Chapter 1

Cyanobacteria: biology, ecology and evolution

Aharon Oren

Department of Plant and Environmental Sciences, The Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel

1.1 Introduction

The first time I observed a prokaryotic microorganism through the microscope was during my first semester as a biology student in Groningen, the Netherlands, in the end of 1969. During the introductory botany course a young faculty member named Wytze Stam showed me filaments of *Anabaena* with many heterocysts, hidden within the leaf cavities of the water fern *Azolla* (see Adams, Duggan and Jackson, 2012 for more information). Later Wytze Stam became a pioneer of molecular systematics studies of cyanobacteria (then called "blue–green algae"), being the first to apply the technique of DNA–DNA hybridization to elucidate taxonomic relationships between different species (Stam and Venema, 1977).

I consider it a special privilege to have been invited to write the introductory chapter to *Cyanobacteria – an Economic Perspective*, considering the fact that I have never worked on economic and biotechnological aspects of cyanobacteria, and that during most of my career my studies concentrated on entirely different types of prokaryotes: anoxygenic phototrophic purple sulfur bacteria during my M.Sc. studies and, later, different groups of halophilic Archaea and Bacteria. Still, the cyanobacteria kept fascinating me, and during several periods of my life I have studied different aspects of this important group of prokaryotes. My Ph.D. studies in Jerusalem centered on the ability of certain cyanobacteria, and in particular a filamentous strain from Solar Lake, Sinai, designated *Oscillatoria limnetica*, to perform not only oxygenic photosynthesis, but also anoxygenic photosynthesis with sulfide as an electron donor, enabling the organisms to lead an anaerobic life (Garlick, Oren, and Padan, 1977; Oren, Padan, and Avron, 1977; Oren and Padan, 1978). The finding that some cyanobacteria also have well-developed modes of survival in the dark under anaerobic conditions, including fermentation and anaerobic respiration with elemental sulfur as electron acceptor (Oren and Shilo, 1979), showed how

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well certain members of the group are adapted to an anaerobic lifestyle.

During my later studies of microbial life at high salt concentrations and the adaptations of microorganisms to hypersaline conditions I developed an interest in solar saltern ponds for the production of salt. Along the salinity gradient in the evaporation ponds beautiful benthic microbial mats often develop, dominated by cyanobacteria. One of the most spectacular displays of cyanobacteria I know is within the crusts of gypsum that accumulate on the bottom of saltern ponds with salinities between 150 and 200 g/l: an upper orange-brown layer of *Aphanothece*-type unicellular species, then a bright dark-green layer of *Phormidium*-type filaments, below which a red layer of photosynthetic purple bacteria is found. This intriguing and very esthetical system became not only one of my favorite objects for research (e.g., Oren, Kühl, and Karsten, 1995; Oren *et al*., 2008, 2009), but also a tool for teaching students about the nature of stratified systems and the influence of different physical and chemical gradients on microbial communities. A brief opportunity to study the microbiology of the hot springs (up to 63°C) on the eastern shore of the Dead Sea in Jordan extended my work on extremophilic cyanobacteria to the thermophiles as well (Ionescu *et al*., 2009, 2010).

In recent years I became involved in an entirely different aspect of the cyanobacteria: problems connected with the systematics and in particular with the nomenclature of the group. In the course of my activity within the International Committee on Systematics of Prokaryotes I realized that the cyanobacteria are a highly problematic group as far as nomenclature is concerned. On the one hand they were traditionally considered to be plants and their nomenclature was therefore regulated by the provisions of the International Code of Botanical Nomenclature (since 2012: the International Code of Nomenclature for algae, fungi, and plants); on the other hand, they belong to the prokaryotic world and as such their nomenclature may be regulated by the International Code of Nomenclature of Prokaryotes (The Bacteriological Code) (Oren, 2004, 2011; Oren and Tindall, 2005). This led to interesting discussions with the cyanobacterial taxonomists (Oren and Komárek, 2010; Oren, Komárek and Hoffmann, 2009). No quick solution of the many remaining nomenclature problems can be expected in the near future.

Thinking about the invitation by the editors of this book to write a chapter entitled "Cyanobacteria – biology, ecology and evolution," it is clear that such an introductory chapter can never cover all aspects. I therefore chose to briefly highlight a number of the topics related to the life of the cyanobacteria that fascinate me most.

