of basal clades of cyanobacteria, which are likely to have changed through time. Moreover, the fossil record of cyanobacteria is almost exclusively estuarine and shallow marine, often from the intertidal zone, or hypersaline lacustrine. However, terrestrial deposits are less commonly preserved in the geological record, and this might bias our view of the fossil ecological ranges.

A couple time calibrated phylogenies based on low-resolution alignments of 16S rRNA gene sequences or on a large multilocus dataset [227,228] suggest that multicellular forms of cyanobacteria were potentially present when the GOE started, implying a pre-GOE origin of the cyanobacterial phylum. Furthermore, their results hint at an acceleration of the diversification rate after the substantial increase of atmospheric oxygen concentration [227]. The acquisition of the multicellularity would be an advantage for UV resistance and substrate adhesion [40]. However, multicellularity is polyphyletic and

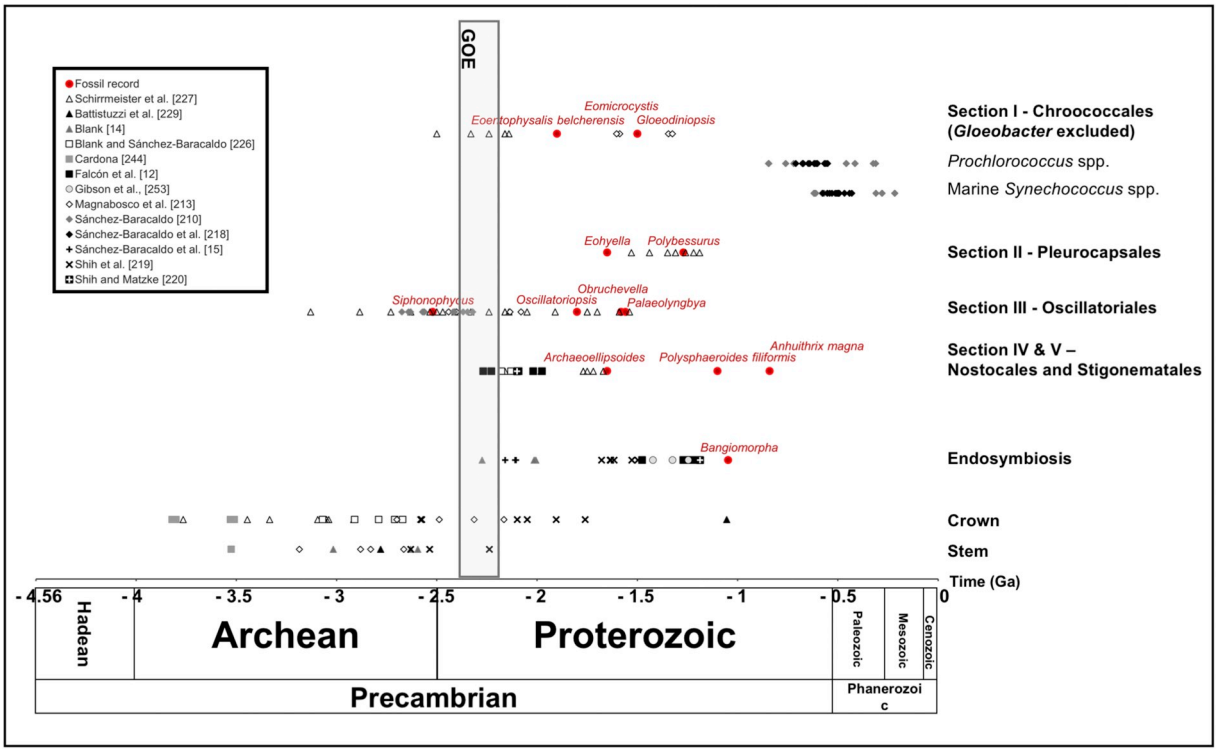

Fig. 3. Microfossils record of unambiguous, probable and possible cyanobacteria (see text for discussion, Table 1, and Supplementary Table 1), and of *Bangiomorpha* as an unambiguous red alga, and minimum median age estimates for the divergence of sections I, II, III, IV and V as described by Rippka et al. [45]; for phylogenetic nodes supporting stem and crown group cyanobacteria according to the literature; and for the primary endosymbiosis. Note that the age of *Polysphaeroides filiformis* considered here corresponds to its record in Baludikay et al. [165].

convergent several times across extant species – especially in cyanobacteria.

Other studies hypothesize that the origin of marine planktonic cyanobacteria would have happened after the evolution of crown groups in freshwater, terrestrial and benthic coastal modern environments [210]. Benthic (terrestrial and coastal) cyanobacteria may have dominated the oxygenic photosynthesis from the late Archean and possibly until the mid-Neoproterozoic [245].

However, these hypotheses remain to be confirmed since the record of Archean cyanobacteria is controversial as explained above, and the fossil record is biased towards benthic forms. Benthic filamentous cyanobacteria forming mats or preserved in silicified stromatolites are preserved preferentially to small planktonic cells sedimenting in the water column. Moreover shallow-water deposits are more common in the Precambrian then deeper sediments.

Non-heterocytous N-fixing unicellular and filamentous *Trichodesmium* spp. would have appeared later, during the late Neoproterozoic [210,218]. This observation possibly coincides with an increase of bioavailable Mo (an essential co-factor of nitrogenase) in the open ocean [40,218,246,247]. However, cyanobacteria likely had to invent a new N_2-fixation machinery that could operate in the presence of the rising O_2, leading to the evolution of heterocytous cyanobacterial taxa, probably as early as the GOE [227], and possibly supported by Paleoproterozoic [134–136] and Neoproterozoic [128] microfossils. However, this hypothesis might be questioned as heterocytous cyanobacteria age estimates resulted from models that used poorly preserved putative fossil akinetes from 2.1 Ga Franceville Gabon. In the Paleoproterozoic redox stratified oceans, cyanobacteria may have performed anoxygenic (rather than oxygenic) photosynthesis using H_2S above euxinic layers, or may have been outcompeted by anoxygenic photosynthetic bacteria metabolizing H_2S or Fe^{2+} above ferruginous water [248]. However, they became important primary producers in the still stratified mid-Proterozoic oceans [38].

4.4. Origin of chloroplast

Chloroplasts form a monophyletic cluster within the Cyanobacteria phylum [12]. This observation is elegantly interpreted as the result of a primary endosymbiosis at the origin of the chloroplast [249]. Although this theory is well accepted in the scientific community (but see Ref. [250] for a more complex model involving Chlamydiales), the precise position of the plastid within the extant diversity of Cyanobacteria has been a matter of discussion. Two major scenarios are opposed, one postulating an ancient origin (early-branching) [13,14,105,202,203,209,211,220] and the other one postulating a (relatively) recent (late-branching) origin [12,208,251]. The hypothesis of an early origin is more frequent in the literature, and it has recently been strengthened by the study of Ponce-Toledo et al. (2017) [13], who identified the early-branching *Gloeomargarita lithophora* as the closest extant relative of plastids. In an attempt to date the primary endosymbiosis, Falcón and colleagues [12] assumed that the closest relative of chloroplasts was a unicellular N-fixing cyanobacterium (late-branching hypothesis) and that it occurred during the middle of the Proterozoic [12] (Fig. 3). However the calibration used included Archean ages for the highly controversial Apex chert microstructures and sterane that were subsequently reassessed as contaminants (see above). Later studies of ATP synthases subunits and elongation factors permitted to estimate the first endosymbiosis event at approximately 0.9 Ga [220]. Taking advantage of the recent discovery of *Gloeomargarita* [13,252], Sanchez-Baraccaldo et al. (2017) estimated the age of the origin of the chloroplast at 1.9 Ga (2.12–1.75 Ga) [15]. This result is similar to the one reported in Ref. [14], although the topologies used in the two studies were slightly different with respect to plastid position. In contrast, Shih et al., 2017 [219] recovered a quite different age for plastids (1.1 Ga). Interestingly, this latter estimate is more similar to the result of [12], even if assuming an early-branching hypothesis for plastid emergence. This suggests that discrepancies in

estimated chloroplast ages rather stem from differences in calibration points and/or dating models than from topologies (early vs late-branching hypotheses). Indeed, if differences do exist in tree topologies concerning chloroplast emergence, the wide age intervals obtained in the various analyses often exceed the branch length variation implied by topological changes. This is not surprising given the very short length of the corresponding internodes in the cyanobacterial backbone.

As exploitable cyanobacterial microfossils are not numerous, a logical strategy is to use the morphologically more complex and more recent eukaryotic algae as calibration points. However, the oldest unambiguous fossil record of eukaryotic algae are silicified multicellular bangiophyte red algae preserved in hypersaline shallow-water environment [195] and recently well dated at 1.047 Ga [253]. These fossils were interpreted as benthic multicellular red algae based on their morphology, longitudinal division pattern, attachment structures, and ecology [195]. Other 1.6 Ga microfossils are interpreted as more divergent Florideophyte red algae based on morphology [254], but their age is debated because of the complex geology of the area [253]. Microfossils interpreted as green algae may also provide an estimation of the minimum age for chloroplast acquisition. Their fossil record ranges from unambiguous 0.6 Ga prasinophytes based on wall ultrastructure [255], 0.8 Ga probable siphonocladalean chlorophytes and probable hydrodictyacean chlorophyte based on distinctive morphology and ecology [134], the latter also found in 1.1–0.9 Ga lower Shaler Group of arctic Canada [256], to 1.65 Ga acritarchs whose putative algal interpretation needs confirmation [257]. Using the new age of 1.047 Ga calibration for *Bangiomorpha*, Gibson et al. [253] estimated the primary chloroplast endosymbiosis at 1.25 Ga, consistent with most of the unambiguous algal fossil record.

