

Cyanobacteria: the bright and dark sides of a charming group

Katia Sciuto · Isabella Moro

Received: 9 September 2014/Revised: 19 February 2015/Accepted: 26 February 2015/
Published online: 20 March 2015
© Springer Science+Business Media Dordrecht 2015

Abstract Cyanobacteria are some of the oldest organisms known. Thanks to their photosynthetic apparatus, capable of splitting water into O₂, protons, and electrons, this large and morphologically diverse group of phototrophic prokaryotes transformed Earth's atmosphere to one suitable for aerobic metabolism and complex life. The long debated Endosymbiotic Theory attributes to cyanobacteria also a significant role in the evolution of life, as important players in plastid origin of higher plants and other photosynthetic eukaryotes. Recent molecular surveys are trying to understand how, exactly, cyanobacteria contributed to plant genome evolution. Their ancient origin and their widespread distribution have recently opened the possibility of including fossil cyanobacterial DNA into the palaeo-reconstructions of various environments and in the calibration of historical records. Cyanobacteria occur in almost every habitat on Earth and can be found in environments subject to stressful conditions, such as desert soils, glaciers, and hot springs. They are common also in urban areas, where they are involved in biodeterioration phenomena. Their great adaptability and versatility are due to a characteristic cell structure, with typical inclusions and particular envelopes. They are the most complex prokaryotes, since they are able to form filaments, colonies, and mats, and they exhibit distinctive ways of movements. To live in different environments, facing biotic and abiotic stresses, cyanobacteria produce also a large array of metabolites, which have potential applications in several fields, such as nutrition, medicine, and agriculture. They have also an important ecological role, not only as primary producers, but also because of their coexistence (often, but not exclusively, in the form of symbiosis) with other organisms to which they supply nitrogen. On the other side, cyanobacteria can have also a negative impact both on the environment and society. In particular they can release a range of toxic compounds, cyanotoxins, diverse in structure and in their effects on human and animal health. In spite of their importance, cyanobacterial identification is not always easy and the use of modern methods (e.g., molecular

Communicated by Anurag chaurasia.

K. Sciuto (✉) · I. Moro
Department of Biology, University of Padua, via U. Bassi 58/B, 35131 Padua, Italy
e-mail: katia.sciuto@unipd.it

sequencing, cytomorphology, and ecophysiology) has led to the revision of traditional taxa and to the discovery of new ones. Currently, the most accepted method for cyanobacterial classification is a polyphasic approach, also including comparison with reference specimens. Moreover, several authors are making efforts to create a unique nomenclature system for cyanobacteria.

Keywords Atmosphere's oxygenation · Biotechnological applications · Evolution of life · Fossil records · Toxins · Systematics

Introduction

Cyanobacteria are widespread microorganisms, able to carry out oxygenic photosynthesis. This feature gave them an important role in the evolution of life on Earth, since they are also among the oldest living beings. For their photoxygenic capability, cyanobacteria represent the primary producers in several habitats, as they are able to survive also to extreme environmental conditions, and thus they still cover an essential role for the development and survival of other life forms in certain environments.

To face biotic and abiotic stressful conditions, these microorganisms have evolved a series of features, giving rise to several different taxa. Taxa differ for morphology, with some having evolved specialized cells, and for biochemical and physiological capabilities, with many species able to fix atmospheric nitrogen and strains able to produce relevant bioactive compounds, among which potent toxins, called cyanotoxins. For all these features, cyanobacteria can have both positive and negative impacts on the environment and on human activities.

In spite of their importance, cyanobacterial systematics, and consequently the identification of given strains, is still problematic, due to their prokaryotic nature and to the presence of cryptic taxa. Currently, a polyphasic approach, including both phenotypic and genetic analyses, is the most accepted method to classify cyanobacteria. Molecular techniques have greatly contributed to shed light on the systematic relationships inside the phylum and to detect new taxa. Recently, the use of genome-based phylogenies has provided new insights in this group of microorganisms.

Following this scheme, the present review aims to point out the huge impact of cyanobacteria on our lives, showing the bright and dark sides of this charming group, updating the readers about the most recent discoveries on these microorganisms, and giving hints to go in depth into the different issues. A summary of the addressed topics is given in Table 1.

Methods

Literature used

This review paper was written based on the literature consulted by the authors during their years of researches. For each of the addressed topics, additional updated literature was found using the Google Scholar web service.

Table 1 Summary of the main addressed topics

Topic	Key-words and key-concepts	References
<i>General features, lifestyles, and distribution</i>		
Cyanobacterial features	Prokaryotic cell Coccolid and filamentous forms Unique cell envelope Extracellular Polysaccharides (EPS) Thylakoid membranes with phycobilisomes Chlorophyll <i>a</i> (with exceptions), carotenoids, and phycobiliproteins Cyanophycin granules, starch, aerotopes Motility in response to environmental parameters Buoyancy Gas vesicles Gliding motility Oscillin Type IV pili Specialized cells Heterocytes and diazocytes (nitrogen fixation) Akinetes (resistance to unfavorable conditions)	Wolk (1973), Stanier and Cohen-Bazire (1977), Andersson and Anderson (1980, Cmiec et al. (1984), Reynolds et al. (1987), Pate (1988), Anagnostidis and Komárek (1990), Grossman et al. (1993), Sherman et al. (1994), Walsby (1994), Hoiczky and Baumeister (1995), Van den Hoek et al. (1995), Ramsing et al. (1997), Sellner (1997), De Philippis and Vincenzini (1998), MacColl (1998), Adams and Duggan (1999), Adams et al. (1999), Brookes et al. (1999), Choi et al. (1999), Hoiczky and Hansel (2000), Adams (2001), Brookes and Ganf (2001), De Philippis et al. (2001), McBride (2001), Bardy et al. (2003), Bhaya (2004), Wolgemuth and Oster (2004), Hoffmann et al. (2005), Moore et al. (2005), Tamaru et al. (2005), Read et al. (2007), Thompson et al. (2009), Flores and Herrero (2010), Hohmann-Marriott and Blankenship (2011), Song et al. (2011)
Cyanobacterial lifestyle and distribution	Found in the most different habitats, even in extreme environments Free-living, epibionts, and symbionts Aquatic and terrestrial Blooms and mats Symbioses between cyanobacteria and animals or plants Symbioses between cyanobacteria and plants are useful in agronomy Several strategies in response to environmental parameters and in defense against grazers Toxin production (cyanotoxins)	Potts (1980), Obukowicz et al. (1981), Carr and Whitton (1982), Friedmann (1982), Skulberg et al. (1984), Lindblad et al. (1987), Lindblad and Bergman (1989), Stal (1995), Sellner (1997), De Philippis and Vincenzini (1998), Paerl et al. (2001), Pajdak-Stós et al. (2001), Carpenter and Foster (2002), Janson (2002), Rai et al. (2002), Sellner et al. (2003), Steindler et al. (2005), Tamaru et al. (2005), Adams et al. (2006), Babica et al. (2006), De Figueiredo et al. (2006), Hirose et al. (2006), Adams and Duggan (2008), Krings et al. (2009), Thompson et al. (2012), Whitton (2012)
Pigments	Hydrosoluble and liposoluble pigments Chlorophyll types and carotenoids Allophycocyanin (APC) C-phycocyanin (C-PC) Phycocerythrin (PE) Phycocerythrocyanin (PEC), the rarest phycobiliprotein A novel type of PE in brackish-adapted picocyanobacteria <i>Acaryochloris marina</i> <i>Prochloron</i> and <i>Prochlorococcus</i> (Prochlorophyta) Scytonemin and mycosporine-like amino acids	Lewin (1976), Withers et al. (1978), Bryant (1982), García-Pichel et al. (1996), Kühl et al. (2005), Lewin (2002), Wiethaus et al. (2010), Gao and García-Pichel (2011), Sciuto et al. (2012), Larsson et al. (2014), Soule and García-Pichel (2014)

Table 1 continued

Topic	Key-words and key-concepts	References
Nitrogen fixation	Nitrogenase enzyme complex, inhibited by O ₂ Heterocyte Diazocyte Temporal separation of oxygenic photosynthesis and nitrogen fixation	Bergman and Carpenter (1991), Capone et al. (1997), Fredriksson and Bergman (1997), Lin et al. (1998), Adams and Duggan (1999), Berman-Frank et al. (2001, 2003), El-Shehawy et al. (2003), Flores and Herrero (2010), Sandh et al. (2012)
<i>Role of cyanobacteria in the evolution of life on earth and fossil records</i>		
Cyanobacterial origin	Fossil records Stromatolites Carbonate rock formation Gypsum deposits Markers of geological times/events Palaeoenvironmental reconstructions Meteorites Life on Mars Panspermia Theories The oldest known cyanobacterial DNA from the late Miocene	Davis and McKay (1996), Golubic and Seong-Joo (1999), Kopp et al. (2005), Altermann et al. (2006), Panieri et al. (2010), Govindjee and Shevela (2011), Hoover (2011), Riding (2011), Schopf et al. (2012), Allwood et al. (2013), Benison and Karmanocky (2014), Jahnke et al. (2014)
Living stromatolites	Laminated benthic microbial deposits Mainly associated with extreme environments Typically found in the intertidal/subtidal zones, but recently also in high-intertidal/supratidal areas	Logan et al. (1974), Hoffman (1976), Cohen et al. (1984), Dill et al. (1986), Reid et al. (1995), Burns et al. (2004), Papineau et al. (2005), Smith et al. (2011), Pepe-Ranney et al. (2012), Cooper et al. (2013)
Oxygenic photosynthesis	Oxygen Evolving Complex Co-presence of two types of reaction centers Horizontal gene transfer Probably the first to evolve oxygenic photosynthesis was a freshwater cyanobacterium	Dismukes et al. (2001), Sánchez-Baracaldo et al. (2005), Johnson (2006), Govindjee and Shevela (2011), Dagan et al. (2013), Nickelsen and Rengstl (2013)
Oxygenation of the atmosphere	When and how O ₂ accumulated? Great Oxygenation Event or Great Oxygen Transition? Coincidence with the evolution of oxygenic photosynthesis?	Dismukes et al. (2001), Rasmussen et al. (2008), Sessions et al. (2009), Govindjee and Shevela (2011), Crowe et al. (2013), Hallmann and Summons (2014), Lyons et al. (2014)
Consequence of atmosphere's oxygenation	Evolution of aerobic respiration O ₃ shield formation Destruction of CH ₄ greenhouse The Snowball Earth glaciation Loss of several life forms and Evolution of new ones Influence of phytoplankton-grazers interaction on diversification of life forms	Dismukes et al. (2001), Kopp et al. (2005), Riding (2006), Sessions et al. (2009), Govindjee and Shevela (2011), Lewy (2013), Ratti et al. (2013)
Endosymbiotic Theory	Primary and secondary endosymbioses Evolution of plastids Horizontal gene transfer	Schimper (1883), Mereschkowsky (1905), (1910), Martin and Kowallik (1999), Sagan (1967), Margulis (1970), Woese (1987), McFadden (2001), Deschamps et al. (2008), Deusch et al. (2008), Reyes-Prieto et al. (2010), Criscuolo and Gribaldo (2011), Dagan et al. (2013), McFadden (2014)

Table 1 continued

Topic	Key-words and key-concepts	References
<i>Positive and negative impacts on the environment and human activities</i>		
Cyanotoxins	Classified in five groups: hepatotoxins, neurotoxins, cytotoxins, dermatotoxins, and irritant toxins Microcystins (MCs) are the most known Often associated with blooms, but also produced by mat- and biofilm-developing genera Often associated with eutrophication, but also from oligotrophic environments Both from freshwater and marine taxa	Codd (1995), Carmichael (1997), Falconer (1998), Jochimsen et al. (1998), Pouria et al. (1998), Codd (2000), Humpage et al. (2000), Carmichael (2001), Chorus (2001), Azevedo et al. (2002), Shen et al. (2002), Sellner et al. (2003), Aboal et al. (2005), Volosko et al. (2008), Paerl and Huisman (2009), Golubic et al. (2010), Žegura et al. (2011), Straubinger-Gansberger et al. (2014)
Uses as food, pharmaceuticals, and in biotechnology	Source of vitamins and proteins Antiviral, antitumor, antibacterial, and anti-HIV activities Algaecides, herbicides, and insecticides H ₂ production as an alternative to fossil fuel	Hallenbeck and Benemann (2002), Dutta et al. (2005), Singh et al. (2005), Kapdan and Kargi (2006), Berry et al. (2008), Dasa and Veziroglu (2008), Gantar and Svirčev (2008), Gerwick et al. (2008), Sharma et al. (2010), Pfeiffer et al. (2011), Zanchett and Oliveira-Filho (2013)
Biodeterioration of cultural heritage	Worldwide colonization of stone monuments, building facades, and caves Biofilm attachment thanks to exopolysaccharide production Deterioration of the substratum Dark stone staining due to protective pigment production	Ortega-Morales et al. (2000), Crispim et al. (2004, 2006), Rindi (2007), Albertano (2012), Cappitelli et al. (2012), Rossi et al. (2012), Keshari and Adhikary (2013)
<i>Hints on cyanobacterial systematics and identification methods</i>		
Taxonomic problems	The species concept is still debated Presence of cryptic species Between algae and bacteria Coexistence of two different nomenclature codes Efforts towards a unique nomenclature system	Stanier et al. (1978), Rippka et al. (1979), Woese (1987), Woese et al. (1970), Oren (2004), Johansen and Casamatta (2005), Komárek and Golubić (2005), Komárek (2006), Oren et al. (2009), Komárek (2010), Sciuto et al. (2012), Palińska and Surosz (2014)
Molecular techniques for cyanobacterial systematics	16S rDNA is the most used molecular marker 16S rDNA identity thresholds Other used loci: 16S-23S ITS, <i>rpoB</i> , <i>rpoC1</i> , <i>gyrB</i> , <i>rbcLX</i> , <i>cpcB-IGS-cpcA</i> , <i>nifD</i> , <i>nifH</i> Entire genome approaches Melainobacteria proposed as a new class under the Cyanobacteria	Woese (1987), Woese et al. (1970), Stackebrandt and Goebel (1994), Wilmotte 1994, Itean et al. (2000), Wilmotte and Herdmann (2001), Seo and Yokota, (2003), Henson et al. (2004), Casamatta et al. (2005), Hoffmann et al. (2005), Rajaniemi et al. (2005), Teneva et al. (2005), Tomitani et al. (2006), Palińska and Marquardt (2008, Kumari et al. (2009), Sciuto et al. (2012), Di Rienzi et al. (2013), Engene et al. (2013), Gupta et al. (2013), Shih et al. (2013), Soo et al. (2014)

Table 1 continued

Topic	Key-words and key-concepts	References
Polyphasic approach	Complementary levels of investigations: morphological, ultrastructural, biochemical, physiological, molecular Recently, comparison with historical specimens The most accepted method	Wilmotte (1994), Hoffmann et al. (2005), Komárek (2006, 2010), Moro et al. (2010), Sciuto et al. (2011, 2012, 2013), Lee et al. (2014), Palińska and Surosz (2014)

For each topic key-words and key-concepts are provided, as well as the related references

Figure preparation

All figures were prepared for publication with the CorelDRAW X4 package (Corel Corporation, Ottawa, Canada). The pictures of living cyanobacteria were previously obtained during different studies. More in detail, light microscopy images were produced with a Leica 5000 microscope, equipped with a digital camera; transmission electron microscopy (TEM) images were obtained using a transmission electron microscope FEI Tecnai G2, operating at 100 kV; and scanning electron microscopy (SEM) images were produced by a scanning electron microscope Cambridge Stereoscan 260 (Cambridge, United Kingdom).