- Cyanobacteria have been around on our planet for a very long time and they were the first organisms to form molecular oxygen and to change the biosphere from anaerobic to largely aerobic.
- Cyanobacteria are a morphologically diverse group, more diverse than any other group of prokaryotes, and some show unique patterns of cell differentiation.
- Many cyanobacteria have a global distribution, and they are excellent model organisms to investigate questions of microbial biogeography and evolution.
- Cyanobacteria are major contributors to the primary production of the oceans, and they are one of the most important groups that fix molecular nitrogen.
- Cyanobacteria are highly efficient in adapting to their environment; many can actively move toward more favorable areas; they adapt their pigmentation according to the intensity and sometimes also to the color of the available light; some show surprising adaptation toward a life under anaerobic conditions; many types thrive at extremes of temperature, salinity, and pH; and when growth conditions are not suitable, some species can survive adverse conditions for long periods.
- Most types of cyanobacteria are relatively easy to grow in the laboratory, and many have been obtained and studied in axenic culture.

Because of my interest in the history of microbiology, I refer throughout the chapter to the historical aspects of the research, trying to show how different concepts and ideas have developed through time.

1.2 Cyanobacteria are ancient microorganisms

The Precambrian has been termed "the age of blue–green algae" (Schopf, 1974), and Schopf and Walter (1982) called the Proterozoic era – the period between

2.5 and 0.54 billion years (Ga) ago when the atmosphere turned from anoxic to oxygenated as a result of oxygenic photosynthesis – "the age of cyanobacteria."

Although there is still considerable controversy about the exact time the cyanobacteria started to appear on Earth, there is be no doubt that they are extremely ancient organisms. There is evidence that oxygenic photosynthesis occurred even in the Archean era (Knoll, 1979; Olson, 2006), possibly even >3.7 Ga ago (Rosing and Frei, 2004). The Precambrian sedimentary record abounds with microfossils that resemble different types of present-day cyanobacteria, and it is generally assumed that the cyanobacteria originated well before 2.5 Ga ago (Schopf, 1970, 1993, 2012; Schopf and Barghoorn, 1967; Schopf and Packer, 1987). Four key rock sequences are known that have survived without major changes in the metamorphosed state from the first billion years (3.8–2.8 Ga) of Archean Earth history:

- the Warrawoona and George Creek Groups of Western Australia, ~3.5 Ga old
- the Onverwacht and associated groups of southern Africa, ~3.5 Ga old
- the Pongola Supergroup of Natal, ~3.1 Ga old
- the Fortescue Group of Western Australia, ~2.8 Ga old (Schopf and Walter, 1982).

The oldest reliable microfossils are those from the Apex chert of northwestern Western Australia and the Fig Tree series of South Africa (3.1 Ga). Some of these, which may or may not have been cyanobacteria, have been referred to as alga-like (Pflug, 1967; Schopf and Barghoorn, 1967; Pflug *et al.*, 1969; Schopf, 1993). But one cannot be certain that such "alga-like" unicellular structures were indeed cyanobacteria.

Much has been written about the nature of the Precambrian stromatolites – layered rocks that resemble the properties of modern stratified microbial mat communities of cyanobacteria – and, since their discovery in the 1960s, the microfossils found in them (Barghoorn and Tyler, 1965; Cloud, 1965; Buick, 1992; Grotzinger and Knoll, 1999). There seems to be little doubt about the cyanobacterial nature of microfossils present in stromatolites of the Transvaal sequence (2.25 Ga) (MacGregor, Truswell, and Eriksson, 1974; Nagy, 1974), and biomarkers possibly derived from cyanobacteria (methylhopanoids – derivatives of 2-methylbacteriohopanepolyols – which occur in many modern species) have been found in organic-rich sediments as old as 2.5 Ga (Summons *et al.*, 1999). Altermann (2007) provided a critical discussion of the different reported claims for the finding of more ancient, 3.8–2.5 Ga-old fossils of cyanobacteria.

The modern stromatolites discovered in the late 1950s in Shark Bay, a slightly hypersaline marine lagoon in Western Australia (Logan, 1961), are often considered as equivalents of the fossil stromatolites that have remained from the Precambrian. These stromatolites have been studied in depth (Bauld, 1984; Stal, 1995, 2012), but it still cannot be ascertained to what extent the communities in Shark Bay indeed resemble the kind of structures built at the time oxygenic phototrophs first colonized the planet and started to release oxygen to the atmosphere.