5. Conclusions

Cyanobacterial fossil record starts unambiguously at 1.89–1.84 Ga and the minimum age for the oxygenic photosynthesis starts with the GOE around 2.4 Ga. *Eoentophysalis, Polybessurus* and *Eohyella* microfossils present a combination of distinctive morphologies, modes of division and ecology that are diagnostic of the cyanobacteria phylum [41]. Therefore, their placement into this phylum is strongly supported, unlike other Proterozoic microfossils that display a simpler morphology widespread among other prokaryotes. Older possible geochemical traces of oxygenation and the metabolisms involved in stromatolites and MISS builders in the Archean are discussed. Moreover, the origin and timing of oxygenic photosynthesis is also still debated although some studies corroborate that the evolution of oxygenic photosynthesis happened right before the GOE which would then be a consequence of this evolution. The origin, timing and environment of the primary endosymbiotic event giving rise to eukaryotic algae are also still debated. Therefore, it is essential to define new biosignatures indicative of cyanobacteria in order to reassess their fossil record and provide new calibration points for molecular clocks. Those biosignatures will combine analyses of the morphology, ultrastructure and ecology of promising microfossils identified in this review, with their molecular (lipids and pigments), metal and isotopic composition. Identifying these fossils, not only as cyanobacteria, but of specific clades within the cyanobacteria, will improve our understanding of their diversification record and provide new calibration points. Coupling these new microfossil calibration points with improved molecular phylogenies and alternative molecular clocks (such as tip-dating) will then enable to date the minimum ages of important biological events such as the origin of oxygenic photosynthesis and the acquisition of chloroplasts among photosynthetic eukaryotic lineages.

Acknowledgments

We thank the editors W. Fischer & J. Valentine for their invitation to write this review for a special issue “How did life come to tolerate and thrive in an oxygenated world?”. Research funding came from the European Research Council StG ELiTE [grant number: FP7/308074], the BELSPO IAP PLANET TOPERS, the FRS-FNRS-FWO EOS ET-HoME project, FRS–FNRS, and the ULiege mini-ARC PUMA project. A. Wilmotte is research associate of the FRS-FNRS. We also thank Prof. A.H. Knoll, Dr T. Hauer, Dr B.K. Baludikay and J. Beghin for providing pictures to illustrate this review. Finally, we also thank anonymous reviewers for their insights and comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.freeradbiomed.2019.05.007.

References

[1] A. Bekker, H.D. Holland, P. Wang, D.R. Iii, H.J. Stein, J.L. Hannah, L.L. Coetzee, N.J. Beukes, Dating the rise of atmospheric oxygen, Nature 427 (2004) 117–120, https://doi.org/10.1038/nature02260.
[2] J.L. Hannah, A. Bekker, H.J. Stein, R.J. Markey, H.D. Holland, Primitive Os and 2316 Ma age for marine shale: implications for Paleoproterozoic glacial events and the rise of atmospheric oxygen, Earth Planet. Sci. Lett. 225 (2004) 43–52, https://doi.org/10.1016/j.epsl.2004.06.013.
[3] J.F. Kasting, What caused the rise of atmospheric O2? Chem. Geol. 362 (2013) 13–25, https://doi.org/10.1016/j.chemgeo.2013.05.039.
[4] L.A. Lewis, Hold the salt: freshwater origin of primary plastids, Proc. Natl. Acad. Sci. Unit. States Am. 114 (2017) 9759–9760, https://doi.org/10.1073/pnas.1712956114.
[5] D.A. Gold, A. Caron, G.P. Fournier, R.E. Summons, Paleoproterozoic sterol biosynthesis and the rise of oxygen, Nature 543 (2017) 420–423, https://doi.org/10.1038/nature21412.
[6] A.J. Roger, S.A. Muñoz-Gómez, R. Kamikawa, The origin and diversification of mitochondria, Curr. Biol. 27 (2017) R1177–R1192, https://doi.org/10.1016/j.cub.2017.09.015.
[7] A.H. Knoll, D. Hewitt, Phylogenetic, functional and geological perspectives on complex multicellularity, Major Transitions Evol. Revisited, MIT Press, Cambridge, 2011, pp. 251–270.
[8] L. Sagan, On the origin of mitosing cells, J. Theor. Biol. 14 (1967) 225–274, https://doi.org/10.1016/0022-5193(67)90079-3.
[9] B.E. Schirrmeister, M. Anisimova, A. Antonelli, H.C. Bagheri, Evolution of cyanobacterial morphotypes. Taxa required for improved phylogenomic approaches, Commun. Integr. Biol. 11 (2011) 45, https://doi.org/10.4161/cib.4.4.16183.
[10] C.F. Delwiche, Tracing the thread of plastid diversity through the tapestry of life, Am. Nat. 154 (1999) S164–S177, https://doi.org/10.1086/303291.
[11] S.J. Giovannoni, S. Turner, G.J. Olsen, S. Barns, D.J. Lane, N.R. Pace, Evolutionary relationships among cyanobacteria and green chloroplasts, J. Bacteriol. 170 (1988) 3584–3592, https://doi.org/10.1128/jb.170.8.3584-3592.1988.
[12] L.I. Falcón, S. Magallón, A. Castillo, Dating the cyanobacterial ancestor of the chloroplast, ISME J. 4 (2010) 777–783, https://doi.org/10.1038/ismej.2010.2.
[13] R.I. Ponce-Toledo, P. Deschamps, P. López-García, Y. Zivanovic, K. Benzerara, D. Moreira, An early-branching freshwater cyanobacterium at the origin of plastids, Curr. Biol. 27 (2017) 386–391, https://doi.org/10.1016/j.cub.2016.11.056.
[14] C.E. Blank, Origin and early evolution of photosynthetic eukaryotes in freshwater environments: reinterpreting proterozoic paleobiology and biogeochemical processes in light of trait evolution, J. Phycol. 49 (2013) 1040–1055, https://doi.org/10.1111/jpy.12111.
[15] P. Sánchez-Baracaldo, J.A. Raven, D. Pisani, A.H. Knoll, Early photosynthetic eukaryotes inhabited low-salinity habitats, Proc. Natl. Acad. Sci. Unit. States Am. 114 (2017) E7737–E7745, https://doi.org/10.1073/pnas.1620089114.
[16] T. Nakov, J.D. Boyko, A.J. Alverson, J.M. Beaulieu, Models with unequal transition rates favor marine origins of Cyanobacteria and photosynthetic eukaryotes, Proc. Natl. Acad. Sci. Unit. States Am. 114 (2017) E10606–E10607, https://doi.org/10.1073/pnas.1716692114.
[17] P. Sánchez-Baracaldo, G. Bianchini, J.P. Huelsenbeck, J.A. Raven, D. Pisani, A.H. Knoll, Reply to Nakov et al.: model choice requires biological insight when studying the ancestral habitat of photosynthetic eukaryotes, Proc. Natl. Acad. Sci. Unit. States Am. 114 (2017) E10608–E10609, https://doi.org/10.1073/pnas.1717417114.
[18] W.W. Fischer, J. Hemp, J.E. Johnson, Evolution of oxygenic photosynthesis, Annu. Rev. Earth Planet Sci. 44 (2016) 647–683, https://doi.org/10.1146/annurev-earth-060313-054810.
[19] M.T. Rosing, R. Frei, U-rich Archaean sea-floor sediments from Greenland - indications of > 3700 Ma oxygenic photosynthesis, Earth Planet. Sci. Lett. 217 (2004) 237–244, https://doi.org/10.1109/SIPS.2006.352605.
[20] Y. Shen, R. Buick, The antiquity of microbial sulfate reduction, Earth Sci. Rev. 64 (2004) 243–272, https://doi.org/10.1016/S0012-8252(03)00054-0.
[21] R. Buick, When did oxygenic photosynthesis evolve? Philos. Trans. R. Soc. B Biol. Sci. 363 (2008) 2731–2743, https://doi.org/10.1098/rstb.2008.0041.
[22] S. Ono, N.J. Beukes, D. Rumble, M.L. Fogel, Early evolution of atmospheric oxygen from multiple-sulfur and carbon isotope records of the 2.9 Ga Mozaan Group of the Pongola Supergroup, Southern Africa, S. Afr. J. Geol. 109 (2006) 97–108, https://