General features, lifestyles, and distribution

Cyanobacteria are a group of *prokaryotic microorganisms*, previously erroneously called blue-green algae, representing the phylum Cyanophyta. They consist of both unicellular coccoid and multicellular filamentous species, able to perform oxygenic photosynthesis as algae and higher plants (Hohmann-Marriott and Blankenship 2011).

Like all prokaryotes, cyanobacterial *cells do not show compartments* (Van den Hoek et al. 1995).

The structure of their *cell envelope* is similar to that of Gram-negative bacteria, including both a peptidoglycan layer and an outer membrane. However the peptidoglycan layer of the cyanobacterial envelope is thicker (10–700 nm) than that of Gram-negative bacteria (2–6 nm), and more similar, also for other features, to that of Gram-positive bacteria. The outer membrane has also a unique composition, different from that of Gram-negative bacteria (Hoiczky and Baumeister 1995; Hoiczky and Hansel 2000) (Fig. 1).

Cyanobacterial cells can release *exocellular polysaccharides* (EPS), composed of different monosaccharides, through a structure called Junctional Pore Complex (JPC) (Wolgemuth and Oster 2004) (Fig. 2). Based on their quantity and compactness, the EPS surrounding cyanobacterial cells are distinguished in capsules, sheaths, and slime (De Philippis et al. 2001). The slime extrusion plays an active role in cyanobacterial gliding motility (Adams 2001), while the more compact capsules and sheaths participate in protecting cells from stresses in extreme habitats and from other harmful conditions (De Philippis and Vincenzini 1998; Tamaru et al. 2005). In many cyanobacterial species the EPS contain aromatic pigments like scytonemin, a cyanobacterial sunscreen for UV A, or oligosaccharide mycosporine-like amino acids (OS-MAAs), which can effectively absorb UV light (Gao and García-Pichel 2011; Soule and García-Pichel 2014).

The cyanobacterial cell shows an intracellular membrane system, the *thylakoid membranes*, occupying much of the cytoplasm. Cyanobacterial thylakoids do not exhibit the

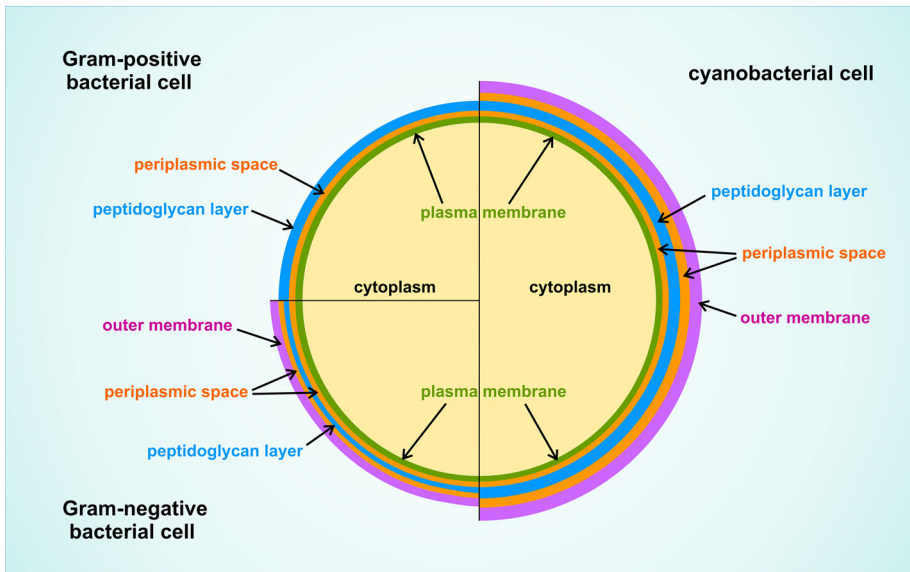
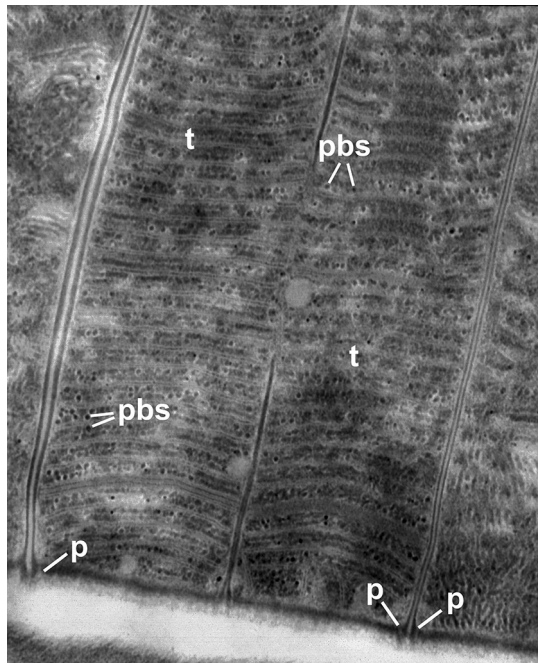


Fig. 1 Schematic representation comparing the cell envelope of a typical Gram-positive bacterial cell, a typical Gram-negative bacterial cell

Fig. 2 Longitudinal section of a filamentous cyanobacterium belonging to the order Oscillatoriales, seen at the transmission electron microscope. The high magnification allows to observe phycobilisomes (*pbs*), attached to the thylakoids (*t*), and the pores (*p*), devoted to polysaccharide excretion



membrane stacking that is such a striking feature of green plant thylakoids (Andersson and Anderson 1980). Most commonly, the membranes take the form of a series of concentric cylinders aligned along the long axis of the cell (Stanier and Cohen-Bazire 1977; Sherman

et al. 1994), but they can assume different arrangements. Thylakoid arrangements were found to be in agreement with phylogenetic reconstructions and, therefore, they are used as a taxonomic character (Anagnostidis and Komárek 1990; Hoffmann et al. 2005).

The cytoplasmic surface of adjacent thylakoid membranes is always separated by a region of cytoplasm where *phycobilisomes* are anchored (Fig. 2). They are light-harvesting structures, associated to Photosystem II (PSII), absorbing visible light in the range of 450–660 nm (Grossman et al. 1993), where chlorophyll *a* has low absorptivity (MacColl 1998).

The phycobilisomes are hemidiscoidal protein complexes, composed of hydrosoluble chromoproteins, the phycobiliproteins (PBPs), arranged in a core and rods. The typical phycobiliproteins are allophycocyanin (APC), C-phycocyanin (C-PC), and phycoerythrin (PE). Only a limited number of cyanobacteria shows phycoerythrocyanin (PEC), a rare PBP (Bryant 1982; García-Pichel et al. 1996; Sciuto et al. 2012), instead of PE. The core contains the APC, while the rods are composed of stacked disks: the disk adjacent to the core is invariably PC and the other disks are PE or PEC (Bryant 1982; MacColl 1998).

Differently from other cyanobacteria, species belonging to the genera *Prochloron* and *Prochlorococcus* are peculiar as regards pigment composition and the light-harvesting machinery. In particular, *Prochloron* is characterized by the absence of phycobilin pigments (Stanier et al. 1978), while *Prochlorococcus* has only remnants of the phycobilisome in the form of the single PE, of the corresponding encoding operon, and of the genes involved in phycobilin biosynthesis (Wiethaus et al. 2010). The absence of classical cyanobacterial phycobilisomes and the unusual presence of chlorophyll *b*, together with chlorophyll *a*, led to the establishment of a new division, the Prochlorophyta (Lewin 1976). After molecular analyses questioning the possible phylogenetic relationship between cyanobacteria and ancestral green-plant chloroplasts, the Prochlorophyta were just considered as aberrant Cyanophyta (Lewin 2002).

Recently, the analysis of genomes, assembled from metagenomic samples collected along a natural salinity gradient in the Baltic Sea, led to observe that brackish-adapted genotypes harbored a novel type of PE, not found in previously sequenced genomes and uncommon in other examined aquatic ecosystems (Larsson et al. 2014). The authors suggest that the PE genes were lost in the ancestor of PC-containing coastal picocyanobacteria and that multiple Horizontal Gene Transfer (HGT) events have reintroduced PE genes into brackish-adapted strains.

As regards the liposoluble photosynthetic pigments, despite the fact that most cyanobacteria show chlorophyll *a* as principal light-harvesting pigment and besides the above mentioned particular composition of Prochlorophyta, a cyanobacterium known as *Acaryochloris marina* uses chlorophyll *d* as pigment and it depends on far-red light for photosynthesis (Kühl et al. 2005).

Cyanobacteria are able to carry out the *biological reduction of nitrogen* (N_2) thanks to the nitrogenase enzyme complex (Berman-Frank et al. 2003). However, since nitrogenase is irreversibly inhibited by molecular oxygen (O_2), nitrogen-fixing cyanobacteria have evolved a number of strategies to protect the nitrogenase enzyme from O_2 , including a temporal separation of oxygenic photosynthesis and nitrogen fixation (Adams and Duggan 1999). In some filamentous strains, instead, vegetative cells can differentiate into *specialized cells*, the *heterocytes*, characterized by a distinctive envelope, consisting of a glycolipid layer that functions as a barrier for O_2 and, externally, of a thicker layer of polysaccharide, protecting the glycolipid layer from physical damage (Flores and Herrero 2010). In this way the heterocyte provides a suitable microanaerobic environment for the fixation of N_2 (Fig. 3). Other planktic marine non-heterocytous cyanobacteria belonging to

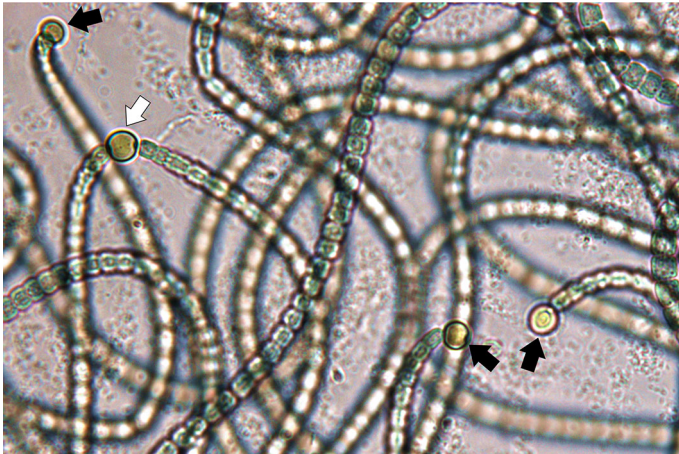


Fig. 3 Light microscopy picture of a filamentous cyanobacterium belonging to the order Nostocales, exhibiting heterocytes both at the ends of filaments (terminal heterocytes, *black arrows*) and inside the filaments (intercalary heterocytes, *white arrow*)

the genus *Trichodesmium* are also able to fix N_2 under fully aerobic conditions, while photosynthetically evolving O_2 (Capone et al. 1997; Berman-Frank et al. 2001). *Trichodesmium* species can, in fact, develop a unique nitrogen-fixing cell type, the *diazocyte* (Bergman and Carpenter 1991; Lin et al. 1998; El-Shehawey et al. 2003; Sandh et al. 2012). These specialized cells are characterized by a reduced number of storage compounds and prominent gas vacuoles (Fredriksson and Bergman 1997).

Cyanobacteria can differentiate other specialized cells, the *akinetes*, spore-like cells, frequently larger than the vegetative ones, characterized by a thick cell wall and by a multilayered extracellular envelope (Adams and Duggan 1999) (Fig. 4). These particular cells are usually produced in response to unfavourable environmental conditions, such as light limitation or phosphate deprivation, which probably result in a shortage of cellular energy (Wolk 1973; Moore et al. 2005; Thompson et al. 2009; Flores and Herrero 2010). When environmental conditions become suitable again for vegetative growth, akinetes germinate into vegetative cells. Moreover, in some taxa, common in meso-eutrophic lakes of temperate regions and dominating the phytoplankton communities during the summer, akinete formation takes place regularly towards the end of the growth season (Cmiec et al. 1984).

Cyanobacteria show specific morphological and physiological features that enable them to colonize different types of substrate and to adapt themselves to great environmental changes. For example, they are *able to move* in diverse directions in response to the variation of light conditions (Ramsing et al. 1997; Choi et al. 1999; Bhaya 2004; Song et al. 2011). In particular, planktic cyanobacteria can perform *vertical migrations by buoyancy regulation* through changes in the cellular content of inclusions, such as cyanophycin and starch, or production of aerotopes, composed of gas vesicles (Reynolds et al. 1987; Sellner 1997; Brookes et al. 1999; Brookes and Ganf 2001). Cyanobacteria can regulate floating through modulation of genes involved in production of gas vesicles and through the aerotope destruction by turgor pressure (Walsby 1994).