1.3 Cyanobacteria are morphologically diverse

Cyanobacteria can be defined to include all known prokaryotes capable of oxygenic photosynthesis. Phylogenetically (as based on the small-subunit ribosomal RNA-based tree of life) they are a coherent group within the domain Bacteria (Bonen, Doolittle, and Fox, 1979; Wilmotte, 1994; Wilmotte and Herdman, 2001). The cyanobacterial lineage also includes the chloroplasts of the eukaryotic cells and plants (Giovannoni *et al.*, 1988).

Descriptions of cyanobacteria started appearing in the botanical literature from the end of the 18th century onwards. In the early times the group was generally referred to as "Schyzophytae," the name "Cyanophyceae" was introduced by Sachs in 1874 and "Cyanophyta" by Smith in 1938. The earliest described genus is probably *Rivularia* (Roth, 1797–1806); *Oscillatoria* and *Nostoc* were published in 1803 by Vaucher, who curiously placed these organisms in the animal kingdom (Fogg *et al.*, 1973). Many species of cyanobacteria were described in the monographs on algae by Lyngbye (1819), Agardh (1824), and Kützing (1845–1849), the first and third of which are beautifully illustrated. These and other 19th century books were the precursors of more recent morphology-based taxonomic treatises on the Cyanophyceae/Cyanophyta

by Geitler (1932) and Desikachary (1959). Morphologically the group is much more diverse than any other group within the prokaryotes, Bacteria and Archaea combined, so that taxonomic schemes are still largely based on morphological characters. However, molecular sequence information is becoming increasingly important in the classification of the cyanobacteria (Wilmotte, 1994; Wilmotte and Herdman, 2001).

The affiliation of the "blue–green algae" with the bacteria rather than with other groups of algae was realized by Ferdinand Cohn already in the second half of the 19th century (Cohn, 1872, 1875, 1897):

> Perhaps the designation of Schyzophytae may recommend itself for this first and simplest division of living organisms, which appears to me naturally delimited from the higher plants, even although its distinguishing characters are negative rather than positive.
> (Cohn, 1875; translation R.Y. Stanier)

After the fundamental division of the living organisms into prokaryotes and eukaryotes had become firmly established in the middle of the 20th century, it was time to re-evaluate the position of the "blue–green algae." In their classic essay entitled 'The concept of a bacterium', Stanier and van Niel (1962) made the following important statement (original emphasis):

> It is now clear that among organisms there are two different organizational patterns. . . the eucaryotic and the procaryotic type. *The distinctive property of bacteria and blue-green algae is the procaryotic nature of their cells*. It is on this basis that they can be clearly segregated from all other protists (namely, all other algae protozoa and fungi), which have eucaryotic cells. (Stanier and van Niel 1962. Reproduced with kind permission from Springer Science + Business Media.)

When, based on the new insights into the nature of the "blue–green algae," Roger Stanier and his colleagues a few years later formally proposed placing the nomenclature of the group under the rules of the International Code of Nomenclature of Bacteria (Stanier *et al.*, 1978), heated discussions started between the bacteriologists and the botanists on the issue of the nomenclatural system under which the group should be treated. Meeting sessions and even entire symposia were devoted to the question (Friedmann and Borowitzka, 1982; Castenholz, 1992; Oren, Komárek, and Hoffmann, 2009; Oren and Komárek, 2010). As explained above, the issue is still largely unresolved.