doi.org/10.2113/gssajg.109.1-2.97.
[23] S.A. Crowe, L.N. Døssing, N.J. Beukes, M. Bau, S.J. Kruger, R. Frei, D.E. Canfield, Atmospheric oxygenation three billion years ago, Nature 501 (2013) 535–538, https://doi.org/10.1038/nature12426.
[24] R. Frei, C. Gaucher, S.W. Poulton, D.E. Canfield, Fluctuations in Precambrian atmospheric oxygenation recorded by chromium isotopes, Nature 461 (2009) 250 https://doi.org/10.1038/nature08266.
[25] N.J. Planavsky, D. Asael, A. Hofmann, C.T. Reinhard, S.V. Lalonde, A. Knudsen, X. Wang, F. Ossa Ossa, E. Pecoits, A.J.B. Smith, N.J. Beukes, A. Bekker, T.M. Johnson, K.O. Konhauser, T.W. Lyons, O.J. Rouxel, Evidence for oxygenic photosynthesis half a billion years before the Great Oxidation Event, Nat. Geosci. 7 (2014) 283–286, https://doi.org/10.1038/ngeo2122.
[26] A.D. Anbar, Y. Duan, T.W. Lyons, G.L. Arnold, B. Kendall, R.A. Creaser, A.J. Kaufman, G.W. Gordon, C. Scott, J. Garvin, R. Buick, A whiff of oxygen before the Great oxidation event? Science 317 (2007) 1903–1906.
[27] T.W. Lyons, C.T. Reinhard, N.J. Planavsky, The rise of oxygen in Earth's early ocean and atmosphere, Nature (2014) 307–315, https://doi.org/10.1038/nature13068.
[28] T. Bosak, B. Liang, M.S. Sim, A.P. Petroff, Morphological record of oxygenic photosynthesis in conical stromatolites, Proc. Natl. Acad. Sci. Unit. States Am. 106 (2009) 10939–10943, https://doi.org/10.1073/pnas.0900885106.
[29] N. Noffke, G. Gerdes, T. Klenke, W.E. Krumbein, Microbially induced sedimentary structures - a new category within the classification of primary sedimentary structures - discussion, J. Sediment. Res. 72 (2001) 587–588, https://doi.org/10.1306/101401720587.
[30] C. Heubeck, An early ecosystem of Archean tidal microbial mats (Moodies Group, South Africa, ca. 3.2 Ga), Geology 37 (2009) 931–934, https://doi.org/10.1130/G30101A.1.
[31] M. Homann, P. Sansjofre, M. Van Zuilen, C. Heubeck, J. Gong, B. Killingsworth, I.S. Foster, A. Airo, M.J. Van Kranendonk, M. Ader, S.V. Lalonde, Microbial life and biogeochemical cycling on land 3,220 million years ago, Nat. Geosci. 11 (2018) 665–671, https://doi.org/10.1038/s41561-018-0190-9.
[32] T. Bosak, A.H. Knoll, A.P. Petroff, The meaning of stromatolites, Annu. Rev. Earth Planet Sci. 41 (2013) 21–44, https://doi.org/10.1146/annurev-earth-042711-105327.
[33] S.P. Slotznick, W.W. Fischer, Examining archean methanotrophy, Earth Planet. Sci. Lett. 441 (2016) 52–59, https://doi.org/10.1016/j.epsl.2016.02.013.
[34] E.P. Suosaari, R.P. Reid, P.E. Playford, J.S. Foster, J.F. Stolz, G. Casaburi, P.D. Hagan, V. Chirayath, I.G. Macintyre, N.J. Planavsky, G.P. Eberli, New multi-scale perspectives on the stromatolites of Shark Bay, western Australia, Sci. Rep. 6 (2016) 1–13, https://doi.org/10.1038/srep20557.
[35] J. Alleon, R.E. Summons, Organic geochemical approaches to understanding early life, Free Radic. Biol. Med. (2019), https://doi.org/10.1016/j.freeradbiomed.2019.03.005.
[36] R. Schinteie, J.J. Brocks, Paleoecology of Neoproterozoic hypersaline environments: biomarker evidence for haloarchaea, methanogens, and cyanobacteria, Geobiology 15 (2017) 641–663, https://doi.org/10.1111/gbi.12245.
[37] S.E. Rashby, A.L. Sessions, R.E. Summons, D.K. Newman, Biosynthesis of 2-methylbacteriohopanepolyols by an anoxygenic phototroph, Proc. Natl. Acad. Sci. Unit. States Am. 104 (2007) 15099–15104, https://doi.org/10.1073/pnas.0704912104.
[38] N. Gueneli, A.M. Mckenna, N. Ohkouchi, C.J. Boreham, J. Beghin, E.J. Javaux, J.J. Brocks, 1.1-billion-year-old Porphyrins establish a marine ecosystem dominated by bacterial primary producers, Proc. Natl. Acad. Sci. Unit. States Am. 115 (2018) E6978–E6986, https://doi.org/10.1073/pnas.1803866115.
[39] H.J. Hofmann, Precambrian microflora, belcher islands, Canada: significance and systematics, J. Paleontol. 50 (1976) 1040–1073.
[40] B.E. Schirrmeister, P. Sanchez-Baracaldo, D. Wacey, Cyanobacterial evolution during the precambrian, Int. J. Astrobiol. 15 (2016) 187–204, https://doi.org/10.1017/S1473550415000579.
[41] A.H. Knoll, S. Golubic, Proterozoic and living cyanobacteria, in: P. Schidlowski, S. Golubic, M. Kimberley, D. McKirdy, Trudinger (Eds.), Early Org. Evol. Implic. Miner. Energy Resour. Springer, 1992, pp. 450–462.
[42] E.J. Javaux, A.H. Knoll, M.R. Walter, TEM evidence for eukaryotic diversity in mid-Proterozoic oceans, Geobiology 2 (2004) 121–132.
[43] S. Willman, P.A. Cohen, Ultrastructural approaches to the microfossil record: assessing biological affinities by use of transmission electron microscopy, Quantifying Evol, Early Life, 2011, pp. 301–320, , https://doi.org/10.1007/978-94-007-0680-4.
[44] R.Y. Stanier, W.R. Sistrom, T.A. Hansen, B.A. Whitton, R.W. Castenholz, N. Pfennig, V.N. Gorlenko, E.N. Kondratieva, K.E. Eimhjellen, R. Whittenbury, R.L. Gherna, H.G. Trüper, Proposal to place the nomenclature of the cyanobacteria (Blue-Green algae) under the rules of the international Code of nomenclature of bacteria, Int. J. Syst. Evol. Microbiol. 28 (1978) 335–336, https://doi.org/10.1099/00207713-28-2-335.
[45] R. Rippka, J. Deruelles, J.B. Waterbury, M. Herdman, R.Y. Stanier, Generic assignments, strain histories and properties of pure cultures of cyanobacteria, Microbiology 111 (1979) 1–61, https://doi.org/10.1099/00221287-111-1-1.
[46] J. Komárek, J. Kaštovský, J. Mareš, J.R. Johansen, Taxonomic classification of cyanoprokaryotes (cyanobacterial genera) 2014, using a polyphasic approach, Preslia 86 (2014) 295–335.
[47] E.J. Javaux, K. Benzerara, Comptes Microfossils, Rendus - Palevol 8 (2009) 605–615, https://doi.org/10.1016/j.crpv.2009.04.004.
[48] W. Altermann, J. Kazmierczak, Archean microfossils : a reappraisal of early life on Earth, Res. Microbiol. 154 (2003) 611–617, https://doi.org/10.1016/j.resmic.2003.08.006.
[49] E.J. Javaux, A.H. Knoll, M. Walter, Recognizing and interpreting the fossils of early eukaryotes, Orig. Life Evol. Biosph. 33 (2003) 75–94, https://doi.org/10.1023/A:1023992712071.
[50] V.N. Sergeev, M. Sharma, Y. Shukla, Proterozoic fossil cyanobacteria, Palaeobotanist 61 (2012) 189–358.
[51] B. Adler, A. de la Pena Moctezuma, Leptospira, Leptospirosis, Vet. Microbiol. 140 (2010) 287–296, https://doi.org/10.1080/00219266.1991.9655201.
[52] J.M. García-Ruiz, S.T. Hyde, A.M. Carnerup, A.G. Christy, M.J. Van Kranendonk, N.J. Welham, Self-assembled silica-carbonate structures and detection of ancient microfossils, Science 302 (2003) 1194–1197, https://doi.org/10.1126/science.1090163.
[53] D. Wacey, M. Saunders, C. Kong, A. Brasier, M. Brasier, 3.46 Ga Apex chert 'microfossils' reinterpreted as mineral artefacts produced during phyllosilicate exfoliation, Gondwana Res. 36 (2016) 296–313, https://doi.org/10.1016/j.gr.2015.07.010.
[54] E.J. Javaux, A.H. Knoll, Micropaleontology of the lower Mesoproterozoic Roper Group , Australia , and implications for early eukaryotic evolution, J. Paleontol. 91 (2017) 199–229, https://doi.org/10.1017/jpa.2016.124.
[55] A.H. Knoll, K.D. Bergmann, J.V. Strauss, Life: the first two billion years, Philos. Trans. R. Soc. B Biol. Sci. 371 (2016), https://doi.org/10.1098/rstb.2015.0493.
[56] J. Rouillard, J.M. García-Ruiz, J. Gong, M.A. van Zuilen, A morphogram for silica-witherite biomorphs and its application to microfossil identification in the early earth rock record, Geobiology 16 (2018) 279–296, https://doi.org/10.1111/gbi.12278.
[57] K. Benzerara, F. Skouri-Panet, J. Li, C. Ferard, M. Gugger, T. Laurent, E. Couradeau, M. Ragon, J. Cosmidis, N. Menguy, I. Margaret-Oliver, R. Tavera, P. Lopez-Garcia, D. Moreira, Intracellular Ca-carbonate biomineralization is widespread in cyanobacteria, Proc. Natl. Acad. Sci. Unit. States Am. 111 (2014) 10933–10938, https://doi.org/10.1073/pnas.1403510111.
[58] E.J. Javaux, C.P. Marshal, A new approach in deciphering early protist paleobiology and evolution: combined microscopy and microchemistry of single Proterozoic acritarchs, Rev. Palaeobot. Palynol. 139 (2006) 1–15, https://doi.org/10.1016/j.revpalbo.2006.01.005.
[59] E.J. Javaux, K. Lepot, The Paleoproterozoic fossil record: implications for the evolution of the biosphere during Earth's middle-age, Earth Sci. Rev. (2018) 68–86, https://doi.org/10.1016/j.earscirev.2017.10.001.
[60] A.H. Knoll, S. Golubic, Anatomy and taphonomy of a precambrian algal stromatolite, Precambrian Res. 10 (1979) 115–151, https://doi.org/10.1016/0301-9268(79)90022-6.
[61] S. Golubic, L. Seong-Joo, Early cyanobacterial fossil record: preservation, palaeoenvironments and identification, Eur. J. Phycol. 34 (1999) 339–348, https://doi.org/10.1080/09670269910001736402org/10.1080/09670269910001736402.
[62] R.W. Castenholz, A. Wilmotte, M. Herdman, R. Rippka, J.B. Waterbury, I. Iteman, L. Hoffmann, B.X. Phylum, Cyanobacteria, Bergey's Manual® Syst. Bacteriol. 437 (2001) 473–599, https://doi.org/10.1007/978-0-387-21609-6_27.
[63] L.E. Graham, L.W. Wilcox, Algae, Prentice Hall, Upper Saddle River, 2000.
[64] J. Šmarda, D. Šmajs, J. Komrska, V. Krzyžánek, S-layers on cell walls of cyanobacteria, Micron 33 (2002) 257–277, https://doi.org/10.1016/S0968-4328(01)00031-2.
[65] S. Pereira, A. Zille, E. Micheletti, P. Moradas-ferreira, R. De Philippis, P. Tamagnini, biosynthesis and assembly (2009) 917–941, https://doi.org/10.1111/j.1574-6976.2009.00183.x.
[66] J.K. Bartley, Actualistic taphonomy of cyanobacteria; implications for the Precambrian fossil record, Palaios 11 (1996) 571–586, https://doi.org/10.2307/3515192.
[67] S.A. Newman, V. Klepac-Ceraj, G. Mariotti, S.B. Pruss, N. Watson, T. Bosak, Experimental fossilization of mat-forming cyanobacteria in coarse-grained siliciclastic sediments, Geobiology 15 (2017) 484–498, https://doi.org/10.1111/gbi.12229.
[68] K. Lepot, P. Compère, E. Gérard, Z. Namsaraev, E. Verleyen, I. Tavernier, D.A. Hodgson, W. Vyverman, B. Gilbert, A. Wilmotte, E.J. Javaux, Organic and mineral imprints in fossil photosynthetic mats of an East Antarctic lake, Geobiology 12 (2014) 424–450, https://doi.org/10.1111/gbi.12096.
[69] K.O. Konhauser, B. Jones, V.R. Phoenix, G. Ferris, R.W. Renaut, The microbial role in hot spring silicification, AMBIO A J. Hum. Environ. 33 (2009) 552–558, https://doi.org/10.1579/0044-7447-33.8.552.
[70] R. Rippka, J. Waterbury, G. Cohen-Bazire, A cyanobacterium which lacks thylakoids, Arch. Microbiol. 100 (1974) 419–436, https://doi.org/10.1007/BF00446333.
[71] J. Komárek, J. Kaštovský, Coincidences of structural and molecular characters in evolutionary lines of cyanobacteria, Arch. Hydrobiol. Suppl. Algol. Stud. 109 (2003) 305–325, https://doi.org/10.1127/1864-1318/2003/0109-0305.
[72] M. Pacton, G.E. Gorin, N. Fiet, Unravelling the origin of ultralaminae in sedimentary organic matter: the contribution of bacteria and photosynthetic organisms, J. Sediment. Res. 78 (2008) 654–667, https://doi.org/10.2110/jsr.2008.075.
[73] A.D. Anbar, Oceans: elements and evolution, Science 322 (2008) 1481–1483, https://doi.org/10.1126/science.1163100.
[74] C.W. Diamond, N.J. Planavsky, C. Wang, T.W. Lyons, What the ~1.4 Ga Xiamaling Formation can and cannot tell us about the mid-Proterozoic ocean, Geobiology 16 (2018) 219–236, https://doi.org/10.1111/gbi.12282.
[75] J. Beghin, R. Guilbaud, S.W. Poulton, N. Gueneli, J.J. Brocks, J.Y. Storme, C. Blanpied, E.J. Javaux, A palaeoecological model for the late mesoproterozoic – early neoproterozoic atar/el Mreïti group, Taoudeni basin, Mauritania, northwestern Africa, Precambrian Res. 299 (2017) 1–14, https://doi.org/10.1016/j.