The non-planktic cyanobacteria are able to move on a surface by a peculiar type of motility, called *gliding motility* (Adams 2001). Differently from buoyancy, gliding is

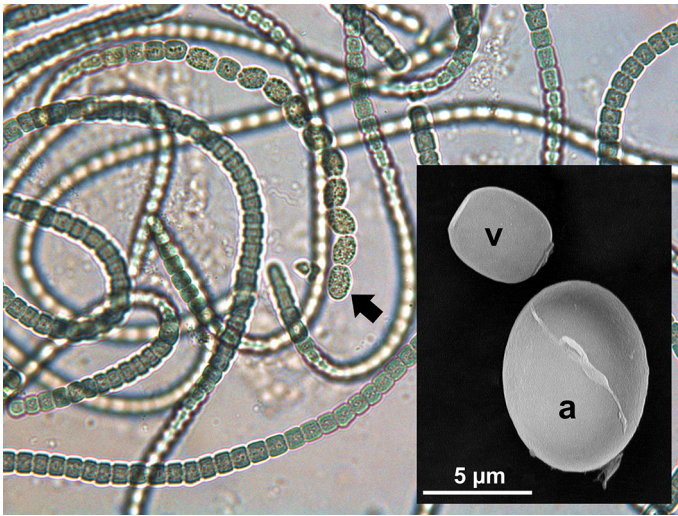


Fig. 4 Light microscopy image of a filamentous cyanobacterium belonging to the order Nostocales, where a chain of akinetes (*arrow*) is visible. In the *box*, an high magnification picture at the scanning electron microscope allows to compare the sizes of a vegetative cell (*v*) with those of an akinete (*a*)

relatively slow and characterized by the lack of cell morphology change during locomotion and, generally, by extracellular slime production (Pate 1988). Gliding does not require flagella and the movement generally is in the same direction of the long axis of the cell. Studies indicate that more than one mechanism is needed to explain the bacterial gliding motility (McBride 2001). Many coccoid cyanobacteria, such as *Synechocystis* species, rely on the extension and retraction of type IV pili, which are located on the cell surface (Bardy et al. 2003). In the filamentous taxa, instead, gliding motility depends on slime extrusion through the JPC, which causes the forward propulsion of trichomes. Moreover, several filamentous cyanobacteria show oscillin fibrils, positioned above a S-layer anchored to the outer membrane, which serve as a screw thread through which slime can flow, leading to the rotation of the trichome around its main axis (Adams et al. 1999; Read et al. 2007).

In particular environmental conditions, cyanobacteria can grow rapidly, forming the notorious *blooms* (Skulberg et al. 1984; Sellner et al. 2003; De Figueiredo et al. 2006). They thrive in highly productive waters by having gas vesicles that allow the migration between radiance-rich surface waters and nutrient-rich bottom waters (Paerl et al. 2001).

Benthic cyanobacteria, instead, can aggregate to form dense multilayered communities, called *mats*, made up of different species, growing on sediments of diverse environments (Stal 1995) (Fig. 5). When these mats entrap sediment particles or minerals they form *stromatolites*, complex lithified aggregates with a well-defined layered structure (Cohen et al. 1984; Pepe-Rannek et al. 2012). Cyanobacteria are found in the most different habitats: in freshwater and in seawater, but also on soil and rocks; moreover, they are able to flourish in physically and chemically stressful environments, including nutrient-deplete, hypersaline, calcified, desiccated and high-irradiance ecosystems, ranging from the tropics to polar regions (Potts 1980; Carr and Whitton 1982; Friedmann 1982, Whitton 2012).

To cope with extreme environmental conditions cyanobacteria have developed many morphological, biochemical, and physiological adaptive strategies. Among the biochemical strategies, an example is the production of EPS to face different environmental

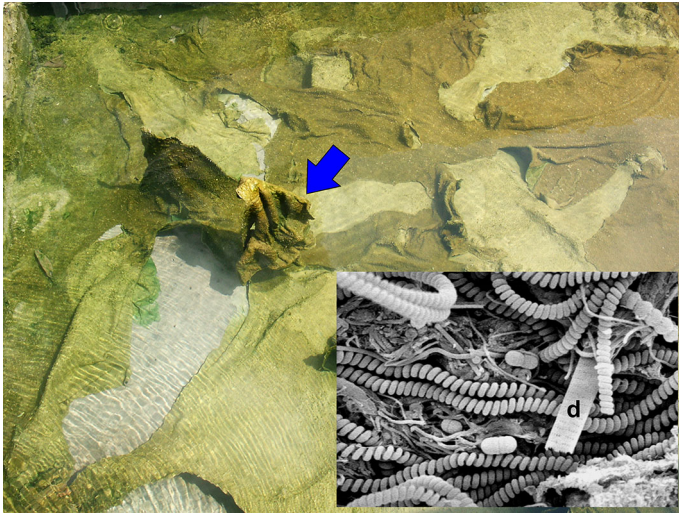


Fig. 5 Cyanobacterial mats growing on the thermal muds of the Euganean thermal District (Padova, Italy). The exopolysaccharides, produced by cyanobacteria to face stressful environmental conditions, strictly pack the cells together, giving them a sheet-like appearance (*arrow*). Natural communities of cyanobacteria are generally composed of several distinct taxa, including both coccoid and filamentous forms, and often associated to other microorganisms, such as diatoms (*d*), as illustrated by the scanning electron microscope picture in the *box*

conditions (De Philippis and Vincenzini 1998). EPS play a crucial role in desert or ice soils (De Philippis and Vincenzini 1998; Tamaru et al. 2005) and are also produced as defense against grazer species (Pajdak-Stós et al. 2001).

Some cyanobacteria live as epibionts and/or as symbionts with or even within other organisms, both animals and plants (Adams et al. 2006; Adams and Duggan 2008; Krings et al. 2009). As epibionts cyanobacteria can be found, for example, on macroalgal thalli, while as symbionts they can be endobionts (intracellular cyanobacteria) or ectobionts (extracellular cyanobacteria) (Rai et al. 2002). *Symbioses* between cyanobacteria and plants are less common, but they are very important in agronomy, where generally the main contribution of the cyanobacterium is the fixation of the atmospheric N_2 , with the consequent supply of fixed nitrogen to their hosts. The major plant hosts are bryophytes, cycads, ferns, and fungi. An important example of symbiotic associations involving cyanobacteria and plants is represented by the relationship between the water-fern *Azolla* and the cyanobacterium *Anabaena*. This symbiosis is particularly interesting because it is permanent, hereditary, and the only known symbiosis between a nitrogen-fixing organism and a Pteridophyte. Another example of symbiosis between cyanobacteria and plants is given by the mutualistic associations involving Cycads and some strains of *Nostoc* and *Anabaena* (Obukowicz et al. 1981; Lindblad et al. 1987; Lindblad and Bergman 1989). The most widespread symbioses occur between cyanobacteria and marine organisms, including animals (sponges, ascidians, echuroid worms, etc.) (Carpenter and Foster 2002; Steindler et al. 2005; Hirose et al. 2006) and algae (diatoms and dinoflagellates) (Janson 2002; Thompson et al. 2012). Usually these symbioses are frequent in oligotrophic waters, where partners can take advantage from the nitrogen fixation or dissolved organic carbon release by cyanobacteria.

Role of cyanobacteria in the evolution of life on earth and fossil records

In several websites cyanobacteria are defined as “*the microbial heroes of Earth’s history*”. They gained this definition, probably first coined by the paleontologist Andrew Knoll (Mullen 2002), for the basic role that these microorganisms played in the evolution of life on our planet.

The first, and probably most recognized, cyanobacterial contribution to life development was the oxygenation of Earth’s atmosphere, and thus the transition from a fundamentally reducing world to an oxidizing one, creating the environmental conditions where we live today. In fact, even if the composition of the early atmosphere on our planet is still debated, it is largely accepted that it was mainly anoxygenic (Hallmann and Summons 2014). In this context, the major innovation provided by cyanobacteria was the evolution of a photosynthetic apparatus able to split water (H_2O) into electrons (e^-), protons (H^+), and O_2 , thus exploiting the most abundant existing substance as an unlimited source of energy. In fact, bacteria able to perform anoxygenic photosynthesis already existed at the time, but they were dependent on the availability of reductants, like molecular hydrogen (H_2) or hydrogen sulfide (H_2S), to produce energy (Dismukes et al. 2001; Govindjee and Shevela 2011).

Cyanobacteria could begin to use water as electron donor thanks to the invention of a structure, currently possessed also by the chloroplasts of algae and higher plants, called *Oxygen Evolving Complex (OEC)* or Water-Oxidizing Complex (WOC). This is an inorganic cluster composed of manganese, calcium, and oxygen, whose formula is Mn_4CaO_5 and which is stabilized by three extrinsic proteins on the lumenal side of PS II: PsbO, PsbU, and PsbV (=cytochrome (Cyt) *c550*) (Dismukes et al. 2001; Govindjee and Shevela 2011; Nickelsen and Rengstl 2013).

A typical Photosystem (PS) is a multisubunit protein/pigment complex, composed of antenna structures, devoted to light absorption and to transfer energy towards the reaction center (RC), and of the just mentioned RC, the enzyme that uses light to reduce molecules. There are two types of RC: the pheophytin-quinone type (RC1), in Photosystem I (PS I), and the iron-sulphur type (RC2), in PS II. Since the anoxygenic photosynthetic bacteria, known so far, possess only one of the two types of RC, a basic step for the origin of cyanobacteria must have been the appearance of an organism holding both the two types of RC, functionally linked together. If RC1 and RC2 evolved in independent lineages and eventually merged in the organism that became the common ancestor of cyanobacteria or if the common ancestor of cyanobacteria evolved with both the RCs and then it gave origin to anoxygenic photosynthetic bacteria by loss of either RC1 or RC2 is still debated (Govindjee and Shevela 2011; Dagan et al. 2013). In both cases the common ancestry of RC1 and RC2 is clear and there is strong evidence that HGT (=Later Gene Transfer, LGT) occurred (Dagan et al. 2013). Moreover, after having analyzed a number of cyanobacterial genomes, Dagan et al. (2013) support the theory by Sánchez-Baracaldo et al. (2005), according to which the organism that first evolved oxygenic photosynthesis was a freshwater cyanobacterium rather than a marine one.

Other inventions, besides the above cited OEC, were necessary to the evolution of oxygenic photosynthesis, but their detailed description is beyond the scope of the present review. For a more in depth illustration of the photosynthetic transport chain components in cyanobacteria, the hypotheses on their evolution, and their comparison with photosynthetic components of other organisms (i.e. anoxygenic photosynthetic bacteria, algae, and higher plants) see Govindjee and Shevela (2011) and Nickelsen and Rengstl (2013). An interesting excursus on the evolution of OEC and the related innovations in the electron

transfer chain components involved in oxygenic photosynthesis is also illustrated online by Johnson (2006).

Sessions et al. (2009) underline how it is ironical that, in spite of the large consensus on the fact that atmosphere oxygenation is a milestone event in the history of Earth, eventually leading to the evolution of a variety of life forms, when and how O₂ first accumulated remain a great enigma. Many researchers are currently trying to understand not just when the biological capability to produce and utilize O₂ first appeared, but also what chemical and physical conditions allowed its current level of accumulation in the atmosphere (Sessions et al. 2009; Hallmann and Summons 2014; Lyons et al. 2014).

The increase of O₂ in the atmosphere, also called the *Great Oxygenation Event* (GOE), has been traditionally estimated to have occurred about 2.6–2.1 billion (Ga) years ago (Govindjee and Shevela 2011; Hallmann and Summons 2014; Lyons et al. 2014), but recent surveys set this date back to about 3 Ga years ago (Crowe et al. 2013), thus pre-dating the evolution of oxygenic photosynthesis by at least 300–400 million years. This finding suggests that cyanobacteria can have a deeper history than what has been thought up to now. In fact, according to the fossil records, represented by stromatolites, cyanobacterial origin has been dated back between 3.7 and 2.4 Ga years ago (Govindjee and Shevela 2011; Kopp et al. 2005), but if the hypothesis by Crowe et al. (2013) is true, these microorganisms could have evolved earlier.

The debate on if the GOE coincided with the evolution of oxygenic photosynthesis or if the latter came before GOE is still open (Rasmussen et al. 2008; Hallmann and Summons 2014), but there is more evidence in favor of a lag phase between the appearance of oxygenic photosynthesis and O₂ accumulation in the atmosphere. It has been supposed that, after oxygenic photosynthesis started to be performed, oxygen oases (i.e. microaerobic regions in the surface ocean containing low O₂, but in sufficient quantity to sustain respiration and O₂-dependent processes) could have persisted for a long period of time before the geological record captured evidence for enhanced atmospheric O₂ levels (Hallmann and Summons 2014). Moreover, recently it has been proposed that rather than a linear unidirectional rise, as traditionally envisioned, O₂ accumulation was like a “roller coaster ride, with dynamic rising and falling oxygen levels in the ocean and atmosphere”, and thus more like a transition (*Great Oxygen Transition*, GOT) (Lyons et al. 2014).

However it happened, the importance of O₂ accumulation in Earth’s atmosphere is unquestionable and it was well described by Donald E. Canfield, who, discussing this issue, stated that: “There is something astonishing in every breath we take. People take oxygen for granted because it is just there and we breathe it all the time, but we have the only planet we know of anywhere that has oxygen on it” (Zimmer 2013). Probably for its centrality in the evolution of life, the O₂ accumulation event in Earth’s atmosphere has been attributed several names besides GOE: the *great oxidation*, the *oxygen revolution*, the *oxygen catastrophe*, and the *oxygen crisis*. The last two names, in particular, highlight how, given the original anoxic conditions of Earth, this change of the atmosphere very probably caused the loss of several life forms, making cyanobacteria responsible for one of the most significant extinction events in Earth’s history (Sessions et al. 2009). On the other hand, some living beings were able to survive, even if confined in anaerobic niches; some others were able to evolve detoxification mechanisms for the dangerous O₂; and even others appeared, capable to take advantage of this new atmospheric substance to produce energy, with a process (aerobic respiration) 18 times more efficient than anaerobic mechanisms (Dismukes et al. 2001).

As oxygenic organisms we are used to think to the importance of Earth’s oxygenation focusing on the fact that we breathe O₂, but the increase of this substance in the atmosphere

entailed much more. In this regard, Kopp et al. (2005) have imagined a different picture in which the evolution of cyanobacteria, and consequently of oxygenic photosynthesis, is delayed, taking place during the Paleoproterozoic rather than in the Archean. In this alternative scenario, O₂ accumulation in the atmosphere caused by cyanobacteria could have *destroyed the greenhouse effect due to methane* (CH₄), which was very probably produced by methanogenic bacteria living in the upper ocean. This CH₄ layer must have contributed to keep the planet warm enough to assure the presence of liquid water. The destruction of CH₄ greenhouse could have led to a decrease of temperatures and eventually to a planetary-scale glaciation, called “Snowball Earth” (2.3–2.2 Ga years ago), thus making cyanobacteria also responsible of one of the “world’s worst climate disasters”.