A recent attempt to classify the cyanobacteria primarily on the basis of morphological traits while incorporating as much "polyphasic" information as possible by including other characteristics was made by the editors and authors of the last edition of *Bergey's Manual of Systematic Bacteriology*, as outlined by Castenholz (2001). In this system, the unicellular types are grouped in Subsections I and II. Cyanobacteria in Subsection I divide by binary fission while those in Subsection II can also undergo multiple divisions. The purple-colored unicellular *Gloeobacter violaceus*, an organism that is unique as it is the only cyanobacterium known that lacks thylakoids (Rippka, Waterbury, and Cohen-Bazire, 1974) roots phylogenetically deeply with Subsection I. Cyanobacteria belonging to Subsection II can form a large number of very small daughter cells named baeocytes, which subsequently grow out to normal-sized cells. Some members of the *Pleurocapsales* (Subsection II) such as *Dermocarpa* and *Hyella* can reach very large cell sizes (up to 30 μm and more), particularly when they are about to divide multiple times to produce baeocytes. The filamentous cyanobacteria are grouped in Subsections III, IV, and V. Subsection III consists of filaments composed of one cell type (the *Oscillatoriales*). Subsections IV and V comprise filamentous cyanobacteria that exhibit cell differentiation, a rare phenomenon among prokaryotes. All representatives belonging to Subsections IV and V are capable of fixing nitrogen. Subsection V is characterized by true branching of trichomes, resulting from the division of cells in more than one plane, forming what may be the most advanced type of morphological structure attained in the prokaryote world.

1.4 Cyanobacteria as model organisms for microbial biogeography studies

Many species of cyanobacteria have a cosmopolitan distribution. An excellent example is the terrestrial *Nostoc commune*, found in both temperate, tropical, and polar regions, on the continents as well as on isolated islands. Some of these cosmopolitan types have become popular objects to test theories about

biogeography and microevolution. The famous statement by Lourens Baas Becking (1934) – "*Alles is overal*: maar *het milieu selecteert*" ("Everything is everywhere: *but*, the environment selects") – has been the starting point for several comparative studies of cyanobacterial populations in similar habitats worldwide. One of those species is the halophilic filamentous organism previously known as *Microcoleus chthonoplastes* and recently renamed *Coleofasciculus chthonoplastes* (Siegesmund *et al*., 2008). An in-depth comparative phenotypic and phylogenetic analysis of material collected from disparate geographical locations only showed very slight differences, if at all (Garcia-Pichel, Prufert-Bebout, and Muyzer, 1996). A similar global dispersal without clear differences between geographically separated populations, as based on sequence comparisons of the ITS (internal transcribed spacer) region between the 16S and the 23S rRNA genes, was observed for the freshwater planktonic *Microcystis aeruginosa* (Van Gremberghe *et al*., 2011). Metagenomic studies showed a remarkably low genomic diversity, with <1% nucleotide divergence in several genes, among geographically widely distributed populations and isolated strains of the marine unicellular nitrogen-fixing *Crocosphaera watsonii* (Zehr *et al*., 2007).

Of special interest as a model for the study of the geographical distribution and evolutionary processes on a local scale are the cyanobacterial communities in hot springs. Distances separating thermal spring areas can be thousands of kilometers, and there are no obvious mechanisms to explain how thermophilic cyanobacteria may migrate between such areas. Yet, surprisingly similar types, unicellular as well as filamentous, are found in springs of similar temperatures and water chemistry worldwide, although thermophilic *Synechococcus* types are absent from the hot springs of Iceland, Alaska, and the Azores (Papke *et al*., 2003). Based on the analysis of 16S and 23S rRNA and ITS sequences, small geographical differences were found that could not be attributed to differences in the chemical properties of the spring waters. Genetic drift caused by geographical isolation was therefore postulated to be in part responsible for the observed evolutionary divergences (Papke *et al*., 2003). More recent genetic analyses of the cyanobacterial communities in hot springs near the eastern shore of the Dead Sea in Jordan have extended these observations of global general similarities combined with minor local differences (Ionescu *et al*., 2010).

1.5 Cyanobacteria are major contributors to the primary production in the oceans

In their monograph on *The Blue–Green Algae*, published in 1973, Fogg *et al*. wrote: ". . . except for *Trichodesmium*, which often forms massive blooms in tropical seas, blue–green algae are generally absent from the open sea. Why this should be so is difficult to explain at present." Thus at the time it was still generally assumed that oxygenic prokaryotes contribute very little to the productivity of the oceans on a global scale.