precamres.2017.07.016.
[76] R. Guilbaud, B.J. Slater, S.W. Poulton, T.H.P. Harvey, J.J. Brocks, B.J. Nettersheim, N.J. Butterfield, Oxygen minimum zones in the early Cambrian ocean, Geochemical Perspect. Lett. (2018) 33–38, https://doi.org/10.7185/geochemlet.1806.
[77] R. Raiswell, D.S. Hardisty, T.W. Lyons, D.E. Canfield, J.D. Owens, N.J. Planavsky, S.W. Poulton, C.T. Reinhard, The iron paleoredox proxies: a guide to the pitfalls, problems and proper practice, Am. J. Sci. 318 (2018) 491–526, https://doi.org/10.2475/05.2018.03.
[78] S.M. Porter, H. Agiæ, L.A. Riedman, Anoxic ecosystems and early eukaryotes, Emerg. Top. Life Sci. 2 (2018) 299–309, https://doi.org/10.1042/ETLS20170162.
[79] A.H. Knoll, Life on a Young Planet, Univ. Press, Princeton, NJ, 2003, p. 277.
[80] A.H. Knoll, S. Worndle, L.C. Kah, Covariance of microfossil assemblages and microbialite textures across an upper mesoproterozoic carbonate platform, Palaios 28 (2013) 453–470, https://doi.org/10.2110/palo.2013.p13-005r.
[81] J.W. Green, A.H. Knoll, K. Swett, Microfossils from oolites and pisolites of the upper proterozoic Eleonore Bay group, central East Greenland, J. Paleontol. 62 (1988) 835–852, https://doi.org/10.1017/S0022336000030109.
[82] S. Golubic, I. Friedman, J. Schneider, The lithobiontic ecological niche, with special reference to microorganisms, SEPM J. Sediment. Res. 51 (1981) 475–478, https://doi.org/10.1306/212F7CB6-2B24-11D7-8648000102C1865D.
[83] J.J. Brocks, G.D. Love, R.E. Summons, A.H. Knoll, G.A. Logan, S.A. Bowden, Biomarker evidence for green and purple sulphur bacteria in a stratified Palaeoproterozoic sea, Nature 437 (2005) 866–870, https://doi.org/10.1038/nature04068.
[84] R.E. Summons, L.L. Jahnke, J.M. Hope, G.A. Logan, 2-Methylhopanoids as biomarkers for cyanobacterial oxygenic photosynthesis, Nature 400 (1999) 554–557.
[85] J.J. Brocks, G.A. Logan, R. Buick, R.E. Summons, Archean molecular fossils and the early rise of eukaryotes, Science 285 (1999) 1033–1036, https://doi.org/10.1126/science.285.5430.1033.
[86] B. Rasmussen, I.R. Fletcher, J.J. Brocks, M.R. Kilburn, Reassessing the first appearance of eukaryotes and cyanobacteria, Nature 455 (2008) 1101–1104, https://doi.org/10.1038/nature07381.
[87] K.L. French, C. Hallmann, J.M. Hope, P.L. Schoon, J.A. Zumberge, Y. Hoshino, C.A. Peters, S.C. George, G.D. Love, J.J. Brocks, R. Buick, R.E. Summons, Reappraisal of hydrocarbon biomarkers in Archean rocks, Proc. Natl. Acad. Sci. Unit. States Am. 112 (2015) 5915–5920, https://doi.org/10.1073/pnas.1419563112.
[88] J. Beghin, J.-Y. Storme, C. Blanpied, N. Gueneli, J.J. Brocks, S.W. Poulton, E.J. Javaux, Microfossils from the late mesoproterozoic – early neoproterozoic atar/el Mreïti group, Taoudeni basin, Mauritania, northwestern Africa, Precambrian Res. 291 (2017) 63–82, https://doi.org/10.1016/J.PRECAMRES.2017.01.009.
[89] C.P. Marshall, E.J. Javaux, A.H. Knoll, M.R. Walter, Combined micro-Fourier transform infrared (FTIR) spectroscopy and micro-Raman spectroscopy of Proterozoic acritarchs: a new approach to Palaeobiology, Precambrian Res. 138 (2005) 208–224, https://doi.org/10.1016/j.precamres.2005.05.006.
[90] B.K. Baludikay, C. François, M.C. Sforna, J. Beghin, Y. Cornet, J.-Y. Storme, N. Fagel, F. Fontaine, R. Littke, D. Baudet, D. Delvaux, E.J. Javaux, Raman microspectroscopy, bitumen reflectance and illite crystallinity scale: comparison of different geothermometry methods on fossiliferous Proterozoic sedimentary basins (DR Congo, Mauritania and Australia), Int. J. Coal Geol. 191 (2018) 80–94, https://doi.org/10.1016/j.coal.2018.03.007.
[91] H.G.M. Edwards, F. Garcia-Pichel, E.M. Newton, D.D. Wynn-Williams, Vibrational Raman spectroscopic study of scytonmenin, the UV-protective cyanobacterial pigment, Spectrochim. Acta (1999) 193–200.
[92] J. Jehlièka, A. Oren, Raman spectroscopy in halophile research, Front. Microbiol. 4 (2013) 1–7, https://doi.org/10.3389/fmicb.2013.00380.
[93] J.-Y. Storme, S. Golubic, A. Wilmotte, J. Kleinteich, D. Velázquez, E.J. Javaux, Raman characterization of the UV-protective pigment gloeocapsin and its role in the survival of cyanobacteria, Astrobiology 15 (2015) 843–857, https://doi.org/10.1089/ast.2015.1292.
[94] V.E. De Oliveira, M.A.C.N. Miranda, M.C.S. Soares, H.G.M. Edwards, L.F.C. De Oliveira, Study of carotenoids in cyanobacteria by Raman spectroscopy, Spectrochim. Acta Part A Mol. Biomol. Spectrosc. 150 (2015) 373–380, https://doi.org/10.1016/j.saa.2015.05.044.
[95] P.J. Proteau, W.H. Gerwick, F. Garcia-Pichel, R. Castenholz, The structure of scytonemin, an ultraviolet sunscreen pigment from the sheaths of cyanobacteria, Experientia 49 (1993) 825–829, https://doi.org/10.1007/BF01923559.
[96] J.M. Fulton, M.A. Arthur, K.H. Freeman, Subboreal aridity and scytonemin in the holocene black sea, Org. Geochem. 49 (2012) 47–55, https://doi.org/10.1016/j.orggeochem.2012.05.008.
[97] D.A. Hodgson, S.W. Wright, N. Davies, Mass Spectrometry and reverse phase HPLC techniques for the identification of degraded fossil pigments in lake sediments and their application in palaeolimnology, J. Paleolimnol. 18 (1997) 335–350, https://doi.org/10.1023/A:1007943119392.
[98] A.H. Knoll, D.E. Canfield, K.O. Konhauser, Fundamentals of Geobiology, John Wiley, 2012, https://doi.org/10.1002/9781118280874.
[99] L.M. Ward, P.M. Shih, The evolution and productivity of carbon fixation pathways in response to changes in oxygen concentration over geological time, Free Radic. Biol. Med. (2019) S0891584918315132.
[100] C.H. House, J.W. Schopf, K.D. McKeegan, C.D. Coath, T.M. Harrison, K.O. Stetter, Carbon isotopic composition of individual Precambrian microfossils, Geology 28 (2000) 707–710, https://doi.org/10.1130/0091-7613(2000)028<0707:CICOIP>2.3.CO;2.
[101] F. Delarue, F. Robert, K. Sugitani, R. Tartèse, R. Duhamel, S. Derenne, Nitrogen isotope signatures of microfossils suggest aerobic metabolism 3.0 Gyr ago, Geochemical Perspect. Lett. 7 (2018) 32–36, https://doi.org/10.7185/geochemlet.1816.
[102] K.H. Williford, T. Ushikubo, J.W. Schopf, K. Lepot, K. Kitajima, J.W. Valley, Preservation and detection of microstructural and taxonomic correlations in the carbon isotopic compositions of individual Precambrian microfossils, Geochem. Cosmochim. Acta 104 (2013) 165–182, https://doi.org/10.1016/j.gca.2012.11.005.
[103] K.O. Konhauser, Bacterial iron biomineralisation in nature, FEMS Microbiol. Rev. 20 (1997) 315–326, https://doi.org/10.1016/S0168-6445(97)00014-4.
[104] J. Li, K. Benzerara, S. Bernard, O. Beyssac, The link between biomineralization and fossilization of bacteria : insights from fi eld and experimental studies, Chem. Geol. 359 (2013) 49–69, https://doi.org/10.1016/j.chemgeo.2013.09.013.
[105] E. Couradeau, K. Benzerara, E. Gérard, D. Moreira, S. Bernard, G.E. Brown, P. López-García, An early-branching microbialite cyanobacterium forms intracellular carbonates, Science 336 (2012) 459–462, https://doi.org/10.1126/science.1216171.
[106] I.I. Brown, D.A. Bryant, D. Casamatta, K.L. Thomas-Keprta, S.A. Sarkisova, G. Shen, J.E. Graham, E.S. Boyd, J.W. Peters, D.H. Garrison, D.S. McKay, Polyphasic characterization of a thermotolerant siderophilic filamentous cyanobacterium that produces intracellular iron deposits, Appl. Environ. Microbiol. 76 (2010) 6664–6672, https://doi.org/10.1128/AEM.00662-10.
[107] K. Lepot, A. Addad, A.H. Knoll, J. Wang, D. Troadec, A. Béché, E.J. Javaux, Iron minerals within specific microfossil morphospecies of the 1.88 Ga Gunflint Formation, Nat. Commun. 8 (2017) 14890, https://doi.org/10.1038/ncomms14890.
[108] J.W. Schopf, B.M. Packer, Early archean (3.3-billion to 3.5-billion-year-old) microfossils from warrawoona group, Australia, Science 237 (1987) 70–73, https://doi.org/10.1126/science.11539686.
[109] D.M. Bower, A. Steele, M.D. Fries, O.R. Green, J.F. Lindsay, Raman imaging spectroscopy of a putative microfossil from the ~3.46 Ga Apex chert: insights from quartz grain orientation, Astrobiology 16 (2016) 169–180, https://doi.org/10.1089/ast.2014.1207.
[110] M.D. Brasier, O.R. Green, J.F. Lindsay, N. McLoughlin, A. Steele, C. Stoakes, Critical testing of Earth's oldest putative fossil assemblage from the ~3.5 Ga Apex chert, Chinaman Creek, Western Australia, Precambrian Res. 140 (2005) 55–102, https://doi.org/10.1016/J.PRECAMRES.2005.06.008.
[111] D.L. Pinti, R. Mineau, V. Clement, Hydrothermal alteration and microfossil artefacts of the 3,465-million-year-old Apex chert, Nat. Geosci. 2 (2009) 640–643, https://doi.org/10.1038/ngeo601.
[112] B.T. De Gregorio, T.G. Sharp, G.J. Flynn, S. Wirick, R.L. Hervig, Biogenic origin for Earth's oldest putative microfossils, Geology 37 (2009) 631–634, https://doi.org/10.1130/G25683A.1.
[113] J.W. Schopf, Microfossils of the early archean Apex chert: new evidence of the antiquity of life, Science 260 (1993) 640–646, https://doi.org/10.1126/science.260.5108.640.
[114] J.W. Schopf, K. Kitajima, M.J. Spicuzza, A.B. Kudryavtsev, J.W. Valley, SIMS analyses of the oldest known assemblage of microfossils document their taxon-correlated carbon isotope compositions, Proc. Natl. Acad. Sci. Unit. States Am. 115 (2017) 53–58, https://doi.org/10.1073/pnas.1718063115.
[115] S. Golubic, H.J. Hofmann, Comparison of holocene and mid-precambrian entophysalidaceae (cyanophyta) in stromatolitic algal mats: cell division and degradation, J. Paleontol. 50 (1976) 1074–1082.
[116] J. Komárek, Cyanoprokaryota 1. Teil: Chroococcales, Subwasserflora von Mitteleuropa. 19 1–548, Spektrum Akademischer Verlag, Heidelberg, 1999.
[117] S. Golubic, R.M.M. Abed, *Entophysalis* mats as environmental regulators, Natl. Acad. Sci. Planet. Biol. (2010) 237–251, https://doi.org/10.1007/978-90-481-3799-2_12.
[118] B.P. Burns, R. Anitori, P. Butterworth, R. Henneberger, F. Goh, M.A. Allen, R. Ibañez-Peral, P.L. Bergquist, M.R. Walter, B.A. Neilan, Modern analogues and the early history of microbial life, Precambrian Res. 173 (2009) 10–18, https://doi.org/10.1016/j.precamres.2009.05.006.
[119] D. Papineau, J.J. Walker, S.J. Mojzsis, N.R. Pace, Composition and structure of microbial communities from stromatolites of Hamelin Pool in Shark Bay, western Australia, appl, Environ. Microbiol. 71 (2005) 4822–4832, https://doi.org/10.1128/AEM.71.8.4822-4832.2005.
[120] H.J. Hofmann, G.D. Jackson, Precambrian (aphebian) microfossils from belcher islands, Hudson Bay, Can. J. Earth Sci. 6 (1969) 1137–1144.
[121] J.W. Green, A.H. Knoll, S. Golubic, K. Swett, Paleobiology of distinctive benthic microfossils from the upper Proterozoic Limestone-Dolomite “Series,” central East Greenland, Am. J. Bot. 74 (1987) 928–940, https://doi.org/10.2307/2443874.
[122] T. Fairchild, The Geologic Setting and Paleobiology of a Late Precambrian Stromatolitic Microflora from South Australia, Doctoral dissertation University of California, 1975.
[123] V.N. Sergeev, Microfossils in cherts from the middle riphean (mesoproterozoic) Avzyan Formation, southern ural Mountains, Russian federation, Precambrian Res. 65 (1994) 231–254, https://doi.org/10.1016/0301-9268(94)90107-4.
[124] A.H. Knoll, Life on a Young Planet: the First Three Billion Years of Evolution on Earth, updated edition, Princeton University Press, 2015.
[125] A. Tribollet, S. Golubic, Reef bioerosion: agents and processes, Coral Reefs an Ecosyst, Transit., 2011, pp. 435–449, , https://doi.org/10.1007/978-94-007-0114-4_25.
[126] Y. Zhang, Proterozoic stromatolitic micro-organisms from Hebei, North China: cell preservation and cell division, Precambrian Res. 38 (1988) 165–175, https://doi.org/10.1016/0301-9268(88)90090-3.
[127] P.M. Visser, B.W. Ibelings, L.R. Mur, A.E. Walsby, The ecophysiology of the