Besides the hypothesis by Kopp et al. (2005), another more acknowledged phenomenon took place following atmosphere’s oxygenation. In fact, it is known that the reaction of O₂ with UV rays, generated by the sun, led to the *formation of a layer of ozone* (O₃), which allowed the freeing of many life forms from the ocean, and thus the colonization of lands, and which, up to now, have protected us and the other living beings from the dangerous mutations potentially caused by UV radiation (Govindjee and Shevela 2011; Lewy 2013). Together with several interesting hypotheses, Lewy (2013) offers an intriguing explanation on the evolution of life, based on the observation of geological deposits called banded iron formations (BIFs). These silica-rich rocks with alternating thin layers of dark and red iron-rich rock revealed to coincide with huge shallow lakes of hydrothermal water. Briefly and simplifying, the author proposes that the about 23.5° inclination of Earth’s rotation axis led to the differentiation of two polar regions with particular irradiation conditions, since they were shaded for half a year from solar illumination. For this reason, shallow lakes in polar regions could have been the terrestrial areas where the primitive life forms evolved for the first time, since they were protected from the dangerous UV rays by the low radiation angle, which reduced radiation intensity, and by the limited duration of solar illumination. Geological records suggest that life forms were incidentally created and eliminated several times in polar regions, because of the changes in the ecological/illumination conditions of this environment. When O₂ producing-cyanobacteria evolved and O₂ started to be accumulated, the interaction between UV rays and O₂ generated the O₃ shield first on the polar regions. Then, this gradually forming O₃ layer extended to lower latitudes, allowing the primitive forms of life to colonize other ecosystems and to diversify. Thus, also for this indirect consequence of their appearance (O₃ shield formation), cyanobacteria greatly contributed to the development of life on Earth.

Cyanobacteria, like other microorganisms, have played also a role as *architects of our planet*. Altermann et al. (2006) suggest that communities of cyanobacteria and heterotrophic bacteria were the principal builders of wide carbonate platforms on Earth and presumably the main contributors to the formation of carbonate rocks during almost 70 % of Earth’s history (3.5–0.5 Ga).

From what hitherto illustrated, the key-role of cyanobacteria in the development and shaping of life on Earth is evident, but their contribution was not limited to that. In fact, it is largely accepted that a symbiosis event, occurred among a free-living cyanobacterium and a phagotrophic organism that must have engulfed it, led to the formation of the first photosynthetic eukaryote. During evolution, the engulfed cyanobacteria must have then given rise to the primary plastids of algae and higher plants. The first to note the resemblance between the plastids of plant cells and free-living cyanobacteria was the ecologist Schimper (1883). This was the starting point for a larger idea, now known as *Endosymbiotic Theory*, on the origin of eukaryotic organelles. The Endosymbiotic Theory was illustrated by Mereschkowsky (Mereschkowsky 1905, 1910; Martin and Kowallik 1999)

and later advanced and supported with microbiological and fossil record evidences by Margulis (Sagan 1967; Margulis 1970). Subsequently, electron microscopy investigations and molecular techniques produced further data in support of this theory (Woese 1987; Deusch et al. 2008; McFadden 2001, 2014).

The Endosymbiotic Theory has undergone several revisions and it is still an intriguing issue in biology. In particular, researchers are trying to understand when the endosymbiotic event occurred and to which lineage the cyanobacterial endosymbiont, precursor of plastids, could have belonged. The phylogenetic reconstructions, carried out up to now, do not agree on the evolutionary position of plastids, leading at least to four possibilities: (1) at the base of cyanobacterial radiation (Crisuolo and Gribaldo 2011); (2) related to members of the genera *Synechococcus* and *Prochlorococcus* (Reyes-Prieto et al. 2010); (3) related to nitrogen-fixing coccoid cyanobacteria corresponding to subgroup V in the classification proposed by Honda et al. (1999) (Deschamps et al. 2008); (4) related to heterocyte-forming cyanobacterial lineages (Deusch et al. 2008). Indeed, HGT, normally occurring among cyanobacteria, greatly complicates the interpretation of results (Dagan et al. 2013, McFadden 2014).

Dagan et al. (2013) illustrate a series of hypotheses about the possible initial benefits of keeping the cyanobacterial endosymbiont, eventually turned into plastids, by the phagotrophic organism: (1) carbohydrate production by the cyanobacterial endosymbiont (traditionally considered the most probable explanation); (2) O₂ production by the cyanobacterium (this hypothesis is valid only if the endosymbiotic event occurred when O₂ levels on Earth were not so high and fossil and geochemical records support this possibility); (3) nitrogen fixation capability of the endosymbiont (this is considered the most probable hypothesis by the authors, based on the observations that in current symbioses between cyanobacteria and other organisms nitrogen fixation is the key-factor to the establishment of the partnership). Probably all these three factors were determinant for the instauration of the symbiosis between the free-living cyanobacterium precursor of modern plastids and the phagotrophic organism that swallowed it.

After the first endosymbiotic event (primary endosymbiosis) further endosymbiotic events took place during evolution, as a consequence of the ingestion, by other phagotrophic organisms, of the life forms originated from the primary endosymbiotic event (secondary endosymbioses) (McFadden 2001). This led to the flourishing of many plant forms, which, in turn, contributed to the diversification of a multiplicity of animals. Conversely, the appearance of plant and animal eukaryotes has been supposed to have an effect on the existing prokaryotes, including cyanobacteria, during Earth's history. Experiments on the interaction between phytoplankton and grazers show how this relationship is one of the driving forces that shaped taxon composition during the evolution of life (Ratti et al. 2013), even if the comparison between microbial carbonate abundance and metazoan diversification shows that animal competition/predation is just one of the factors that has influenced microbial communities over time (Riding 2006).

All the hypotheses on the formation of Earth's atmosphere and on the evolution of life on Earth have been drawn mainly based on *fossil records*, which, in the case of cyanobacteria, include body fossils, chemical fossils, and trace fossils (Golubic and Seong-Joo 1999).

Among the best known cyanobacterial fossil records there are stromatolites. *Stromatolites*, “laminated benthic microbial deposits”, are a subcategory of microbialites, i.e. “organo-sedimentary deposits produced by microbial communities” (Riding 2011). Besides fossil stromatolites, there are also contemporary occurrences, mainly associated with extreme environments, where competition and/or predation pressures are limited, and

which are typically found in the intertidal and subtidal zones. Among the most famous there are the stromatolites from the hypersaline coastal lagoon of Hamelin Pool at Shark Bay, Western Australia (Logan et al. 1974; Hoffman 1976; Burns et al. 2004; Papineau et al. 2005). Other living stromatolites are those growing in current-swept channels between Exuma Islands, in Bahamas (Dill et al. 1986; Reid et al. 1995), and those from hot springs in Yellowstone National Park (Pepe-Ranney et al. 2012). Recently, however, they have been found on a high-intertidal to supratidal rock platform of Morgan Bay, South Africa (Smith et al. 2011), as well as in the supratidal zone of the Giant's Causeway Coast, Northern Ireland (Cooper et al. 2013).

Fossil cyanobacteria, in general, have been proposed as *markers of geological times and geological events*. In this regard, Jahnke et al. (2014) define modern evaporitic microbial ecosystems as “important living archives for understanding early life on Earth” and Panieri et al. (2010) succeeded in sequencing the oldest known DNA from fossilized cyanobacteria, embedded in primary gypsum crystals from the late Miocene, and suggest the importance of using fossil cyanobacterial traces in palaeoenvironmental reconstructions of ancient life.

The study of fossil cyanobacteria, together with other fossilized microorganisms, is currently important also in the light of the so-called *Panspermia Theories*, i.e. several hypotheses on the possibility that life exists in the outer space and that from there it was transported to Earth by meteorites, asteroids or comets (Davis and McKay 1996). Hoover (2011) studied some filamentous forms found in CII carbonaceous meteorites. Based on environmental scanning electron microscopy (ESEM), field emission scanning electron microscopy (FESEM), and energy dispersive X-ray spectroscopy (EDS), he concluded that the investigated filaments were fossils of cyanobacteria and other trichomic prokaryotes, embedded in the meteorites before these entered Earth's atmosphere, thus strongly suggesting the existence of life forms outside Earth. This idea has been criticized by some, but, now, astrobiologists are investigating the fossilized biological communities, made up by cyanobacteria and other microorganisms (e.g., diatoms and green algae), found as inclusions in gypsum deposits from different Earth's sites (Australia, Crete, Cyprus, Italy, Mexico, Peru). Since similar deposits of sulfate minerals, like gypsum, are abundant on Mars, the comparison between Martian sediments and the terrestrial ones can give new insights on the existence of past, and probably current, life on Mars (Schopf et al. 2012; Allwood et al. 2013; Benison and Karmanocky 2014).

Positive and negative impacts on the environment and human activities

In the last few decades, certain altered hydrologic parameters or anthropogenic excessive release of nutrients into the environment may benefit various species of cyanobacteria that can rapidly multiply causing “blooms” (Babica et al. 2006). Cyanobacterial blooms are common in freshwater environments throughout the world, while in marine waters they are limited to only few taxa. These blooms are composed of an high number of planktic cyanobacterial species, which can regulate buoyancy through gas vesicle production and through changes in intracellular pools of several compounds (Skulberg et al. 1984; Sellner 1997; Sellner et al. 2003; De Figueiredo et al. 2006).

Sometimes these blooms can also involve *harmful cyanobacteria*, able to produce toxic peptides and alkaloids, called *cyanotoxins*, which can cause serious environmental problems, in particular in freshwater ecosystems and water reservoirs for fishing, drinking or irrigation uses (Codd 1995; Carmichael 2001; Chorus 2001; Sellner et al. 2003; Paerl and

Huisman 2009; Straubinger-Gansberger et al. 2014). Bloom-forming genera with members able to produce toxins comprise: *Anabaenopsis*, *Aphanizomenon*, *Cylindrospermopsis*, *Dolichospermum*, *Microcystis*, *Nodularia*, *Planktothrix*, and *Raphidiopsis* (Voloshko et al. 2008). However, also mat- and biofilm-developing genera, such as *Anabaena*, *Lyngbya*, *Oscillatoria*, and *Phormidium*, include toxic species (Voloshko et al. 2008).

Even if cyanotoxin producing cyanobacteria are usually associated with blooms and therefore with eutrophication, studies have shown cyanotoxin production even in typical oligotrophic environments, such as high-ecological-integrity carbonate streams, and by typical oligotrophic taxa (i.e. taxa living in environments with poor supply of nutrients), such as *Rivularia* (Aboal et al. 2005). Besides the most studied toxic cyanobacteria from freshwater habitats, marine benthic cyanobacteria can also produce cyanotoxins that are transferred along the food chain and affect fishes and mollusks (Golubic et al. 2010). Cyanotoxins are, in fact, a potential risk for both human and animal health and, in some cases, they can cause acute diseases, such as cancer or even death (Jochimsen et al. 1998; Pouria et al. 1998; Azevedo et al. 2002). Based on the physiological systems, i.e. organs, tissues, or cells, that they can primarily affect, cyanotoxins are classified into five important groups (Žegura et al. 2011). There are hepatotoxins, of which microcystins (MCs) are the most known (Carmichael 1997, 2001; Falconer 1998; Codd 2000); neurotoxins (Carmichael 1997, 2001; Falconer 1998; Codd 2000); cytotoxins (Humpage et al. 2000; Shen et al. 2002); dermatotoxins; and irritant toxins (lipopolysaccharides) (Falconer 1998; Codd 2000).

Besides the negative impacts on environment and human activities by cyanobacterial presence due to toxin production, these photosynthetic prokaryotes have also some positive effects. Some cyanotoxins, in fact, have proved to be *bioactive compounds* with antiviral, antitumor, antibacterial, and anti-HIV activities (Singh et al. 2005; Sharma et al. 2010; Zanchett and Oliveira-Filho 2013). In particular, several cyanobacteria living in marine environments, most of which belonging to the order Oscillatoriales, are able to produce exciting potential pharmaceuticals, with promising anti-carcinogenic effects or other anti-disease activities (Gerwick et al. 2008). Another positive aspect derived from cyanobacterial toxin production has been suggested by studies on the ecological roles of some of these specific compounds as allelochemicals, inhibiting competing sympatric macrophytes, algae, and microbes. These allelochemicals, playing a role in defense against potential predators and grazers, can be employed for the development of algaecides, herbicides, and insecticides (Berry et al. 2008).

Cyanobacteria are also considered as *health food stores* throughout the world, since they are an excellent source of vitamins and proteins (Singh et al. 2005; Gantar and Svirčev 2008; Sharma et al. 2010; Pfeiffer et al. 2011; Ohmori and Ehira 2014).

Among the advantages deriving from the cyanobacterial use there is the highly promising capability by these microorganisms to produce H_2 (Hallenbeck and Benemann 2002; Dutta et al. 2005). H_2 is one of the most desired alternative to the limited fossil fuel, representing an efficient, clean energy source, with renew potential ability. In recent years *H_2 production* from renewable sources (it can be realized by anaerobic and photosynthetic microorganisms using carbohydrate rich and non-toxic raw materials), also known as “green technology”, has received considerable attention (Kapdan and Kargi 2006; Dasa and Veziroglu 2008).

Cyanobacteria live in very different terrestrial environments, such as rocks, desert crusts, and modern and ancient stone monuments (Albertano 2012; Keshari and Adhikary 2013). Important stone temples, caves, mortar monuments, as well as building facades of many countries, like India, Mexico, Brazil, and USA, are now disfigured due to

cyanobacterial biofilm formation, leading to deterioration of the substratum (Ortega-Morales et al. 2000; Crispim et al. 2006; Cappitelli et al. 2012; Rossi et al. 2012; Keshari and Adhikary 2013, 2014). The ability to colonize these substrata is due to exocellular polysaccharide production, allowing the formation of biofilms that penetrate up to a maximum depth of about 1 mm (Cappitelli et al. 2012; Rossi et al. 2012). In this way, cyanobacteria can cause *biodeterioration of cultural heritage*, characterized by dark pigmentation of the stone (Crispim et al. 2004; Rindi 2007; Cappitelli et al. 2012). This dark stone discoloration is correlated with the secretion of protective pigments in the polysaccharide layers, namely scytonemins, mycosporine-like amino acids (MAAs), and carotenoids (Cappitelli et al. 2012; Keshari and Adhikary 2013). Since they are protective against UV radiation, these pigments allow the persistence of cyanobacteria even on surfaces exposed to high light intensities (Rossi et al. 2012).

Hints on cyanobacterial systematics and identification methods

In spite of the huge impact cyanobacteria can have both on the environment and on human activities, the identification and classification of these microorganisms are complex and many taxa are problematic from a systematic point of view.

As for other microorganisms, *identification problems* are often due to small cell sizes and morphologies that can look very similar among phylogenetically distinct entities. In particular, cyanobacteria show the phenomenon of “*cryptic species*”, i.e. organisms potentially attributable to the same species from a morphological point of view, but that are genetically distinct (Sciuto et al. 2012). Moreover, like for other organisms without sexual reproduction, *the species concept* for the phylum Cyanobacteria is still debated (Johansen and Casamatta 2005; Komárek 2006, 2010; Palińska and Surosz 2014) and, therefore, species boundaries are often difficult to be traced. This is a problem, for example, during ecological surveys, in which researchers have to do with the existence of different ecotypes of a species, exploiting separate ecological niches in the same environment.