Today it is clear that a significant part of the carbon dioxide fixation in the oceans can be attributed to the activity of unicellular cyanobacteria, mostly organisms belonging to novel types discovered only in the past few decades. Some of these differ in pigmentation from the classic cyanobacterial pattern, which is characterized by chlorophyll *a* and phycobiliproteins as the main photosynthetic pigments. The first indications of the importance of small unicellular cyanobacteria in the plankton of the oceans came from electron microscopic studies by Sieburth and coworkers in the late 1970s (Johnson and Sieburth, 1979 and references therein) and from the observation of numerous orange-autofluorescent cells of phycoerythrin-rich cyanobacteria of the genus *Synechococcus* in the North Atlantic by Waterbury *et al*. (1979). *Synechococcus* is now known as a major contributor to the oceanic primary production (Scanlan, 2012). This type of *Synechococcus* has been isolated (Waterbury *et al*., 1979). Some strains display an unusual type of swimming motility, the mechanism of which is still unclear (Waterbury *et al*., 1985). The finding of *Prochlorococcus*, another member of the oxygenic picoplankton, containing divinyl chlorophyll *a* and *b* and lacking phycobilisomes (Chisholm *et al*., 1988, 1992; Partensky, Hess, and Vaulot, 1999; Post, 2006; Scanlan and West, 2002) showed that the cyanobacteria may contribute even more to global carbon dioxide

fixation. More recently we learned about the existence of the chlorophyll *d*-containing *Acaryochloris* and the nitrogen-fixing *Crocosphaera watsonii*, all organisms widely distributed in the world's oceans (Waterbury, Watson, and Valois, 1988; Zehr *et al.*, 2007). These discoveries have changed our conceptions of oceanic primary production (Paerl, 2012). Carr (1999) nicely summarized this when he wrote:

> The discovery about twenty years ago that a significant proportion of the primary production of the open oceans was driven by hitherto unrecognized unicellular cyanobacteria was of great moment to biological oceanography and extended the global role of these organisms by a vast scale.

The discovery of *Prochlorococcus* as a member of the cyanobacteria that contains a derivative of chlorophyll *b* was preceded by the recognition of other "Prochlorophyta" in aquatic environments. The first was *Prochloron*, a yet uncultured symbiont of marine ascidians (Lewin, 1975, 1977; Lewin and Withers, 1975). A decade later came the publication of the discovery of *Prochlorothrix hollandica*, a filamentous oxygenic photoautotrophic prokaryote containing chlorophyll *a* and *b*, from a freshwater lake in the Netherlands (Burger-Wiersma *et al.*, 1986; Burger-Wiersma, Stal, and Mur, 1989). When then the unicellular *Prochlorococcus* was found as a major component of the picoplankton in the photic zone of the oceans (Chisholm *et al.*, 1988; Partensky, Hess, and Vaulot, 1999), it became clear that such cyanobacteria with unusual types of chlorophyll are widespread. At one point it was proposed that the "Prochlorophyta" should be separated from the cyanobacteria as a separate phylum, but this is not justified on the basis of molecular phylogenetic, 16S rRNA-based studies: *Prochloron*, *Prochlorothrix*, and *Prochlorococcus* are three independent lineages of cyanobacteria. *Prochlorococcus* has unique divinyl-chlorophyll *a* and divinyl-chlorophyll *b* photopigments and only minor amounts of phycobiliprotein pigments. *Prochlorothrix* and *Prochloron* are the only prokaryotes known to possess chlorophyll *b* (Kühl, Chen, and Larkum, 2007).

The unicellular chlorophyll *d*-containing *Acaryochloris* was discovered during an attempt to isolate *Prochloron* from didemnid ascidians (Miyashita *et al.*, 1996, 1997, 2003). The long-wavelength absorption peak of chlorophyll *d* is shifted to the red by about 30 nm as compared to chlorophyll *a*, showing an *in vivo* absorption peak at 710–720 nm. *Acaryochloris* does not contain phycobilisomes, but some phycocyanin and allophycocyanin may be present to function in light harvesting. Phylogenetically it does not show a close relationship to any of the other subgroups of unicellular cyanobacteria. In the ascidians it does not grow as a symbiont within the animal but rather forms dense cell patches in biofilms growing below the ascidian. It was also found as small epiphytic patches on a red macroalga. *Acaryochloris* is highly light-adapted and does not suffer from photoinhibition at high irradiance levels (Partensky and Garczarek, 2003; Kühl *et al.*, 2005; Kühl, Chen, and Larkum, 2007). Another chlorophyll *d*-producing cyanobacterium related to *Acaryochloris* was isolated from the hypersaline Salton Sea of California, and was shown to harbor an unusual hybrid proteobacterial/cyanobacterial small-subunit rRNA gene (Miller *et al.*, 2005).