harmful cyanobacterium *Microcystis*, in: J. Huisman, H. Matthijs, P.M. Visser (Eds.), Harmful Cyanobacteria, Springer, Dordrecht, 2005, pp. 109–142, , https://doi.org/10.1007/1-4020-3022-3_6.
[128] K. Pang, Q. Tang, L. Chen, B. Wan, C. Niu, X. Yuan, S. Xiao, Nitrogen-fixing heterocystous cyanobacteria in the tonian period, Curr. Biol. 28 (2018) 616–622, https://doi.org/10.1016/j.cub.2018.01.008 e1.
[129] C.P. Wolk, A. Ernst, J. Elhai, Heterocyst metabolism and development, in: D.A. Bryant (Ed.), Mol. Biol. Cyanobacteria. Adv. Photosynth. Springer, Dordrecht, 1994.
[130] R.N. Kaplan-Levy, O. Hadas, M.L. Summers, J. Rücker, A. Sukenik, Akinetes: Dormant cells of Cyanobacteria, in: E. Lubzens, et al. (Ed.), Dormancy and Resistance in Harsh Environments, Springer, Berlin, 2010, pp. 5–27.
[131] J. Komárek, Cyanoprokaryota. 3. Teil: Heterocytous genera, Süßwasserflora von Mitteleuropa, Springer Spektrum, 2013.
[132] S. Golubic, V.N. Sergeev, A.H. Knoll, Mesoproterozoic *Archaeoellipsoides*: akinetes of heterocystous cyanobacteria, Lethaia 28 (1995) 285–298.
[133] V.N. Sergeev, A.H. Knoll, J.P. Grotzinger, Paleobiology of the mesoproterozoic Billyakh group, anabar uplift, northern Siberia, J. Paleontol. 69 (1995) 1–37.
[134] N.J. Butterfield, Proterozoic photosynthesis - a critical review, Palaeontology 58 (2015) 953–972, https://doi.org/10.1111/pala.12211.
[135] B. Amard, J. Bertrand-Sarfati, Microfossils in 2000 Ma old cherty stromatolites of the Franceville group, Gabon, Precambrian Res. 81 (1997) 197–221, https://doi.org/10.1016/S0301-9268(96)00035-6.
[136] A. Tomitani, A.H. Knoll, C.M. Cavanaugh, T. Ohno, The evolutionary diversification of cyanobacteria: molecular-phylogenetic and paleontological perspectives, Proc. Natl. Acad. Sci. Unit. States Am. 103 (2006) 5442–5447, https://doi.org/10.1073/pnas.0600999103.
[137] H.N. Schulz-Vogt, E.R. Angert, F. Garcia-Pichel, Giant bacteria, Encycl. Life Sci. (2007) 1–7, https://doi.org/10.1002/9780470015902.a0020371.
[138] V.K. Golovenok, M.Y. Belova, Riphean microbiotas in cherts of the Billyakh group on the anabar uplift, Paleontol. Zh. 4 (1984) 20–30.
[139] Y. Zhang, Proterozoic stromatolite microfloras of the Gaoyuzhuang Formation (early sinian: riphean), hebei, China, J. Paleontol. 55 (1981) 485–506.
[140] J.W. Schopf, Microflora of the bitter Springs Formation, late precambrian, central Australia, J. Paleontol. 42 (1968) 651–688.
[141] V.N. Sergeev, M. Sharma, Y. Shukla, Mesoproterozoic silicified microbiotas of Russia and India-Characteristics and Contrasts, Palaeobotanist 57 (2008) 323–358.
[142] J. Komárková, J. Jezberová, O. Komárek, E. Zapomìlová, Variability of *Chroococcus* (cyanobacteria) morphospecies with regard to phylogenetic relationships, Hydrobiologia 639 (2010) 69–83, https://doi.org/10.1007/s10750-009-0015-3.
[143] H. Nozaki, Morphology, sexual reproduction and taxonomy of *Volvox carteri* f. *kawasakiensis* f. nov. (Chlorophyta) from Japan, Phycologia 27 (1988) 209–220, https://doi.org/10.2216/i0031-8884-27-2-209.1.
[144] M. Shi, Q. Feng, M.Z. Khan, S. Zhu, An eukaryote-bearing microbiota from the early mesoproterozoic Gaoyuzhuang Formation, Tianjin, China and its significance, Precambrian Res. 303 (2017) 709–726, https://doi.org/10.1016/j.precamres.2017.09.013.
[145] X.L. Song, *Obruchevella* from the early cambrian meishaucun stage of the meishucun section, jinning, yunnan, China, Geol. Mag. 121 (1984) 179–183.
[146] E. Reitlinger, Kimbrijskie foraminifery yakutii (cambrian foraminifers of yakutsk), byullelin 'moskovskogo obs, Ispytateki Prir. Geol. 23 (1948) 77–81.
[147] C. Mankiewicz, *Obruchevella* and other microfossils in the Burgess Shale: preservation and affinity, J. Paleontol. 66 (1992) 717–729, https://doi.org/10.1017/S0022336000020758.
[148] V.A. Luchinina, Paleoal'gologicheskaya Kharakteristika Rannego Kembriya Sibirskoi Platformy (Paleoalgological Characteristics of the Lower Cambrian of the Siberian Plat Form), Nauka, Novosibirsk, 1975, p. 100.
[149] C. Sili, G. Torzillo, A. Vonshak, Arthrospira (*Spirulina*), in: B.A. Whitton (Ed.), Ecol. Cyanobacteria II Their Divers. Sp. Time, Springer, 2012, pp. 677–706, , https://doi.org/10.1007/978-94-007-3855-3_25.
[150] G. Giesberger, Some observations on the culture, physiology and morphology of some brown-red *Rhodospirillum*-species, Antonie Leeuwenhoek 13 (1947) 137–148.
[151] K.V.N.S. Lakshmi, B. Divyasree, E.V.V. Ramprasad, C. Sasikala, C.V. Ramana, Reclassification of *Rhodospirillum photometricum* Molisch 1907, *Rhodospirillum sulfurexigens* Anil Kumar et al. 2008 and *Rhodospirillum oryzae* Lakshmi et al. 2013 in a new genus, *Pararhodospirillum* gen. nov., as *Pararhodospirillum photometricum* comb. nov, Int. J. Syst. Evol. Microbiol. 64 (2013) 1154–1159, https://doi.org/10.1099/ijs.0.059147-0.
[152] J.W. Schopf, The paleobiological record of photosynthesis, Photosynth. Res. 107 (2011) 87–101, https://doi.org/10.1007/s11120-010-9577-1.
[153] N.J. Butterfield, A.H. Knoll, K. Swett, Paleobiology of the neoproterozoic svanbergfjellet formation, Spitsbergen, Foss. Strat. 34 (1994) 1–84.
[154] C. V Mendelson, J.W. Schopf, Proterozoic microfossils from the sukhaya tunguska, shorikha, and yudoma formations of the siberian platform, USSR, J. Paleontol. 56 (1982) 42–83.
[155] A.H. Knoll, P.K. Strother, S. Rossi, Distribution and diagenesis of microfossils from the lower proterozoic duck creek dolomite, Western Australia, Precambrian Res. 38 (1988) 257–279, https://doi.org/10.1016/0301-9268(88)90005-8.
[156] H.N. Schulz-Vogt, Beggiatoa, in: D. Springer (Ed.), Encycl. Geobiol. 2011, pp. 111–112.
[157] A. Permyakov, S. Osipova, N. Bondarenko, L. Obolkina, O. Timoshkin, C. Boedeker, B. Geist, A.R. Schäffner, Proteins homologous to aquaporins of higher plants in the freshwater alga *Ulothrix zonata* (Ulotrichales, Chlorophyta), Eur. J. Phycol. 51 (2016) 99–106, https://doi.org/10.1080/09670262.2015.1106588.
[158] F.A. Macdonald, M.D. Schmitz, J.L. Crowley, C.F. Roots, D.S. Jones, A.C. Maloof, J.V. Strauss, P.A. Cohen, D.T. Johnston, D.P. Schrag, Calibrating the cryogenian, Science 327 (2010) 1241–1243, https://doi.org/10.1126/science.1183325.
[159] P.Y. Zhang, X.L. Yan, Microfossils from the Gaoyuzhuang Formation in laishui county, hebei, China, Acta Geol. Sin. 58 (1984) 196–203.
[160] M.S. Yakschin, Algal microbiota from the lower riphean deposits of the anabar uplift, Nauk. Novosib (1991) 61.
[161] J.H. Oehler, Experimental studies in Precambrian paleontology: structural and chemical changes in blue-green algae during simulated fossilization in synthetic chert, Bull. Geol. Soc. Am. 87 (1976) 117–129, https://doi.org/10.1130/0016-7606(1976)87<117:ESIPPS>2.0.CO;2.
[162] B.V. Timofeev, T.N. Hermann, N.S. Mikhailova, Microphytofossils of the Precambrian, Cambrian, and Ordovician, Nauk. Leningr., 1976.
[163] H.J. Hofmann, G.D. Jackson, Shale-facies Microfossils from the Proterozoic Bylot Supergroup, Baffin Island, Canada, 1994, pp. 1–34.
[164] N.G. Vorob'eva, V.N. Sergeev, P.Y. Petrov, Kotuikan Formation assemblage: a diverse organic-walled microbiota in the Mesoproterozoic Anabar succession, northern Siberia, Precambrian Res. 256 (2015) 201–222, https://doi.org/10.1016/j.precamres.2014.11.011.
[165] B.K. Baludikay, J. Storme, C. François, D. Baudet, E.J. Javaux, A diverse and exquisitely preserved organic-walled microfossil assemblage from the Meso – neoproterozoic Mbuji-Mayi Supergroup (Democratic Republic of Congo) and implications for Proterozoic biostratigraphy, Precambrian Res. 281 (2016) 166–184, https://doi.org/10.1016/j.precamres.2016.05.017.
[166] N.G. Vorob'eva, V.N. Sergeev, A.H. Knoll, Neoproterozoic microfossils from the northeastern margin of the East european platform, J. Paleontol. 83 (2009) 161–196, https://doi.org/10.1666/08-064.1.
[167] J. Mareš, Y. Lara, I. Dadáková, T. Hauer, B. Uher, A. Wilmotte, J. Kaštovský, Phylogenetic analysis of cultivation-resistant terrestrial cyanobacteria with massive sheaths (*Stigonema* spp. and *Petalonema alatum*, Nostocales, Cyanobacteria) using single-cell and filament sequencing of environmental samples, J. Phycol. 51 (2015) 288–297, https://doi.org/10.1111/jpy.12273.
[168] E.J. Javaux, K. Lepot, M.A. Van Zuilen, V.A. Melezhik, P. V Medvedev, Palaeoproterozoic microfossils, in: V.A. Melezhik (Ed.), Read. Arch. Earth's Oxyg. Springer, 2013, pp. 1352–1370.
[169] L.C. Kah, A.H. Knoll, Microbenthic distribution of Proterozoic tidal flats: environmental and taphonomic considerations, Geology 24 (1996) 79–82, https://doi.org/10.1130/0091-7613(1996)024<0079:MDOPTF>2.3.CO;2.
[170] C. Klein, N.J. Beukes, J.W. Schopf, Filamentous microfossils in the early proterozoic transvaal Supergroup: their morphology, significance, and paleoenvironmental setting, Precambrian 36 (1987) 81–94.
[171] A.H. Knoll, K. Swett, J. Mark, Paleobiology of a neoproterozoic tidal flat/lagoonal complex: the draken conglomerate formation, Spitsbergen, J. Paleontol. 65 (1991) 531–570, https://doi.org/10.1017/S0022336000030663.
[172] S.G. Lekele Baghekema, K. Lepot, A. Riboulleau, A. Fadel, A. Trentesaux, A. El Albani, Nanoscale analysis of preservation of ca. 2.1 Ga old Francevillian microfossils, Gabon, Precambrian Res. (2017) 1–18, https://doi.org/10.1016/j.precamres.2017.08.024.
[173] M. Sharma, Small-sized akinetes from the mesoproterozoic salkhan Limestone, semri group, Bihar, India, J. Palaeontol. Soc. India 51 (2006) 109–118, https://doi.org/10.1177/1471301211408123.
[174] Z. Yun, Stromatolitic microbiota from the middle proterozoic wumishan formation (jixian group) of the ming tombs, beijing, China, Precambrian Res. 30 (1985) 277–302.
[175] R.J. Horodyski, J.A. Donaldson, Microfossils from the middle proterozoic dismal lakes General geology the Dismal Lakes Group is exposed in a sinuous belt that extends for a distance of more than 300 km from the north shore of Great Bear Lake al- most to the coast of Coronation Gulf, Precambrian Res. 11 (1980).
[176] V.N. Sergeev, A.H. Knoll, S.P. Kolosova, P.N. Kolosov, Microfossils in cherts from the mesoproterozoic (middle riphean) debengda formation, the olenek uplift, northeastern Siberia, Stratigr. Geol. Correl. 2 (1994) 19–33 http://europepmc.org/abstract/MED/11539429.
[177] V.N. Sergeev, Paleobiology of the neoproterozoic (upper riphean) shorikha and burovaya silicified microbiotas, turukhansk uplift, Siberia, J. Paleontol. 75 (2001) 427–448.
[178] V.K. Golovenok, M.Y. Belova, Riphean microbiotas in cherts of the yeniseyskiy kryazh (ridge), Paleontol. Zh. 2 (1985) 94–103.
[179] V.N. Sergeev, R.N. Ogurtsova, Microbiota from the lower cambrian phosphatic deposits of the maly karatau (south Kazakhstan), Izv. Akad. Nauk. SSSR - Seriya Geol. 3 (1989) 58–66.
[180] M.D. Muir, Microfossils from the middle precambrian McArthur group, northern territory, Australia, Orig. Life 5 (1974) 105–118.
[181] D.S. McMenamin, S. Kumar, S.M. Awramik, Microbial fossils from the kheinjua formation, middle proterozoic semri group (lower vindhyan) son valley area, central India, Precambrian Res. 21 (1983) 247–271, https://doi.org/10.1016/0301-9268(83)90043-8.
[182] D.Z. Oehler, Microflora of the middle proterozoic balbirini dolomite (McArthur group) of Australia, Alcheringa 2 (1978) 269–309.
[183] S. Kumar, P. Srivastava, Middle to late proterozoic microbiota from the deoban Limestone, garhwal himalaya, India, Precambrian Res. 56 (1992) 291–318, https://doi.org/10.1016/0301-9268(92)90106-X.
[184] X. Liu, Z. Lin, Z. Zhang, X. Xu, A study of late Precambrian microfossil algal community from Jinning County, Jiangshu Province, Acta Micropalaeontol. Sin. 1 (1984) 171–182.
[185] V.N. Sergeev, Silicified Microfossils from the Precambrian: Nature, Classification,