The *coexistence of two different nomenclature codes*, Botanical and Bacteriological, has made the situation even more complex. In fact, since they were considered as algae, cyanobacteria were initially classified based on botanical principles and their nomenclature was ruled under the International Code of Botanical Nomenclature (ICBN). In 1978, after the recognition of the prokaryotic nature of cyanobacteria, Stanier and colleagues proposed to rule the nomenclature of these microorganisms under the International Code of Nomenclature of Bacteria (ICNB), now International Code of Nomenclature of Prokaryotes (ICNP), using bacteriological criteria to classify them. Thus, in 1979 Rippka et al. created a bacteriological classification code also for cyanobacteria. However, only after the use of molecular techniques, in particular based on ribosomal gene sequences, cyanobacteria were confirmed as members of the domain Eubacteria (Woese et al. 1970; Woese 1987). For more than 30 years, taxonomists have been trying to find a solution that will lead to the *creation of a unique nomenclature system for cyanobacteria* (Oren 2004; Komarek 2006, 2010; Oren et al. 2009; Palińska and Surosz 2014). In this regard, a first, concrete effort was the elaboration by Komárek and Golubić (2005) of a special nomenclatural guide for cyanobacteria, “*Cyano-Guide*”, under which nomenclatural procedures respecting all the major prescriptions and recommendations of both Codes are provided.

Among the different methods used to classify cyanobacteria, undoubtedly, *the advent of molecular techniques has greatly contributed to their systematics*, to the identification of new taxa, and to try to define taxon boundaries. Besides the above mentioned

acknowledgment of their prokaryotic nature based on ribosomal gene analyses (Woese et al. 1970; Woese 1987), the information obtained from 16S rDNA gene phylogenetic reconstructions, together with morphological, ultrastructural, and pigment composition data, led Hoffmann et al. (2005) to propose a classification of cyanobacteria in which the phylum Cyanobacteria, class Cyanophyceae, is divided into four sub-classes: Gloeobacteriophycidae, Synechococcophycidae, Oscillatorophycidae, and Nostochophycidae. According to Hoffmann and collaborators the main phenotypic features to be considered diagnostic are: (1) presence/absence of thylakoids, (2) thylakoid arrangement, (3) presence of differentiated cells.

Indeed, as for other prokaryotes, the 16S rDNA gene is currently the most used marker for molecular and phylogenetic studies on cyanobacteria (e.g., Wilmotte 1994; Wilmotte and Herdmann 2001; Casamatta et al. 2005; Palińska and Marquardt 2008; Engene et al. 2013). Related to this, there is the criterion proposed by Stackebrandt and Goebel (1994) to attribute bacterial strains to the same species or to the same genus. The criterion, widely used also for cyanobacteria, is based on the correlation between DNA–DNA reassociation percentage of the genomic DNAs of two bacterial strains with the identity percentage between their 16S rDNA gene sequences. Stackebrandt and Goebel observed that, in most cases, two bacterial strains belonging to a same genus, based on the DNA–DNA reassociation percentage, shared also an identity of at least 95 % between their 16S rDNA sequences, while two bacterial strains belonging to a same species showed a 16S rDNA identity of at least 97.5 %. Even if a further tool for the hard task to classify cyanobacteria, these threshold values cannot be taken alone to establish if cyanobacterial strains belong to the same genus and/or species, as proven by some studies (e.g., Sciuto et al. 2012).

Other used molecular markers for cyanobacterial phylogeny and classification are: 16S–23S intergenic transcribed spacer (ITS), *rpoB* gene, *rpoC1* gene, *gyrB* gene, *rbcLX* gene, *cpcB*-IGS-*cpcA* operon, *nifD* and *nifH* genes (e.g., Iteman et al. 2000; Seo and Yokota, 2003; Henson et al. 2004; Rajaniemi et al. 2005; Teneva et al. 2005; Tomitani et al. 2006). Several molecular techniques can be used to identify and classify cyanobacteria, as illustrated, for example, by Kumari et al. (2009) and Gupta et al. (2013).

In the last 2 years, *entire genome approaches* have been used to reconstruct cyanobacterial phylogeny (Shih et al. 2013; Soo et al. 2014). Besides other information, these studies give new insights on the systematics of the phylum. In particular Soo et al. (2014) have suggested to include, under the phylum Cyanobacteria, another group of prokaryotes, the Melainabacteria, found in human gut and different water sources (Di Rienzi et al. 2013). In the phylogenetic reconstructions by Soo and colleagues, this non-photosynthetic bacterial lineage is strongly monophyletic with the rest of cyanobacteria, besides sharing with them some ancestral traits, such as the structure of cell envelope. If this proposal is accepted, the phylum Cyanobacteria will be composed of two classes, the Oxyphotobacteria and the Melainabacteria, and will lose one of the main features that, traditionally, has universally characterized it: the ability to perform oxygenic photosynthesis.

Even if the level of information obtained from entire genome analyses is evident, at the moment it is still not applicable by several research groups and, in particular, it is not used for routine identification of cyanobacterial strains. Currently, a *polyphasic approach*, including several complementary levels of investigations (i.e. morphological, ultrastructural, biochemical, physiological, molecular) is the most accepted method to characterize and identify cyanobacteria (e.g., Wilmotte 1994; Komárek 2006, 2010; Moro et al. 2010; Sciuto et al. 2011; Lee et al. 2014). Recently, the importance of comparing new isolated

strains with reference ones, in particular *historical specimens*, to more precisely characterize them has been also underlined (Sciuto et al. 2012, 2013; Palińska and Surosz 2014).

In the last years the use of a polyphasic approach and, in particular, the application of molecular techniques have led to the revision of the traditional cyanobacterial systematics and to the discovery of several new taxa, with a corresponding increase of papers characterizing new cyanobacterial entities or reporting changes to cyanobacterial taxonomy and nomenclature (see Fig. 1 in Lee et al. 2014 for an exemplifying summary). Therefore an accurate study of recent literature and the subsequent acceptance of verified and evidently valid modifications will be an essential part in the process of *renovation of the cyanobacterial classification system*.

Conclusions

Cyanobacteria are among the oldest living beings, widespread in several habitats, including those considered extreme, thanks to a series of adaptive strategies. The variety of environments where they can be found is associated with a range of forms and lifestyles, as well as with a series of features that can be exploited in different human activities. They had also a key-role to develop and shape life on our planet as we know it today.

Nevertheless, cyanobacterial identification, the first and important step in each applied field, is a complex issue, due to the chaos in their present-day systematics. The speed with which new ways to exploit these microorganisms are found, thanks to progress in biotechnological techniques, is not accompanied by a solution allowing to unambiguously identify new isolated strains. In the future, efforts shall be devoted not just to find new applications for cyanobacteria, but to solve their systematic problems. This will help to increase the knowledge on these organisms, as small in size as huge in their impact on our lives, whose biodiversity is still largely underestimated.

Acknowledgments We thank the anonymous reviewers for their constructive and accurate comments, which helped us to improve this review paper.

References

- Aboal M, Puig MA, Asencio AD (2005) Production of microcystins in calcareous Mediterranean streams: the Alharabe River, Segura River basin in south-east Spain. *J Appl Phycol* 17:231–243. doi:[10.1007/s10811-005-2999-z](https://doi.org/10.1007/s10811-005-2999-z)
- Adams DG (2001) How do cyanobacteria glide? *Microbiol Today* 28:131–133
- Adams DG, Duggan PS (1999) Tansley Review No. 107. Heterocyst and akinete differentiation in cyanobacteria. *New Phytol* 144:3–33. doi:[10.1046/j.1469-8137.1999.00505.x](https://doi.org/10.1046/j.1469-8137.1999.00505.x)
- Adams DG, Duggan PS (2008) Cyanobacteria-bryophyte symbioses. *J Exp Bot* 59:1047–1058. doi:[10.1093/jxb/ern005](https://doi.org/10.1093/jxb/ern005)
- Adams DG, Ashworth D, Nelmes B (1999) Fibrillar array in the cell wall of a gliding filamentous cyanobacterium. *J Bacteriol* 181:884–892
- Adams DG, Bergman B, Nierzwicki-Bauer SA, Rai AN, Schüßler A (2006) Cyanobacterial-plant symbioses. In: Dworkin M, Falkow S, Rosenberg E, Schleifer KH, Stackebrandt E (eds) *The prokaryotes: a handbook on the biology of bacteria*, vol 1, 3rd edn., Symbiotic associations, biotechnology, applied microbiology Springer, New York, pp 331–363
- Albertano P (2012) Cyanobacterial biofilms in monuments and caves. In: Whitton BA (ed) *Ecology of cyanobacteria. II: their diversity in space and time*. Springer, Dordrecht, pp 317–343. doi:[10.1007/978-94-007-3855-3](https://doi.org/10.1007/978-94-007-3855-3)

- Allwood AC, Burch IW, Rouchy JM, Coleman M (2013) Morphological biosignatures in gypsum: diverse formation processes of messinian (≈ 6.0 ma) gypsum stromatolites. *Astrobiology* 13:870–886. doi:[10.1089/ast.2013.1021](https://doi.org/10.1089/ast.2013.1021)
- Altermann W, Kazmierczak J, Oren A, Wright DT (2006) Cyanobacterial calcification and its rock-building potential during 3.5 billion years of Earth history. *Geobiology* 4:147–166. doi:[10.1111/j.1472-4669.2006.00076.x](https://doi.org/10.1111/j.1472-4669.2006.00076.x)
- Anagnostidis K, Komárek J (1990) Modern approach to the classification system of the cyanophytes. 5: stigonematales. *Arch. Hydrobiol Algal Stud* 59:1–73
- Andersson B, Anderson JM (1980) Lateral heterogeneity in the distribution of chlorophyll-protein complexes of the thylakoid membranes of spinach chloroplasts. *Bioenergetics* 593:427–440. doi:[10.1016/0005-2728\(80\)90078-X](https://doi.org/10.1016/0005-2728(80)90078-X)
- Azevedo SMFO, Carmichael WW, Jochimsen EM, Rinehart KL, Lau S, Shaw GR, Eaglesham GK (2002) Human intoxication by microcystins during renal dialysis treatment in Caruaru—Brazil. *Toxicology* 181:441–446
- Babica P, Bláha L, Maršálek B (2006) Exploring the natural role of microcystins—a review of effects on photoautotrophic organisms. *J Phycol* 42:9–20. doi:[10.1111/j.1529-8817.2006.00176.x](https://doi.org/10.1111/j.1529-8817.2006.00176.x)
- Bardy SL, Ng SYM, Jarrell KF (2003) Prokaryotic motility structures. *Microbiology* 149:295–304
- Benison KC, Karmanocky FJ (2014) Could microorganisms be preserved in Mars gypsum? Insights from terrestrial examples. *Geology* 42:615–618. doi:[10.1130/G35542.1](https://doi.org/10.1130/G35542.1)
- Bergman B, Carpenter EJ (1991) Nitrogenase confined to randomly distributed trichomes in the marine cyanobacterium *Trichodesmium thiebautii*. *J Phycol* 27:158–165. doi:[10.1111/j.0022-3646.1991.00158.x](https://doi.org/10.1111/j.0022-3646.1991.00158.x)
- Berman-Frank I, Lundgren P, Chen YB, Küpper H, Kolber Z, Bergman B, Falkowski P (2001) Segregation of nitrogen fixation and oxygenic photosynthesis in the marine cyanobacterium *Trichodesmium*. *Science* 294:1534–1537. doi:[10.1126/science.1064082](https://doi.org/10.1126/science.1064082)
- Berman-Frank I, Lundgren P, Falkowski P (2003) Nitrogen fixation and photosynthetic oxygen evolution in cyanobacteria. *Res Microbiol* 154:157–164. doi:[10.1016/S0923-2508\(03\)00029-9](https://doi.org/10.1016/S0923-2508(03)00029-9)
- Berry JP, Gantar M, Perez MH, Berry G, Noriega FG (2008) Cyanobacterial toxins as allelochemicals with potential applications as algacides, herbicides and insecticides. *Mar Drugs* 6:117–146. doi:[10.3390/md20080007](https://doi.org/10.3390/md20080007)
- Bhaya D (2004) Light matters: phototaxis and signal transduction in unicellular cyanobacteria. *Mol Microbiol* 53:745–754. doi:[10.1111/j.1365-2958.2004.04160.x](https://doi.org/10.1111/j.1365-2958.2004.04160.x)
- Brookes JD, Ganf GG (2001) Variations in the buoyancy response of *Microcystis aeruginosa* to nitrogen, phosphorus and light. *J Plankton Res* 23:1399–1411. doi:[10.1093/plankt/23.12.1399](https://doi.org/10.1093/plankt/23.12.1399)
- Brookes JD, Ganf GG, Green D, Whittington J (1999) The influence of light and nutrients on buoyancy, filament aggregation and flotation of *Anabaena circinalis*. *J Plankton Res* 21:327–341. doi:[10.1093/plankt/21.2.327](https://doi.org/10.1093/plankt/21.2.327)
- Bryant DA (1982) Phycoerythrocyanin and phycoerythrin: properties and occurrence in cyanobacteria. *J Gen Microbiol* 128:835–844
- Burns BP, Goh F, Allen M, Neilan BA (2004) Microbial diversity of extant stromatolites in the hypersaline marine environment of Shark Bay, Australia. *Environ Microbiol* 6:1096–1101. doi:[10.1111/j.1462-2920.2004.00651.x](https://doi.org/10.1111/j.1462-2920.2004.00651.x)
- Capone DG, Zehr JP, Paerl HW, Bergman B, Carpenter EJ (1997) *Trichodesmium*, a globally significant marine cyanobacterium. *Science* 276:1221–1229. doi:[10.1126/science.276.5316.1221](https://doi.org/10.1126/science.276.5316.1221)
- Cappitelli F, Salvadori O, Albanese D, Villa F, Sorlini C (2012) Cyanobacteria cause black staining of the National Museum of the American Indian Building, Washington, DC, USA. *Biofouling* 28:257–266. doi:[10.1080/08927014.2012.671304](https://doi.org/10.1080/08927014.2012.671304)
- Carmichael WW (1997) The cyanotoxins. In: Callow JA (ed) *Advances in botanical research*, vol 27. Academic Press, London, pp 211–256
- Carmichael WW (2001) Health effects of toxin producing cyanobacteria: the ‘CyanoHABS’. *Hum Ecol Risk Assess* 7:1393–1407. doi:[10.1080/20018091095087](https://doi.org/10.1080/20018091095087)
- Carpenter EJ, Foster R (2002) Marine symbioses. In: Rai AN, Bergman B, Rasmussen U (eds) *Cyanobacteria in symbiosis*. Kluwer Academic Publishers, Dordrecht, pp 11–18
- Carr NG, Whitton BA (1982) *The biology of cyanobacteria*. Blackwell Scientific Publications, Oxford
- Casamatta DA, Johansen JR, Vis ML, Broadwater ST (2005) Molecular and morphological characterization of ten polar and near-polar strains within the *Oscillatoriales* (cyanobacteria). *J Phycol* 41:421–438. doi:[10.1111/j.1529-8817.2005.04062.x](https://doi.org/10.1111/j.1529-8817.2005.04062.x)
- Choi J, Chung Y, Moon Y, Kimt C, Watanabe M, Song P, Joe C, Bogorad L, Park YM (1999) Photo-movement of the gliding Cyanobacterium *Synechocystis* sp. PCC 6803. *Photochem Photobiol* 70:95–102. doi:[10.1111/j.1751-1097.1999.tb01954.x](https://doi.org/10.1111/j.1751-1097.1999.tb01954.x)