1.6 Cyanobacterial nitrogen fixation – different strategies

Cyanobacteria are of great importance in the global nitrogen cycle as one of the major groups of prokaryotes capable of fixing gaseous nitrogen. The process is performed by many different types, unicellular as well as filamentous, with and without heterocysts (Stewart, 1980). Although the connection between cyanobacteria and biological nitrogen fixation was suspected for a long time, the first real proof that nitrogen is fixed was published only in 1969 for a unicellular representative (*Gloeocapsa* sp.) (Wyatt and Silvey, 1969). The presence of nitrogenase in heterocysts was documented in the same year (Stewart, Haystead, and Pearson, 1969).

Nitrogenase, the enzyme complex responsible for the reduction of nitrogen to ammonium ions, is irreversibly inactivated by molecular oxygen, the product of oxygenic photosynthesis. Therefore the two processes are basically incompatible. Various strategies have evolved in different groups of cyanobacteria to overcome this problem. One is based on spatial separation of the nitrogen-fixation process and oxygenic

photosynthesis; a second strategy is temporal separation: oxygen production during daytime and nitrogen fixation at night; it was recently discovered that some unicellular marine cyanobacteria may be altogether unable to evolve oxygen, and thus can maintain an active nitrogenase system. Even today the diverse mechanisms used by different types of cyanobacteria to combine nitrogen fixation with an aerobic mode of life are not completely clear.

The function of heterocysts, empty-looking thick-walled cells within filaments of pigmented cells, has for a long time baffled scientists, who called these structures "botanical enigmas" (Fritsch, 1951). In 1968 the role of the heterocyst as the site of nitrogen fixation could still be questioned (Fay *et al.*, 1968): up to that time some workers considered the heterocysts as some kind of spores, dormant cells that allegedly were able to germinate under suitable conditions (Wolk, 1965). However, by 1853 Ferdinand Cohn had made a clear statement that these special cells cannot develop into new filaments:

> Nach diesen Beobachtungen scheint bei Anabaena, nicht wie bei Nostoc verrucosum nach Thuret, der ganze vielzellige Faden sondern jede einzelne vegetative Zelle, desselben im Stande zu sein, zu einem neuen Fadenhaufen sich zu vermehren, während die Dauerzellen keiner weiteren Entwicklung fähig sind. [According to these observations it is clear that in *Anabaena*, unlike in *Nostoc verrucosum* (Thuret), not the entire multicellular filament, but every single vegetative cell is able to multiply and develop into a new mass of filaments, while the resistant cells are incapable of further development] (Cohn, 1853).

Today we know that nitrogenase is located in the heterocyst, that these cells have lost the capacity of oxygenic photosynthesis and carbon dioxide fixation, but have retained photosystem I to supply the energy required for the nitrogen-fixation process. Respiration and oxidative phosphorylation also occur, so that nitrogen fixation does not strictly depend on light. The thick cell envelope serves as a gas diffusion barrier, providing a certain degree of protection of the nitrogenase against inactivation by oxygen (Haselkorn, 1978; Wolk, 1988). In *Anabaena*, heterocyst differentiation is controlled by a small diffusible peptide (Yoon and Golden, 1998). Heterocysts are found in Subsections IV and V (see the above section on morphological diversity). Heterocystous types are often found in symbiotic associations between cyanobacteria and eukaryotic organisms, based on the nitrogen-fixing ability of the prokaryotic partner. The *Azolla–Anabaena* symbiosis mentioned at the beginning of this chapter is a well-known case. Even more unusual is the intracellular occurrence of *Richelia intracellularis*, short filaments with a large terminal heterocyst, inside large marine pennate diatoms of the genera *Rhizosolenia* and *Hemiaulus*.

Not all nitrogen-fixing cyanobacteria produce specialized differentiated cells to harbor the nitrogenase. Temporal separation of photosynthetic oxygen production and nitrogen fixation is another strategy, used both by filamentous and unicellular species. When grown in media devoid of bound nitrogen under alternating light–dark cycles, an *Oscillatoria* sp. fixes nitrogen in the dark periods (Stal and Krumbein, 1985). A similar phenomenon was documented in the marine unicellular cyanobacterium *Crocosphaera watsonii* (Waterbury, Watson, and Valois, 1988).