and Biostratigraphic Significance, Geos, Moscow, 2006.
[186] P.K. Strother, A.H. Knoll, E.S. Barghoorn, Micro-organisms from the late precambrian narssarssuk formation, north-western Greenland, Palaeontology 26 (1983) 1–32.
[187] R.P. Anderson, S. McMahon, U. Bold, F.A. Macdonald, D.E.G. Briggs, Palaeobiology of the early ediacaran shuurgat formation, zavkhan terrane, southwestern Mongolia, J. Syst. Palaeontol. 15 (2017) 947–968, https://doi.org/10.1080/14772019.2016.1259272.
[188] R. Prasad, S.N. Uniyal, Asher, Organic-walled microfossils from the proterozoic vindhyan Supergroup of son valley, Madhya Pradesh , India, Palaeobotanist 54 (2005) 13–60.
[189] A.H. Knoll, K. Swett, E. Burkhardt, Paleoenvironmental distribution of microfossils and stromatolites in the upper proterozoic backlundtoppen formation, spitsbergen, J. Paleontol. 63 (1989) 129–145.
[190] D.A. Sprinkel, G. Waanders, Stratigraphy, organic microfossils, and thermal maturity of the neoproterozoic uinta Mountains group in the eastern uinta Mountains, northeastern Utah, in: D. C.M, J.L. Pederson, D.A. Sprinkel, B.J. Kowallis (Eds.), Uinta Mt. Geol, 2005, pp. 63–73.
[191] V.K. Singh, R. Babu, M. Shukla, Heterolithic prokeryotes from the coated grains bearing carbonate facies of Bhander Group, Madhya Pradesh, India, J. Appl. Biosci. 37 (2011) 80–90.
[192] K. Nagovitsin, Tappania-bearing association of the Siberian platform: biodiversity, stratigraphic position and geochronological constraints, Precambrian Res. 173 (2009) 137–145, https://doi.org/10.1016/j.precamres.2009.02.005.
[193] J. Samuelsson, P.R. Dawes, G. Vidal, Organic-walled microfossils from the proterozoic thule Supergroup, northwest Greenland, Precambrian Res. 96 (1999) 1–23, https://doi.org/10.1016/S0301-9268(98)00123-5.
[194] B. Prasad, R. Asher, Acritarch biostratigraphy and lithostratigraphic classification of proterozoic and lower paleozoic sediments (Pre-unconformity sequence) of ganga basin, India, paleontogr, Indica 5 (2001) 151.
[195] N.J. Butterfield, A.H. Knoll, K. Swett, A bangiophyte red alga from the proterozoic of arctic Canada, Science 250 (1990) 104–107, https://doi.org/10.1126/science.11538072.
[196] V.K. Golovenok, M.Y. Belova, Microfossils in cherts from the sukhaya tunguska formation, riphean, turukhansk uplift, dokl, Earth Sci. 323 (1992) 114–118.
[197] K.E. Nagovitsin, Silicified microbiotas of the upper riphean of the yenisei ridge: news in paleontology and stratigraphy, Geol .Geof. 41 (2000) 7–31.
[198] J.W. Schopf, Biostratigraphic usefulness of stromatolitic precambrian microbiotas: a preliminary analysis, Precambrian Res. 5 (1977) 143–173.
[199] V.N. Sergeev, N.G. Vorob'eva, P. Yu Petrov, The biostratigraphic conundrum of Siberia: do true Tonian–Cryogenian microfossils occur in Mesoproterozoic rocks? Precambrian Res. 299 (2017) 282–302, https://doi.org/10.1016/j.precamres.2017.07.024.
[200] N.G. Vorob'eva, V.N. Sergeev, A.H. Knoll, Neoproterozoic microfossils from the margin of the East European Platform and the search for a biostratigraphic model of lower Ediacaran rocks, Precambrian Res. 173 (2009) 163–169, https://doi.org/10.1016/j.precamres.2009.04.001.
[201] P.M. Shih, D. Wu, A. Latifi, S.D. Axen, D.P. Fewer, E. Talla, A. Calteau, F. Cai, N. Tandeau de Marsac, R. Rippka, M. Herdman, K. Sivonen, T. Coursin, T. Laurent, L. Goodwin, M. Nolan, K.W. Davenport, C.S. Han, E.M. Rubin, J.A. Eisen, T. Woyke, M. Gugger, C.A. Kerfeld, Improving the coverage of the cyanobacterial phylum using diversity-driven genome sequencing, Proc. Natl. Acad. Sci. Unit. States Am. 110 (2013) 1053–1058, https://doi.org/10.1073/pnas.1217107110.
[202] N. Rodríguez-Ezpeleta, H. Brinkmann, S.C. Burey, B. Roure, G. Burger, W. Löffelhardt, H.J. Bohnert, H. Philippe, B.F. Lang, Monophyly of primary photosynthetic eukaryotes: green plants, red algae, and glaucophytes, Curr. Biol. 15 (2005) 1325–1330 https://doi.org/10.1016/j.cub.2005.06.040.
[203] A. Criscuolo, S. Gribaldo, Large-scale phylogenomic analyses indicate a deep origin of primary plastids within cyanobacteria, Mol. Biol. Evol. 28 (2011) 3019–3032, https://doi.org/10.1093/molbev/msr108.
[204] L. Cornet, L. Meunier, M. Van Vlierberghe, R.R. Léonard, B. Durieu, Y. Lara, A. Misztak, D. Sirjacobs, E.J. Javaux, H. Philippe, A. Wilmotte, D. Baurain, Consensus assessment of the contamination level of publicly available cyanobacterial genomes, PLoS One 13 (2018) 1–26, https://doi.org/10.1371/journal.pone.0200323.
[205] P. Dvořák, A. Poulíčková, P. Hašler, M. Belli, D.A. Casamatta, A. Papini, Species concepts and speciation factors in cyanobacteria, with connection to the problems of diversity and classification, Biodivers. Conserv. 24 (2015) 739–757, https://doi.org/10.1007/s10531-015-0888-6.
[206] L. Cornet, A. Wilmotte, E.J. Javaux, D. Baurain, A constrained SSU-rRNA phylogeny reveals the unsequenced diversity of photosynthetic Cyanobacteria (Oxyphotobacteria), BMC Res. Notes 11 (2018) 435, https://doi.org/10.1186/s13104-018-3543-y.
[207] T. Dagan, M. Roettger, K. Stucken, G. Landan, R. Koch, P. Major, S.B. Gould, V.V. Goremykin, R. Rippka, N.T. De Marsac, M. Gugger, P.J. Lockhart, J.F. Allen, I. Brune, I. Maus, A. Pühler, W.F. Martin, Genomes of stigonematalean cyanobacteria (subsection V) and the evolution of oxygenic photosynthesis from prokaryotes to plastids, Genome Biol. Evol. 5 (2013) 31–44, https://doi.org/10.1093/gbe/evs117.
[208] J.A.G. Ochoa de Alda, R. Esteban, M.L. Diago, J. Houmard, The plastid ancestor originated among one of the major cyanobacterial lineages, Nat. Commun. 5 (2014) 4937 https://doi.org/10.1038/ncomms5937.
[209] B. Li, C.J. Cox, J.S. Lopes, P.G. Foster, T.M. Embley, Compositional biases among synonymous substitutions cause conflict between gene and protein trees for plastid origins, Mol. Biol. Evol. 31 (2014) 1697–1709, https://doi.org/10.1093/molbev/msu105.