- Chorus I (2001) Cyanotoxins: occurrence, causes, consequences. Springer, Berlin
- Cmiech HA, Reynolds CS, Leedale GF (1984) Seasonal periodicity, heterocyst differentiation and sporulation of planktonic Cyanophyceae in a shallow lake, with special reference to *Anabaena solitaria*. Br Phycol J 19:245–257. doi:10.1080/00071618400650271
- Codd GA (1995) Cyanobacterial toxins: occurrence, properties and biological significance. Water Sci Technol 32:149–156. doi:10.1016/0273-1223(95)00692-3
- Codd GA (2000) Cyanobacterial toxins, the perception of water quality, and the prioritisation of eutrophication control. Ecol Eng 16:51–60. doi:10.1016/S0925-8574(00)00089-6
- Cohen Y, Castenholz RW, Halvorson HO (1984) Microbial mats: stromatolites. Alan R. Liss, Inc., New York
- Cooper JAG, Smith AM, Arnscheidt J (2013) Contemporary stromatolite formation in high intertidal rock pools, Giant's Causeway, Northern Ireland: preliminary observations. J Coastal Res 65:1675–1680. doi:10.2112/SI65-283.1
- Crisuolo A, Gribaldo S (2011) Large-scale phylogenomic analyses indicate a deep origin of primary plastids within cyanobacteria. Mol Biol Evol 28:3019–3032. doi:10.1093/molbev/msr108
- Crispim CA, Gaylarde CC, Gaylarde PM (2004) Biofilms on church walls in Porto Alegre, RS, Brazil, with special attention to cyanobacteria. Int Biodeter Biodeg 54:121–124. doi:10.1016/j.ibiod.2004.03.001
- Crispim CA, Gaylarde PM, Gaylarde CC, Neilan BA (2006) Deteriogenic cyanobacteria on historic buildings in Brazil detected by culture and molecular techniques. Int Biodeter Biodeg 57:239–243. doi:10.1016/j.ibiod.2006.03.001
- Crowe SA, Døssing LN, Beukes NJ, Bau M, Kruger SJ, Frei R, Canfield DE (2013) Atmospheric oxygenation three billion years ago. Nature 501:535–538. doi:10.1038/nature12426
- Dagan T, Roettger M, Stucken K et al (2013) Genomes of stigonematalean cyanobacteria (Subsection V) and the evolution of oxygenic photosynthesis from prokaryotes to plastids. Genome Biol Evol 5:31–44. doi:10.1093/gbe/evs117
- Dasa D, Veziroglu TN (2008) Advances in biological hydrogen production processes. Int J Hydrogen Energy 33:6046–6057. doi:10.1016/j.ijhydene.2008.07.098
- Davis WL, McKay CP (1996) Origins of life: a comparison of theories and applications to Mars. Orig Life Evol Biosph 26:61–73. doi:10.1007/BF01808160
- De Figueiredo DR, Reboleira ASSP, Antunes SC, Abrantes N, Azeiteiro U, Gonçalves F, Pereira MJ (2006) The effect of environmental parameters and cyanobacterial blooms on phytoplankton dynamics of a Portuguese temperate lake. Hydrobiologia 568:145–157. doi:10.1007/s10750-006-0196-y
- De Philippis R, Vincenzini M (1998) Exocellular polysaccharides from cyanobacteria and their possible applications. FEMS Microbiol Rev 22:151–175. doi:10.1111/j.1574-6976.1998.tb00365.x
- De Philippis R, Sili C, Paperi R, Vincenzini M (2001) Exopolysaccharide-producing cyanobacteria and their possible exploitation: a review. J Appl Phycol 13:293–299
- Deschamps P, Colleoni C, Nakamura Y, Suzuki E, Putaux JL, Buleon A, Haebel S, Ritte G, Steup M, Falcon LI et al (2008) Metabolic symbiosis and the birth of the plant kingdom. Mol Biol Evol 25:536–548. doi:10.1093/molbev/msm280
- Deusch O, Landan G, Roettger M, Gruenheit N, Kowallik KV, Allen JF, Martin W, Dagan T (2008) Genes of cyanobacterial origin in plant nuclear genomes point to a heterocyst-forming plastid ancestor. Mol Biol Evol 25:748–761. doi:10.1093/molbev/msn022
- Di Rienzi SC, Sharon I, Wrighton KC et al (2013) The human gut and groundwater harbor nonphotosynthetic bacteria belonging to a new candidate phylum sibling to cyanobacteria. Life 2:e01102. doi:10.7554/eLife.01102
- Dill RF, Shinn EA, Jones AT, Kelly K, Steinen RP (1986) Giant subtidal stromatolites forming in normal salinity waters. Nature 324:55–58. doi:10.1038/324055a0
- Dismukes GC, Klimov VV, Baranov SV, Kozlov YuN, DasGupta J, Tyryshkin A (2001) The origin of atmospheric oxygen on Earth: the innovation of oxygenic photosynthesis. Proc Natl Acad Sci USA 98:2170–2175. doi:10.1073/pnas.061514798
- Dutta D, De D, Chaudhuri S, Bhattacharya SK (2005) Hydrogen production by cyanobacteria. Microb Cell Fact 4:36. doi:10.1186/1475-2859-4-36
- El-Shehawey R, Lugomela C, Ernst A, Bergman B (2003) Diurnal expression of *hetR* and diazocyst development in the filamentous non-heterocystous cyanobacterium *Trichodesmium erythraeum*. Microbiology 149:1139–1146. doi:10.1099/mic.0.26170-0
- Engene N, Gunasekera SP, Gerwick WH, Paul VJ (2013) Phylogenetic inferences reveal a large extent of novel biodiversity in chemically rich tropical marine cyanobacteria. Appl Environ Microbiol 79:1882–1888. doi:10.1128/AEM.03793-12
- Falconer IR (1998) Algal toxins and human health. In: Hrubec J (ed) Handbook of environmental chemistry, vol 5 (Part C). Springer, Berlin, pp 53–82

- Flores E, Herrero A (2010) Compartmentalized function through cell differentiation in filamentous cyanobacteria. *Nat Rev Microbiol* 8:39–50. doi:[10.1038/nrmicro2242](https://doi.org/10.1038/nrmicro2242)
- Fredriksson C, Bergman B (1997) Ultrastructural characterization of cells specialised for nitrogen fixation in a non-heterocystous cyanobacterium, *Trichodesmium* spp. *Protoplasma* 197:76–85. doi:[10.1007/BF01279886](https://doi.org/10.1007/BF01279886)
- Friedmann EI (1982) Endolithic microorganisms in the Antarctic cold desert. *Science* 215:1045–1053. doi:[10.1126/science.215.4536.1045](https://doi.org/10.1126/science.215.4536.1045)
- Gantar M, Svirčev Z (2008) Microalgae and cyanobacteria: food for thought. *J Phycol* 44:260–268. doi:[10.1111/j.1529-8817.2008.00469.x](https://doi.org/10.1111/j.1529-8817.2008.00469.x)
- Gao Q, García-Pichel F (2011) Microbial ultraviolet sunscreens. *Nat Rev Microbiol* 9:791–802. doi:[10.1038/nrmicro2649](https://doi.org/10.1038/nrmicro2649)
- García-Pichel F, Prufert-Bebout L, Muyzer G (1996) Phenotypic and phylogenetic analyses show *Microcoleus chthonoplastes* to be a cosmopolitan cyanobacterium. *Appl Environ Microbiol* 62:3284–3291
- Gerwick WH, Coates RC, Engene N, Gerwick L, Grindberg RV, Jones AC, Sorrels CM (2008) Giant marine cyanobacteria produce exciting potential pharmaceuticals. *Microbe* 3:277–284
- Golubic S, Seong-Joo L (1999) Early cyanobacterial fossil record: preservation, palaeoenvironments and identification. *Eur J Phycol* 34:339–348. doi:[10.1080/09670269910001736402](https://doi.org/10.1080/09670269910001736402)
- Golubic S, Abed RMM, Palińska K, Pauillac S, Chinain M, Laurent D (2010) Marine toxic cyanobacteria: diversity, environmental responses and hazards. *Toxicon* 56:836–841. doi:[10.1016/j.toxicon.2009.07.023](https://doi.org/10.1016/j.toxicon.2009.07.023)
- Govindjee, Shevela D (2011) Adventures with cyanobacteria: a personal perspective. *Front Plant Sci* 2:28. doi:[10.3389/fpls.2011.00028](https://doi.org/10.3389/fpls.2011.00028)
- Grossman AR, Schaefer MR, Chiang GG, Collier JL (1993) The phycobilisome, a light-harvesting complex responsive to environmental conditions. *Microbiol Rev* 57:725–749
- Gupta V, Ratha SK, Sood A, Chaudhary V, Prasanna R (2013) New insights into the biodiversity and applications of cyanobacteria (blue-green algae)—prospects and challenges. *Algal Res* 2:69–97. doi:[10.1016/j.algal.2013.01.006](https://doi.org/10.1016/j.algal.2013.01.006)
- Hallenbeck PC, Benemann JR (2002) Biological hydrogen production: fundamentals and limiting processes. *Int J Hydrogen Energ* 27:1185–1193. doi:[10.1016/S0360-3199\(02\)00131-3](https://doi.org/10.1016/S0360-3199(02)00131-3)
- Hallmann C, Summons RE (2014) Paleobiological clues to early atmospheric evolution. In: Holland H, Turekian K (eds) *Treatise on geochemistry*, vol 6, 2nd edn., The Atmosphere-history Elsevier, Oxford, pp 139–155
- Henson BJ, Watson LE, Barnum SR (2004) The evolutionary history of nitrogen fixation, as assessed by NifD. *J Mol Evol* 58:390–399. doi:[10.1099/ijms.0.02821-0](https://doi.org/10.1099/ijms.0.02821-0)
- Hirose E, Hirose M, Neilan BA (2006) Localization of symbiotic cyanobacteria in the colonial Ascidian *Trididemnum miniatum* (Didemniidae, Ascidiacea). *Zool Sci* 23:435–442. doi:[10.2108/zsj.23.435](https://doi.org/10.2108/zsj.23.435)
- Hoffman P (1976) Stromatolite morphogenesis in Shark Bay, Western Australia. *Dev Sedimentol* 20:261–271. doi:[10.1016/S0070-4571\(08\)71139-7](https://doi.org/10.1016/S0070-4571(08)71139-7)
- Hoffmann L, Komárek J, Kašrovský J (2005) System of cyanoprokaryotes (Cyanobacteria)-state 2004. *Algol Stud* 117:95–115. doi:[10.1127/1864-1318/2005/0117-0095](https://doi.org/10.1127/1864-1318/2005/0117-0095)
- Hohmann-Marriott MF, Blankenship RE (2011) Evolution of photosynthesis. *Annu Rev Plant Biol* 62:515–548. doi:[10.1146/annurev-arplant-042110-103811](https://doi.org/10.1146/annurev-arplant-042110-103811)
- Hoiczky E, Baumeister W (1995) Envelope structure of four gliding filamentous cyanobacteria. *J Bacteriol* 177:2387–2395
- Hoiczky E, Hansel A (2000) Cyanobacterial cell walls: news from an unusual prokaryotic envelope. *J Bacteriol* 182:1191–1199. doi:[10.1128/JB.182.5.1191-1199.2000](https://doi.org/10.1128/JB.182.5.1191-1199.2000)
- Honda D, Yokota A, Sugiyama J (1999) Detection of seven major evolutionary lineages in cyanobacteria based on the 16S rRNA gene sequence analysis with new sequences of five marine *Synechococcus* strains. *J Mol Evol* 48:723–739
- Hoover RB (2011) Fossils of Cyanobacteria in CI1 Carbonaceous Meteorites: Implications to Life on Comets, Europa, and Enceladus. *Journal of Cosmology*, volume 13. <http://journalofcosmology.com/Life102.html>. Accessed 17 Jul 2014
- Humpage AR, Fenech M, Thomas P, Falconer IR (2000) Micronucleus induction and chromosome loss in transformed human white cells indicate clastogenic and aneugenic action of the cyanobacterial toxin, cylindrospermopsin. *Mutat Res* 472:155–164. doi:[10.1016/S1383-5718\(00\)00144-3](https://doi.org/10.1016/S1383-5718(00)00144-3)
- Iteman I, Rippka R, Tandeau de Marsac N, Herdman M (2000) Comparison of conserved structural and regulatory domains within divergent 16S–23S rRNA spacer sequences of cyanobacteria. *Microbiology* 146:1275–1286