Although it had already been observed more than half a century ago that nitrogen fixation in tropical seas is often associated with the presence of the filamentous non-heterocystous cyanobacterium *Trichodesmium* (Dugdale, Menzel, and Ryther, 1961), the properties of this organism are still to a large extent enigmatic: it lacks heterocysts but fixes nitrogen only in the light (Capone and Carpenter, 1982; Capone *et al.*, 1997; Zehr *et al.*, 1999). *Trichodesmium* blooms consist of long filaments that cluster to form aggregates of different morphologies. These aggregates can move great distances through the water column, their buoyancy being regulated by presence of gas vesicles (see below). It was previously hypothesized that the aggregates allowed interior cells to act as "heterocysts" (Carpenter and Price, 1976), but this does not appear to be the case. There are indications that nitrogenase is present in a subset of the cells in the trichome, termed "diazocytes" (Fredriksson and Bergmann, 1997). However, it is uncertain whether such diazocytes are terminally differentiated cells like the heterocysts. More likely, these cells turn temporarily into nitrogen-fixing cells. Therefore this strategy has been considered as a combination of spatial and temporal separation (Berman-Frank *et al.*, 2001). Nitrogen fixation starts at the end of the night and lasts until midday. Thereafter, nitrogenase activity declines and the enzyme is rapidly and irreversibly inactivated in

the dark. The nitrogen-fixing cells are kept anoxic by a high rate of respiration. The relatively low solubility of oxygen in warm seawater may limit the geographic distribution of *Trichodesmium* to oceanic areas with water temperatures above 25°C. Under such conditions heterocysts are not required (Staal, Meysman, and Stal, 2003).

Even more curious is the recent discovery of unicellular cyanobacteria, abundant in tropical and subtropical oceans, that perform nitrogen fixation during the day. Their occurrence was first reported in the subtropical north Pacific Ocean in 2001 (Zehr *et al.*, 2001). These cells lack photosystem II and are thus incapable of oxygenic photosynthesis. Analysis of their genome indicates that they lack the enzymes of the Calvin cycle, the tricarboxylic acid cycle, and the pathways for the biosynthesis of some amino acids. These organisms have not yet been isolated, and they probably depend on some form of organic carbon provided by as yet unidentified other members of the marine ecosystem. Indeed most cyanobacteria are obligate photoautotrophs (Smith, London, and Stanier, 1967), but facultative photoheterotrophy and even chemoheterotrophy has been demonstrated in some species (Rippka, 1972). Thus there are precedents for heterotrophic growth of cyanobacteria, at least in laboratory culture. The interrelationships between this new form of marine life and the other organisms present in the oceanic waters are still entirely unknown (Zehr *et al.*, 2008; Tripp *et al.*, 2010; Bothe, Tripp, and Zehr, 2011).

1.7 Cyanobacteria use different strategies to move to areas where conditions are most favorable

Many cyanobacteria have the ability to move and to position themselves within a water column or within a benthic microbial mat so that conditions of light, nutrients, and other environmental parameters are the best achievable. There are basically two methods to reach this goal: passive movement based on the regulation of the buoyancy of the cells, and active motility at the expense of energy.

The presence of "gas vacuoles" – clusters of gas vesicles – in some cyanobacteria was already known in the 19th century. The first reports probably date from 1895, when three articles documented the buoyancy of different aquatic cyanobacteria and the sensitivity of the gas vesicles to pressurization (Ahlborn, 1895; Klebahn, 1895, Strodtmann, 1895). Gas vesicles are hollow cylinders built of protein subunits. The main protein that composes the vesicles (GvpA) is extremely hydrophobic, so that the inner side of the vesicle wall strongly repels water. A second protein, GvpC, strengthens the structure of the vesicles at the outer side. Gasses diffuse freely through the wall of the vesicles, so that these become filled with a gas mixture that reflects the composition of the gasses dissolved in the surrounding water. The number of gas vesicles per cell can be regulated to increase or decrease the buoyancy of the cells (Walsby, 1981, 1987, 1994). Among the genera whose distribution in aquatic environments is strongly dependent on the gas-vesicle content of the cells one can mention *Microcystis* and *Anabaena*, which often form dense blooms in nutrient-rich lakes, and *Trichodesmium*, mentioned above as one of the main marine nitrogen-fixing organisms. The large number of gas vesicles at the periphery of the *Trichodesmium* cells and the occurrence of the buoyant filaments in large bundles allow the masses of red, phycoerythrin-rich patches of cyanobacteria to float to the sea surface.