[210] P. Sánchez-Baracaldo, Origin of marine planktonic cyanobacteria, Sci. Rep. 5 (2015) 14–17, https://doi.org/10.1038/srep17418.
[211] J.C. Uyeda, L.J. Harmon, C.E. Blank, A comprehensive study of cyanobacterial morphological and ecological evolutionary dynamics through deep geologic time, PLoS One 11 (2016) e0162539https://doi.org/10.1371/journal.pone.0162539.
[212] J.M. Walter, F.H. Coutinho, B.E. Dutilh, J. Swings, F.L. Thompson, C.C. Thompson, Ecogenomics and taxonomy of Cyanobacteria phylum, Front. Microbiol. 8 (2017) 1–18, https://doi.org/10.3389/fmicb.2017.02132.
[213] C. Magnabosco, K.R. Moore, J.M. Wolfe, G.P. Fournier, Dating phototrophic microbial lineages with reticulate gene histories, Geobiology 16 (2018) 179–189, https://doi.org/10.1111/gbi.12273.
[214] H. Philippe, H. Brinkmann, D.V. Lavrov, D.T.J. Littlewood, M. Manuel, G. Wörheide, D. Baurain, Resolving difficult phylogenetic questions: why more sequences are not enough, PLoS Biol. 9 (2011) e1000602https://doi.org/10.1371/journal.pbio.1000602.
[215] H. Philippe, D.M. de Vienne, V. Ranwez, B. Roure, D. Baurain, F. Delsuc, Pitfalls in supermatrix phylogenomics, Eur. J. Taxon. No 283 Pitfalls Supermatrix Phylogenomics 283 (2017) 1–25, https://doi.org/10.5852/ejt.2017.283.
[216] P. Simion, H. Philippe, D. Baurain, M. Jager, D.J. Richter, A. Di Franco, B. Roure, N. Satoh, E. Queinnec, A. Ereskovsky, A large and consistent phylogenomic dataset supports sponges as the sister group to all other animals, Curr. Biol. 27 (2017) 958–967.
[217] I. Irisarri, D. Baurain, H. Brinkmann, F. Delsuc, J.-Y. Sire, A. Kupfer, J. Petersen, M. Jarek, A. Meyer, M. Vences, Phylotranscriptomic consolidation of the jawed vertebrate timetree, Nat. Ecol. Evol. 1 (2017) 1370–1378.
[218] P. Sánchez-Baracaldo, A. Ridgwell, J.A. Raven, A neoproterozoic transition in the marine nitrogen cycle, Curr. Biol. 24 (2014) 652–657, https://doi.org/10.1016/j.cub.2014.01.041.
[219] P.M. Shih, J. Hemp, L.M. Ward, N.J. Matzke, W.W. Fischer, Crown group Oxyphotobacteria postdate the rise of oxygen, Geobiology 15 (2017) 19–29, https://doi.org/10.1111/gbi.12200.
[220] P.M. Shih, N.J. Matzke, Primary endosymbiosis events date to the later Proterozoic with cross-calibrated phylogenetic dating of duplicated ATPase proteins, Proc. Natl. Acad. Sci. Unit. States Am. 110 (2013) 12355–12360, https://doi.org/10.1073/pnas.1305813110.
[221] A. Gavryushkina, T.A. Heath, D.T. Ksepka, T. Stadler, D. Welch, A.J. Drummond, Bayesian total-evidence dating reveals the recent crown radiation of penguins, Syst. Biol. 66 (2017) 57–73.
[222] F. Ronquist, N. Lartillot, M.J. Phillips, Closing the gap between rocks and clocks using total-evidence dating, Phil. Trans. R. Soc. B. 371 (2016) 20150136.
[223] P.-S. Seo, A. Yokota, The phylogenetic relationships of cyanobacteria inferred from 16S rRNA, gyrB, rpoC1 and rpoD1 gene sequences, J. Gen. Appl. Microbiol. 49 (2003) 191–203, https://doi.org/10.2323/jgam.49.191.
[224] L. Hoffmann, J. Komárek, J. Kaštovský, System of cyanoprokaryotes (cyanobacteria) – state in 2004, Arch. Hydrobiol. Suppl. Algol. Stud. 117 (2005) 95–115, https://doi.org/10.1127/1864-1318/2005/0117-0095.
[225] R.S. Gupta, D.W. Mathews, Signature proteins for the major clades of Cyanobacteria, BMC Evol. Biol. 10 (2010) 1–20, https://doi.org/10.1186/1471-2148-10-24.
[226] C.E. Blank, P. Sanchez-Baracaldo, Timing of morphological and ecological innovations in the cyanobacteria – a key to understanding the rise in atmospheric oxygen, Geobiology 8 (2010) 1–23, https://doi.org/10.1111/j.1472-4669.2009.00220.x.
[227] B.E. Schirrmeister, J.M. de Vos, A. Antonelli, H.C. Bagheri, Evolution of multicellularity coincided with increased diversification of cyanobacteria and the Great Oxidation Event, Proc. Natl. Acad. Sci. Unit. States Am. 110 (2013) 1791–1796, https://doi.org/10.1073/pnas.1209927110.
[228] B.E. Schirrmeister, M. Gugger, P.C.J. Donoghue, Cyanobacteria and the Great oxidation event: evidence from genes and fossils, Palaeontology 58 (2015) 769–785, https://doi.org/10.1111/pala.12178.
[229] F.U. Battistuzzi, A. Feijao, S.B. Hedges, A genomic timescale of prokaryote evolution: insights into the origin of methanogenesis, phototrophy, and the colonization of land, BMC Evol. Biol. 4 (2004) 1–14, https://doi.org/10.1186/1471-2148-4-44.
[230] S.C. Di Rienzi, I. Sharon, K.C. Wrighton, O. Koren, L.A. Hug, B.C. Thomas, J.K. Goodrich, J.T. Bell, T.D. Spector, J.F. Banfield, R.E. Ley, The human gut and groundwater harbor non-photosynthetic bacteria belonging to a new candidate phylum sibling to Cyanobacteria, Elife 2013 (2013) 1–25, https://doi.org/10.7554/eLife.01102.001.
[231] R.M. Soo, J. Hemp, D.H. Parks, W.W. Fischer, P. Hugenholtz, On the origins of oxygenic photosynthesis and aerobic respiration in Cyanobacteria, Science 355 (80) (2017) 1436–1440, https://doi.org/10.1126/science.aal3794.
[232] W.F. Martin, D.A. Bryant, J.T. Beatty, A physiological perspective on the origin and evolution of photosynthesis, FEMS Microbiol. Rev. 42 (2018) 205–231, https://doi.org/10.1093/FEMSRE/FUX056.
[233] J.M. Olson, The evolution of photosynthesis, Science 168 (1970) 438 LP-446 http://science.sciencemag.org/content/168/3930/438.abstract.
[234] J.M. Olson, B.K. Pierson, Origin and evolution of photosynthetic reaction centers, Orig. Life Evol. Biosph. 17 (1987) 419–430, https://doi.org/10.1007/BF02386479.
[235] J.F. Allen, W. Martin, Out of thin air, Nature 445 (2007) 610–612 https://doi.org/10.1038/445610a.
[236] A.Y. Mulkidjanian, E.V. Koonin, K.S. Makarova, S.L. Mekhedov, A. Sorokin, Y.I. Wolf, A. Dufresne, F. Partensky, H. Burd, D. Kaznadzey, R. Haselkorn, M.Y. Galperin, The cyanobacterial genome core and the origin of photosynthesis, Proc. Natl. Acad. Sci. Unit. States Am. 103 (2006) 13126–13131, https://doi.org/