- Jahnke LL, Turk-Kubo KA, Parenteau MN, Green SJ, Kubo MDY, Vogel M, Summons RE, Des Marais DJ (2014) Molecular and lipid biomarker analysis of a gypsum-hosted endoevaporitic microbial community. *Geobiology* 12:62–82. doi:10.1111/jbi.12068
- Janson S (2002) Cyanobacteria in symbiosis with diatoms. In: Rai AN, Bergman B, Rasmussen U (eds) Cyanobacteria in symbiosis. Kluwer Academic Publishers, Dordrecht, pp 1–10
- Jochimsen EM, Carmichael WW, An JS, Cardo DM, Cookson ST, Holmes CEM, Antunes MB, Lyra TM, Barreto VST, Azevedo SMFO, Jarvis WR (1998) Liver failure in death after exposure to microcystins at a hemodialysis center in Brazil. *N Engl J Med* 338:873–878
- Johansen JR, Casamatta DA (2005) Recognizing cyanobacterial diversity through adoption of a new species paradigm. *Arch Hydrobiol/Algal Stud* 117:71–93. doi:10.1127/1864-1318/2005/0117-0071
- Johnson JD (2006) The Manganese-calcium oxide cluster of Photosystem II and its assimilation by the Cyanobacteria. <http://www.chm.bris.ac.uk/motm/oec/motm.htm#Ref1>. Accessed 22 Jul 2014
- Kapdan IK, Kargi F (2006) Bio-hydrogen production from waste materials. *Enzyme Microb Tech* 38:569–582. doi:10.1016/j.enzmictec.2005.09.015
- Keshari N, Adhikary SP (2013) Characterization of cyanobacteria isolated from biofilms on stone monuments at Santiniketan, India. *Biofouling* 29:525–536. doi:10.1080/08927014.2013.794224
- Keshari N, Adhikary SP (2014) Diversity of cyanobacteria on stone monuments and building facades of India and their phylogenetic analysis. *Int Biodeter Biodegr* 90:45–51. doi:10.1016/j.ibiod.2014.01.014
- Komárek J (2006) Cyanobacterial taxonomy: current problems and prospects for the integration of traditional and molecular approaches. *Algae* 21:349–375. doi:10.4490/algae.2006.21.4.349
- Komárek J (2010) Recent changes (2008) in cyanobacteria taxonomy based on a combination of molecular background with phenotype and ecological consequences (genus and species concept). *Hydrobiologia* 639:245–259. doi:10.1007/s10750-009-0031-3
- Komárek J, Golubić S (2005) Proposal for unified nomenclatural rules for cyanobacteria vs. cyanophytes: cyano-guide. *Algal Stud* 117:17–18
- Kopp RE, Kirschvink JL, Hilburn IA, Nash CZ (2005) The Paleoproterozoic snowball Earth: a climate disaster triggered by the evolution of oxygenic photosynthesis. *Proc Natl Acad Sci USA* 102:11131–11136. doi:10.1073/pnas.0504878102
- Krings M, Hass H, Kerp H, Taylor TN, Agerer R, Dotzler N (2009) Endophytic cyanobacteria in a 400-million-yr-old land plant: a scenario for the origin of a symbiosis? *Rev Palaeobot Palynol* 153:62–69. doi:10.1016/j.revpalbo.2008.06.006
- Kühl M, Chen M, Ralph PJ, Schreiber U, Larkum AWD (2005) A niche for cyanobacteria containing chlorophyll d. *Nature* 433:820. doi:10.1038/433820a
- Kumari N, Srivastava AK, Bhargava P, Rai LC (2009) Molecular approaches towards assessment of cyanobacterial biodiversity. *Afr J Biotechnol* 8:4284–4298
- Larsson J, Celepli N, Ininbergs K, Dupont CL, Yooséph S, Bergman B, Ekman M (2014) Picocyanobacteria containing a novel pigment gene cluster dominate the brackish water Baltic Sea. *ISME J* 8:1892–1903. doi:10.1038/ismej.2014.35
- Lee E, Ryan UM, Monis P, McGregor GB, Bath A, Gordon C, Papparini A (2014) Polyphasic identification of cyanobacterial isolates from Australia. *Water Res* 59:248–261. doi:10.1016/j.watres.2014.04.023
- Lewin RA (1976) Prochlorophyta as a proposed new division of algae. *Nature* 261:697–698
- Lewin RA (2002) Prochlorophyta—a matter of class distinctions. *Photosynth Res* 73:59–61
- Lewy Z (2013) Life on earth originated where later microbial oxygenic photosynthesis precipitated banded iron formation, suppressing life diversification for 1.4 Ga. *Int J Geosci* 4:1382–1391. doi:10.4236/ijg.2013.410135
- Lin S, Henze S, Lundgren P, Bergman B, Carpenter EJ (1998) Whole-cell immunolocalization of nitrogenase in marine diazotrophic cyanobacteria, *Trichodesmium* spp. *Appl Environ Microbiol* 64:3052–3064
- Lindblad P, Bergman B (1989) Occurrence and localization of phycoerythrin in symbiotic *Nostoc* of *Cycas revoluta* and in the free-living isolated *Nostoc* 7422. *Plant Physiol* 89:783–785
- Lindblad P, Rai AN, Bergman B (1987) The *Cycas revoluta*-*Nostoc* symbiosis: enzyme activities of nitrogen and carbon metabolism in the cyanobiont. *Microbiology* 133:1695–1699
- Logan BW, Hoffman P, Gebelein CD (1974) Algal mats, cryptalgal fabrics, and structures, Hamelin Pool, Western Australia. *AAPG Mem* 22:140–194
- Lyons TW, Reinhard CT, Planavsky NJ (2014) The rise of oxygen in Earth's early ocean and atmosphere. *Nature* 506:307–315. doi:10.1038/nature13068
- MacColl R (1998) Cyanobacterial phycobilisomes. *J Struct Biol* 124:311–334
- Margulis L (1970) *Origin of Eukaryotic Cells*. Yale University Press, New Haven

- Martin W, Kowallik K (1999) Annotated English translation of Mereschkowsky's 1905 paper 'Über Natur und Ursprung der Chromatophoren im Pflanzenreiche'. *Eur J Phycol* 34:287–295. doi:[10.1080/09670269910001736342](https://doi.org/10.1080/09670269910001736342)
- McBride MJ (2001) Bacterial gliding motility: multiple mechanisms for cell movement over surfaces. *Annu Rev Microbiol* 55:49–75. doi:[10.1146/annurev.micro.55.1.49](https://doi.org/10.1146/annurev.micro.55.1.49)
- McFadden GI (2001) Primary and secondary endosymbiosis and the origin of plastids. *J Phycol* 37:951–959. doi:[10.1046/j.1529-8817.2001.01126.x](https://doi.org/10.1046/j.1529-8817.2001.01126.x)
- McFadden GI (2014) Origin and evolution of plastids and photosynthesis in eukaryotes. *Cold Spring Harb Perspect Biol* 6:a016105. doi:[10.1101/cshperspect.a016105](https://doi.org/10.1101/cshperspect.a016105)
- Mereschkowski C (1905) Über Natur und Ursprung der Chromatophoren im Pflanzenreiche. *Biol Centralbl* 25:593–604 (addendum in 25:689–691)
- Mereschkowsky K (1910) Theorie der zwei Plasmaarten als Grundlage der Symbiogenesis, einer neuen Lehre von der Entstehung der Organismen. *Biol Centralbl* 30:353–367
- Moore D, O'Donohue M, Garnett C, Critchley C, Shaw G (2005) Factors affecting akinete differentiation in *Cylindrospermopsis raciborskii* (nostocales, cyanobacteria). *Freshw Biol* 50:345–352. doi:[10.1111/j.1365-2427.2004.01324.x](https://doi.org/10.1111/j.1365-2427.2004.01324.x)
- Moro I, Rascio N, La Rocca N, Sciuto K, Albertano P, Bruno L, Andreoli C (2010) Polyphasic characterization of a thermo-tolerant filamentous cyanobacterium isolated from the Euganean thermal muds (Padova, Italy). *Eur J Phycol* 45:143–154. doi:[10.1080/09670260903564391](https://doi.org/10.1080/09670260903564391)
- Mullen L (2002) Tracking the path of green slime. *Astrobiology Magazine*. <http://www.astrobio.net/topic/origins/extreme-life/tracking-the-path-of-green-slime/>. Accessed 23 July 2014
- Nickelsen J, Rengstl B (2013) Photosystem II assembly: from cyanobacteria to plants. *Annu Rev Plant Biol* 64:609–635. doi:[10.1146/annurev-arplant-050312-120124](https://doi.org/10.1146/annurev-arplant-050312-120124)
- Obukowicz M, Schaller M, Kennedy GS (1981) Ultrastructure and phenolic histochemistry of the *Cycas revoluta-Anabaena* symbiosis. *New Phytol* 87:751–759
- Ohmori M, Ehira S (2014) *Spirulina*: an example of cyanobacteria as nutraceuticals. In: Sharma NK, Rai AK, Stal LJ (eds) *Cyanobacteria: an economic perspective*. Wiley, Oxford, pp 103–118
- Oren A (2004) A proposal for further integration of the cyanobacteria under the bacteriological Code. *Int J Syst Evol Microbiol* 54:1895–1902. doi:[10.1099/ijs.0.03008-0](https://doi.org/10.1099/ijs.0.03008-0)
- Oren A, Komárek J, Hoffmann L (2009) Nomenclature of the cyanophyta/cyanobacteria/cyanoprokaryotes—What has happened since IAC Luxembourg? *Algol Stud* 130:17–26. doi:[10.1127/1864-1318/2009/0130-0017](https://doi.org/10.1127/1864-1318/2009/0130-0017)
- Ortega-Morales O, Guezennec J, Hernández-Duque G, Gaylarde CC, Gaylarde PM (2000) Phototrophic biofilms on ancient mayan buildings in Yucatan, Mexico. *Curr Microbiol* 40:81–85. doi:[10.1007/s002849910015](https://doi.org/10.1007/s002849910015)
- Paerl HW, Huisman J (2009) Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environ Microbiol Rep* 1:27–37. doi:[10.1111/j.1758-2229.2008.00004.x](https://doi.org/10.1111/j.1758-2229.2008.00004.x)
- Paerl HW, Fulton RS, Moisaner PH, Dyble J (2001) Harmful freshwater algal blooms, with an emphasis on cyanobacteria. *Sci World* 1:76–113. doi:[10.1100/tsw.2001.16](https://doi.org/10.1100/tsw.2001.16)
- Pajdak-Stós A, Fialkowska E, Fyda J (2001) *Phormidium autumnale* (Cyanobacteria) defense against three ciliate grazer species. *Aquat Microb Ecol* 23:237–244
- Palińska KA, Marquardt J (2008) Genotypic and phenotypic analysis of strains assigned to the widespread cyanobacterial morphospecies *Phormidium autumnale* (Oscillatoriales). *Arch Microbiol* 189:325–335. doi:[10.1007/s00203-007-0323-9](https://doi.org/10.1007/s00203-007-0323-9)
- Palińska KA, Surosz W (2014) Taxonomy of cyanobacteria: a contribution to consensus approach. *Hydrobiologia* 740:1–11. doi:[10.1007/s10750-014-1971-9](https://doi.org/10.1007/s10750-014-1971-9)
- Panieri G, Lugli S, Manzi V, Roveri M, Schreiber CB, Palinska KA (2010) Ribosomal RNA gene fragments from fossilized cyanobacteria identified in primary gypsum from the late Miocene, Italy. *Geobiology* 8:101–111. doi:[10.1111/j.1472-4669.2009.00230.x](https://doi.org/10.1111/j.1472-4669.2009.00230.x)
- Papineau D, Walker JJ, Mojzsis SJ, Pace NR (2005) Composition and structure of microbial communities from Stromatolites of Hamelin Pool in Shark Bay, Western Australia. *Appl Environ Microbiol* 71:4822–4832. doi:[10.1128/AEM.71.8.4822-4832.2005](https://doi.org/10.1128/AEM.71.8.4822-4832.2005)
- Pate JL (1988) Gliding motility in prokaryotic cells. *Can J Microbiol* 34:459–465
- Pepe-Ranney C, Berelson WM, Corsetti FA, Treants M, Spear JR (2012) Cyanobacterial construction of hot spring siliceous stromatolites in Yellowstone National Park. *Environ Microbiol*. doi:[10.1111/j.1462-2920.2012.02698.x](https://doi.org/10.1111/j.1462-2920.2012.02698.x)
- Pfeiffer C, Bauer T, Surek B, Schömig E, Gründemann D (2011) Cyanobacteria produce high levels of ergothioneine. *Food Chem* 129:1766–1769. doi:[10.1016/j.foodchem.2011.06.047](https://doi.org/10.1016/j.foodchem.2011.06.047)
- Potts M (1980) Blue-green algae (cyanobacteria) in marine coastal environments of the Sinai Peninsula; distribution, zonation, stratification and taxonomic diversity. *Phycologia* 19:60–73