10.1073/pnas.0605709103.
[237] Y. Cohen, B.B. Jorgensen, N.P. Revsbech, R. Poplawski, Adaptation to hydrogen sulfide of oxygenic and anoxygenic photosynthesis among cyanobacteria, Appl. Environ. Microbiol. 51 (1986) 398–407.
[238] J.M. Klatt, D. de Beer, S. Häusler, L. Polerecky, Cyanobacteria in sulfidic spring microbial mats can perform oxygenic and anoxygenic photosynthesis simultaneously during an entire diurnal period, Front. Microbiol. 7 (2016) 1–10, https://doi.org/10.3389/fmicb.2016.01973.
[239] R.E. Blankenship, Origin and early evolution of photosynthesis, Photosynth. Res. 33 (1992) 91–111, https://doi.org/10.1007/BF00039173.
[240] P. Mathis, Compared structure of plant and bacterial photosynthetic reaction centers. Evolutionary implications, Biochim. Biophys. Acta Bioenerg. 1018 (1990) 163–167, https://doi.org/10.1016/0005-2728(90)90240-5.
[241] H. Brinkmann, M. Göker, M. Koblížek, I. Wagner-Döbler, J. Petersen, Horizontal operon transfer, plasmids, and the evolution of photosynthesis in Rhodobacteraceae, ISME J. 12 (2018) 1994–2010, https://doi.org/10.1038/s41396-018-0150-9.
[242] S.V. Shestakov, E.A. Karbysheva, The origin and evolution of cyanobacteria, Biol. Bull. Rev. 7 (2017) 259–272, https://doi.org/10.1134/S2079086417040090.
[243] W.W. Fischer, J. Hemp, J.E. Johnson, Manganese and the evolution of photosynthesis, Orig. Life Evol. Biosph. 45 (2015) 351–357, https://doi.org/10.1007/s11084-015-9442-5.
[244] T. Cardona, Early archean origin of heterodimeric photosystem I, Heliyon 4 (2018) e00548, , https://doi.org/10.1016/j.heliyon.2018.e00548.
[245] S. V Lalonde, K.O. Konhauser, Benthic perspective on Earth's oldest evidence for oxygenic photosynthesis, Proc. Natl. Acad. Sci. Unit. States Am. 112 (2015) 995–1000 http://www.pnas.org/content/112/4/995.abstract.
[246] G.L. Arnold, A.D. Anbar, J. Barling, T.W. Lyons, Molybdenum isotope evidence for widespread anoxia in mid-proterozoic oceans, Science 304 (2004) 87–90, https://doi.org/10.1126/science.1091785.
[247] A.D. Anbar, A.H. Knoll, proterozoic ocean chemistry and evolution: a bioinorganic bridge? Science 297 (2002) 1137–1142, https://doi.org/10.1126/science.1069651.
[248] D.T. Johnston, F. Wolfe-Simon, A. Pearson, A.H. Knoll, Anoxygenic photosynthesis modulated Proterozoic oxygen and sustained Earth's middle age, Proc. Natl. Acad. Sci. Unit. States Am. 106 (2009) 16925–16929, https://doi.org/10.1073/pnas.0909248106.
[249] J.M. Archibald, The puzzle of plastid evolution, Curr. Biol. 19 (2009) R81–R88 https://doi.org/10.1016/j.cub.2008.11.067.
[250] U. Cenci, D. Bhattacharya, A.P.M. Weber, C. Colleoni, A. Subtil, S.G. Ball, Biotic host–pathogen interactions as major drivers of plastid endosymbiosis, Trends Plant Sci. 22 (2017) 316–328 https://doi.org/10.1016/j.tplants.2016.12.007.
[251] P. Deschamps, C. Plancke, C. Colleoni, C. D'Hulst, D. Dauvillée, J.N. Raj, S. Ball, E. Suzuki, Y. Nakamura, J.-L. Putaux, A. Buléon, S. Haebel, G. Ritte, M. Steup, L.I. Falcón, D. Moreira, W. Löffelhardt, Metabolic symbiosis and the birth of the plant kingdom, Mol. Biol. Evol. 25 (2007) 536–548, https://doi.org/10.1093/molbev/msm280.
[252] M. Ragon, K. Benzerara, D. Moreira, R. Tavera, P. López-García, 16S rDNA-based analysis reveals cosmopolitan occurrence but limited diversity of two cyanobacterial lineages with contrasted patterns of intracellular carbonate mineralization, Front. Microbiol. 5 (2014) 1–11, https://doi.org/10.3389/fmicb.2014.00331.
[253] T.M. Gibson, P.M. Shih, V.M. Cumming, W.W. Fischer, P.W. Crockford, M.S.W. Hodgskiss, S. Wörndle, R.A. Creaser, R.H. Rainbird, T.M. Skulski, G.P. Halverson, Precise age of Bangiomorpha pubescens dates the origin of eukaryotic photosynthesis, Geology 46 (2018) 135–138, https://doi.org/10.1130/G39829.1.
[254] S. Bengtson, T. Sallstedt, V. Belivanova, M. Whitehouse, Three-dimensional preservation of cellular and subcellular structures suggests 1.6 billion-year-old crown-group red algae, PLoS Biol. 15 (2017) e2000735https://doi.org/10.1371/journal.pbio.2000735.
[255] K.R. Arouri, P.F. Greenwood, M.R. Walter, Biological affinities of Neoproterozoic acritarchs from Australia: microscopic and chemical characterisation, Org. Geochem. 31 (2000) 75–89, https://doi.org/10.1016/S0146-6380(99)00145-X.
[256] C.C. Loron, R.H. Rainbird, E.C. Turner, J.W. Greenman, E.J. Javaux, Organic-walled microfossils from the late mesoproterozoic to early neoproterozoic lower shaler Supergroup (arctic Canada): diversity and biostratigraphic significance, Precambrian Res. 321 (2019) 349–374, https://doi.org/10.1016/j.precamres.2018.12.024.
[257] H. Agiæ, M. Moczyd³owska, L.M. Yin, Affinity, life cycle, and intracellular complexity of organic-walled microfossils from the Mesoproterozoic of Shanxi, China, J. Paleontol. 89 (2015) 28–50, https://doi.org/10.1017/jpa.2014.4.