- Pouria S, de Andrade A, Barbosa J, Cavalcanti RL, Barreto VTS, Ward CJ, Preiser W, Poon GK, Neild GH, Codd GA (1998) Fatal microcystin intoxication in haemodialysis unit in Caruaru, Brazil. *Lancet* 352:21–26. doi:[10.1016/S0140-6736\(97\)12285-1](https://doi.org/10.1016/S0140-6736(97)12285-1)
- Rai AN, Bergman B, Rasmussen U (2002) Cyanobacteria in symbiosis. Kluwer Academic, Dordrecht
- Rajaniemi R, Hrouzek P, Kaštovská K, Willame R, Rantala A, Hoffmann L, Komárek J, Sivonen K (2005) Phylogenetic and morphological evaluation of the genera *Anabaena*, *Aphanizomenon*, *Trichormus* and *Nostoc* (nostocales, cyanobacteria). *Int J Syst Evol Microbiol* 55:11–26. doi:[10.1099/ijs.0.63276-0](https://doi.org/10.1099/ijs.0.63276-0)
- Ramsing NB, Ferris MJ, Ward DM (1997) Light-induced motility of thermophilic *Synechococcus* isolates from Octopus Spring, Yellowstone National Park. *Appl Environ Microbiol* 63:2347–2354
- Rasmussen B, Fletcher IR, Brocks JJ, Kilburn MR (2008) Reassessing the first appearance of eukaryotes and cyanobacteria. *Nature* 455:1101–1104. doi:[10.1038/nature07381](https://doi.org/10.1038/nature07381)
- Ratti S, Knoll AH, Giordano M (2013) Grazers and phytoplankton growth in the oceans: an experimental and evolutionary perspective. *PLoS One* 8:e77349. doi:[10.1371/journal.pone.0077349](https://doi.org/10.1371/journal.pone.0077349)
- Read N, Connell S, Adams DG (2007) Nanoscale visualization of a fibrillar array in the cell wall of filamentous cyanobacteria and its implications for gliding motility. *J Bacteriol* 189:7361–7366
- Reid RP, Macintyre IG, Steneck RS, Browne KM, Miller TE (1995) Stromatolites in the Exuma Cays, Bahamas: uncommonly common. *Facies* 33:1–18. doi:[10.1007/BF02537442](https://doi.org/10.1007/BF02537442)
- Reyes-Prieto A, Yoon HS, Moustafa A, Yang EC, Andersen RA, Boo SM, Nakayama T, Ishida K, Bhattacharya D (2010) Differential gene retention in plastids of common recent origin. *Mol Biol Evol* 27:1530–1537. doi:[10.1093/molbev/msq032](https://doi.org/10.1093/molbev/msq032)
- Reynolds CS, Oliver RL, Walsby AE (1987) Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. *N.Z. J Mar Freshw Res* 21:379–390
- Riding R (2006) Microbial carbonate abundance compared with fluctuations in metazoan diversity over geological time. *Sediment Geol* 185:229–238. doi:[10.1016/j.sedgeo.2005.12.015](https://doi.org/10.1016/j.sedgeo.2005.12.015)
- Riding R (2011) Microbialites, stromatolites, and thrombolites. In: Reitner J, Thiel V (eds) *Encyclopedia of geobiology, encyclopedia of earth science series*. Springer, Heidelberg, pp 635–654. doi:[10.1007/978-1-4020-9212-1_196](https://doi.org/10.1007/978-1-4020-9212-1_196)
- Rindi F (2007) Diversity, distribution and ecology of green algae and cyanobacteria in urban habitats. In: Seckbach J (ed) *Algae and cyanobacteria in extreme environments*. Springer, Dordrecht, pp 619–638. doi:[10.1007/978-1-4020-6112-7_34](https://doi.org/10.1007/978-1-4020-6112-7_34)
- Rippka R, Deruelles J, Waterbury JB, Herdman M, Stanier RY (1979) Generic assignments, strain histories and properties of pure cultures of cyanobacteria. *J Gen Microbiol* 111:1–61. doi:[10.1099/00221287-111-1-1](https://doi.org/10.1099/00221287-111-1-1)
- Rossi F, Micheletti E, Bruno L, Adhikary SP, Albertano P, De Philippis R (2012) Characteristics and role of the exocellular polysaccharides produced by five cyanobacteria isolated from phototrophic biofilms growing on stone monuments. *Biofouling* 28:215–224. doi:[10.1080/08927014.2012.663751](https://doi.org/10.1080/08927014.2012.663751)
- Sagan L (1967) On the origin of mitosing cells. *J Theor Biol* 14:255–274
- Sánchez-Baracaldo P, Hayes PK, Blank CE (2005) Morphological and habitat evolution in the cyanobacteria using a compartmentalization approach. *Geobiology* 3:145–165. doi:[10.1111/j.1472-4669.2005.00050.x](https://doi.org/10.1111/j.1472-4669.2005.00050.x)
- Sandh G, Xu L, Bergman B (2012) Diazocyte development in the marine diazotrophic cyanobacterium *Trichodesmium*. *Microbiology* 158:345–352. doi:[10.1099/mic.0.051268-0](https://doi.org/10.1099/mic.0.051268-0)
- Schimper AFW (1883) Über die Entwicklung der Chlorophyllkörner und Farbkörper. *Bot. Zeitung*. 41:105–114, 121–131, 137–146, 153–162
- Schopf JW, Farmer JD, Foster IS, Kudryavtsev AB, Gallardo VA, Espinoza C (2012) Gypsum-permineralized microfossils and their relevance to the search for life on Mars. *Astrobiology* 12:619–633. doi:[10.1089/ast.2012.0827](https://doi.org/10.1089/ast.2012.0827)
- Sciuto K, Rascio N, Andreoli C, Moro I (2011) Polyphasic characterization of ITD-01, a cyanobacterium isolated from the Ischia Thermal District (Naples, Italy). *Fottea* 11:31–39
- Sciuto K, Andreoli C, Rascio N, La Rocca N, Moro I (2012) Polyphasic approach and typification of selected *Phormidium* strains (cyanobacteria). *Cladistics* 28:357–374. doi:[10.1111/j.1096-0031.2011.00386.x](https://doi.org/10.1111/j.1096-0031.2011.00386.x)
- Sciuto K, Wolf MA, Schiavon M, Moro I (2013) Barcoding PATHS: a new database for plant and algal type and historical specimens. *Taxon* 62:647–648. doi:[10.12705/623.32](https://doi.org/10.12705/623.32)
- Sellner KG (1997) Physiology, ecology, and toxic properties of marine cyanobacteria blooms. *Limnol Oceanogr* 42:1089–1104. doi:[10.1016/j.ecss.2006.05.022](https://doi.org/10.1016/j.ecss.2006.05.022)
- Sellner KG, Doucette GJ, Kirkpatrick GJ (2003) Harmful algal blooms: causes, impacts and detection. *J Ind Microbiol Biotechnol* 3:383–406. doi:[10.1007/s10295-003-0074-9](https://doi.org/10.1007/s10295-003-0074-9)
- Seo P, Yokota A (2003) The phylogenetic relationships of cyanobacteria inferred from 16S rRNA, *gyrB*, *rpoC1* and *rpoD1* gene sequences. *J Gen Appl Microbiol* 49:191–203

- Sessions AL, Doughty DM, Welander PV, Summons RE, Newman DK (2009) The continuing puzzle of the great oxidation event. *Curr Biol* 19:R567–R574. doi:[10.1016/j.cub.2009.05.054](https://doi.org/10.1016/j.cub.2009.05.054)
- Sharma NK, Tiwari SP, Tripathi K, Rai AK (2011) Sustainability and cyanobacteria (blue-green algae): facts and challenges. *J Appl Phycol* 23:1059–1081. doi:[10.1007/s10811-010-9626-3](https://doi.org/10.1007/s10811-010-9626-3)
- Shen X, Lam PKS, Shaw GR, Wickramasinghe W (2002) Genotoxicity investigation of a cyanobacterial toxin, cylindrospermopsin. *Toxicol* 40:1499–1501. doi:[10.1016/S0041-0101\(02\)00151-4](https://doi.org/10.1016/S0041-0101(02)00151-4)
- Sherman DM, Troyan TA, Sherman LA (1994) Localisation of membrane proteins in the cyanobacterium *Synechococcus* sp. PCC 7942. Radial asymmetry in the photosynthetic complexes. *Plant Physiol* 106:251–262. doi:[10.1104/pp.106.1.251](https://doi.org/10.1104/pp.106.1.251)
- Shih PM, Wu D, Latifi A, Axen SD, Fewer DP, Talla E, Calteau A, Cai F, Tandeau de Marsac N, Rippka R, Herdman M, Sivonen K, Coursin T, Laurent T, Goodwin L, Nolan M, Davenport KW, Han CS, Rubin EM, Eisen JA, Woyke T, Gugger M, Kerfeld CA (2013) Improving the coverage of the cyanobacterial phylum using diversity-driven genome sequencing. *Proc Natl Acad Sci USA* 110:1053–1058. doi:[10.1073/pnas.1217107110](https://doi.org/10.1073/pnas.1217107110)
- Singh S, Kate BN, Banerjee UC (2005) Bioactive compounds from cyanobacteria and microalgae: an overview. *Crit Rev Biotechnol* 25:73–95. doi:[10.1080/07388550500248498](https://doi.org/10.1080/07388550500248498)
- Skulberg MO, Codd GA, Carmichael WW (1984) Toxic blue-green algae in Portuguese freshwaters. *Arch Hydrobiol* 130:439–451
- Smith AM, Andrews JE, Uken R, Thackeray Z, Perissinotto R, Leuci R, Marca-Bell A (2011) Rock pool tufa stromatolites on a modern South African wave-cut platform: partial analogues for Archaean stromatolites? *Terra Nova* 23:375–381. doi:[10.1111/j.1365-3121.2011.01022.x](https://doi.org/10.1111/j.1365-3121.2011.01022.x)
- Song JY, Cho HS, Cho JI, Jeon JS, Lagarias JC, Park YI (2011) Near-UV cyanobacteriochrome signaling system elicits negative phototaxis in the cyanobacterium *Synechocystis* sp. PCC 6803. *Proc Natl Acad Sci USA* 108:10780–10785. doi:[10.1073/pnas.1104242108](https://doi.org/10.1073/pnas.1104242108)
- Soo RM, Skennerton CT, Sekiguchi Y et al (2014) An expanded genomic representation of the phylum cyanobacteria. *Genome Biol Evol* 6:1031–1045. doi:[10.1093/gbe/evu073](https://doi.org/10.1093/gbe/evu073)
- Soule T, García-Pichel F (2014) Ultraviolet photoprotective compounds from cyanobacteria in biomedical applications. In: Sharma NK, Rai AK, Stal LJ (eds) *Cyanobacteria: an economic perspective*. Wiley, Chichester, pp 119–144. doi:[10.1002/9781118402238.ch8](https://doi.org/10.1002/9781118402238.ch8)
- Stackebrandt E, Goebel BM (1994) Taxonomic note: a place for DNA-DNA reassociation and 16S rRNA sequence analysis in the present species definition in bacteriology. *Int J Syst Bacteriol* 44:846–849. doi:[10.1099/00207713-44-4-846](https://doi.org/10.1099/00207713-44-4-846)
- Stal LJ (1995) Physiological ecology of cyanobacteria in microbial mats and other communities. *New Phytol* 131:1–32. doi:[10.1111/j.1469-8137.1995.tb03051.x](https://doi.org/10.1111/j.1469-8137.1995.tb03051.x)
- Stanier RY, Cohen-Bazire G (1977) Phototrophic prokaryotes: the cyanobacteria. *Annu Rev Microbiol* 31:225–274
- Stanier RY, Sistrom WR, Hansen TA et al (1978) 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 Bacteriol* 28:35–36. doi:[10.1099/00207713-28-2-335](https://doi.org/10.1099/00207713-28-2-335)
- Steindler L, Huchon D, Avni A, Ilan M (2005) 16S rRNA phylogeny of sponge-associated cyanobacteria. *Appl Environ Microbiol* 71:4127–4131. doi:[10.1128/AEM.71.7.4127-4131.2005](https://doi.org/10.1128/AEM.71.7.4127-4131.2005)
- Straubinger-Gansberger N, Gruber M, Kaggwa MN, Lawton L, Omondi Oduor S, Schagerl M (2014) Sudden flamingo deaths in Kenyan Rift Valley lakes. *Wildl Biol* 20:185–189. doi:[10.2981/wlb.00018](https://doi.org/10.2981/wlb.00018)
- Tamaru Y, Takani Y, Yoshida T, Sakamoto T (2005) Crucial role of extracellular polysaccharides in desiccation and freezing tolerance in the terrestrial cyanobacterium *Nostoc commune*. *Appl Environ Microbiol* 71:7327–7333. doi:[10.1128/AEM.71.11.7327-7333.2005](https://doi.org/10.1128/AEM.71.11.7327-7333.2005)
- Teneva I, Dzhabazov B, Mladenov R, Schirmer K (2005) Molecular and phylogenetic characterization of *Phormidium* species (Cyanoprokaryota) using the *cpcB*-IGS-*cpcA* locus. *J Phycol* 41:188–194. doi:[10.1111/j.1529-8817.2005.04054.x](https://doi.org/10.1111/j.1529-8817.2005.04054.x)
- Thompson PA, Jameson I, Blackburn SI (2009) The influence of light quality on akinete formation and germination in the toxic cyanobacterium *Anabaena circinalis*. *Harmful Algae* 8:504–512. doi:[10.1016/j.hal.2008.10.004](https://doi.org/10.1016/j.hal.2008.10.004)
- Thompson AW, Foster RA, Krupke A, Carter BJ, Musat N, Vault D, Kuypers MMM, Zehr JP (2012) Unicellular cyanobacterium symbiotic with a single-celled eukaryotic alga. *Science* 337:1546–1550. doi:[10.1126/science.1222700](https://doi.org/10.1126/science.1222700)
- Tomitani A, Knoll AH, Cavanaugh CM, Ohno T (2006) The evolutionary diversification of cyanobacteria: molecular-phylogenetic and paleontological perspectives. *Proc Natl Acad Sci USA* 103:5442–5447. doi:[10.1073/pnas.0600999103](https://doi.org/10.1073/pnas.0600999103)
- van den Hoek C, Mann D, Jahns HM (1995) *Algae: an introduction to phycology*. Cambridge University Press, United Kingdom

- Voloshko L, Kopecky J, Safronova T, Pljusich A, Titova N, Hrouzek P, Drabkova V (2008) Toxins and other bioactive compounds produced by cyanobacteria in Lake Ladoga. *Est J Ecol* 57:100–110. doi:[10.3176/eco.2008.2.02](https://doi.org/10.3176/eco.2008.2.02)
- Walsby AE (1994) Gas vesicles. *Microbiol Rev* 58:94–144
- Whitton BA (2012) Ecology of cyanobacteria II: their diversity in space and time. Springer, Dordrecht
- Wiethaus J, Busch AWU, Dammeyer T, Frankenberg-Dinkel N (2010) Phycobiliproteins in *Prochlorococcus marinus*: biosynthesis of pigments and their assembly into proteins. *Eur. J Cell Biol* 89:1005–1010. doi:[10.1016/j.ejcb.2010.06.017](https://doi.org/10.1016/j.ejcb.2010.06.017)
- Wilmotte A (1994) Molecular evolution and taxonomy of the cyanobacteria. In: Bryant DA (ed) The molecular biology of cyanobacteria. Kluwer Academic Publishers, Dordrecht, pp 1–25
- Wilmotte A, Herdmann M (2001) Phylogenetic relationships among cyanobacteria based on 16S rRNA sequences. In: Boone DR, Castenholz RW (eds) *Bergey's manual of systematic bacteriology*, vol 1. Springer, New York, pp 487–493
- Withers NW, Alberte RS, Lewin RA, Thornber JP, Britton G, Goodwin TW (1978) Photosynthetic unit size, carotenoids, and chlorophyll-protein composition of *Prochloron* sp., a prokaryotic green alga. *Proc Natl Acad Sci USA* 75:2301–2305
- Woese CR (1987) Bacterial evolution. *Microbiol Rev* 51:221–271
- Woese CR, Kandler O, Wheelis ML (1970) Towards a natural system of organisms: proposal for the domains archaea, bacteria, and eukarya. *Proc Natl Acad Sci USA* 87:4576–4579
- Wolgemuth CW, Oster G (2004) The junctional pore complex and the propulsion of bacterial cells. *J Mol Microbiol Biotechnol* 7:72–77. doi:[10.1159/000077871](https://doi.org/10.1159/000077871)
- Wolk CP (1973) Physiology and cytological chemistry of blue-green algae. *Bact Rev* 37:32–101
- Zanchett G, Oliveira-Filho EC (2013) Cyanobacteria and cyanotoxins: from impacts on aquatic ecosystems and human health to anticarcinogenic effects. *Toxins* 5:1896–1917. doi:[10.3390/toxins5101896](https://doi.org/10.3390/toxins5101896)
- Žegura B, Štraser A, Filipič M (2011) Genotoxicity and potential carcinogenicity of cyanobacterial toxins—a review. *Mutat Res* 727:16–41. doi:[10.1016/j.mrrev.2011.01.002](https://doi.org/10.1016/j.mrrev.2011.01.002)
- Zimmer C (2013) Earth's oxygen: a mystery easy to take for granted. *New York Times*. <http://www.nytimes.com/2013/10/03/science/earths-oxygen-a-mystery-easy-to-take-for-granted.html>. Accessed 23 July 2014