Active movement by cyanobacteria is possible as well. Many species display gliding movement: self-propulsion over a solid substrate or along other trichomes. Gliding movements are slow, generally in the order of 1–10 μm/s. Genera noted for their conspicuous movements are *Oscillatoria* and *Spirulina*, gliding being accompanied by the rotation of the trichome along its axis. The direction of movement can be triggered by gradients of environmental parameters, notably the intensity and quality of the light available, but other factors can be important as well, including even the salinity of the medium. Thus, "halotaxis," where cells move in the direction of optimal salt concentrations, was recently identified in the cyanobacterial community in an intertidal hypersaline microbial mat (Kohls *et al.*, 2010).

Gliding movement is strictly dependent on the presence of a solid substratum. Occurrence of flagella, being the most common mode of active movement in the world of prokaryotes, has not yet been documented

for cyanobacteria. Therefore, the discovery of marine unicellular *Synechococcus* cells that actively swim in the water, without the requirement for a solid surface, came as a great surprise (Waterbury *et al.*, 1985). Electron microscopic examination did not reveal the presence of flagella or any other cellular structures connected with locomotion. The mode of swimming motility of these marine planktonic organisms is poorly understood and its function is obscure (Brahamsha, 1996).

1.8 Some cyanobacteria change color as a function of light quality

Cyanobacteria can be many different colors: green, blue–green, brown, purple, red, and even almost black. The color of the cells, and accordingly the range of wavelengths absorbed by the photosynthetic apparatus, depends on the types of pigments present and the amounts and ratios in which these pigments are found. A pigment common to nearly all is the green chlorophyll *a*, which is the pigment of the reaction centers of both photosystem I and photosystem II. Exceptional cases such as *Prochlorococcus* and *Acaryochloris* were discussed earlier. Different types of carotenoids (echinenone, myxoxanthophyll, and others) are commonly present as well. And, with very few exceptions, cyanobacteria have phycobilisomes attached to the thylakoid membranes. The phycobilisome is a macromolecular complex composed of phycobiliproteins, which can constitute up to 40% of the soluble cellular protein. Allophycocyanin (maximum absorbance 650 nm) is found in the core substructure, the part of the phycobilisome that is in direct association with the photosynthetic reaction center. The blue phycocyanin (absorption peak 620 nm), the red phycoerythrin (565 nm) and the comparatively rare phycoerythrocyanin (570 nm) are present in rods that emanate from the core. Two subunit forms (α and β) exist of each of these phycobiliproteins, and these are assembled as heterodimers into higher-order structures; these aggregates are the building blocks of the phycobilisome (Bazire, 1971; Glaser and Cohen- Glaser, 1983; Grossman *et al.*, 1993; Carr, 1999; Stal, 2007).

Certain species, notably strains of *Oscillatoria* and *Phormidium*, change their color as a function of the spectral properties of the light in which they are grown. The phenomenon is known as "complementary chromatic adaptation." It was first observed by Theodor Wilhelm Engelmann in 1883. When the organisms are illuminated with a spectrum of light, they assume, over the course of a day or two, a color complementary to that part of the spectrum in which they are growing. Engelmann therefore suggested that the pigmentation is usually such as to permit the most efficient use of the wavelengths available in the particular habitat in which the cells grow. Complementary chromatic adaptation was studied intensively in the first decades of the 20th century (Engelmann, 1902; Gaidukov, 1902; Boresch, 1922). Today we know that the phenomenon is caused by a change in the ratio in which the different phycobiliproteins are incorporated into the rods of the phycobilisomes. When the cells are exposed to red light, more blue phycocyanin is produced; when illuminated with green light, the red phycoerythrin is preferentially synthesized. The result is the creation of a new form of phycobilisome that is capable of more efficient harvesting of the most prevalent wavelengths of light in the environment (Tandeau de Marsac, 1977, 1983; Wyman and Fay, 1987; Kehoe and Grossmann, 1999).

1.9 A facultative anaerobic lifestyle is common in many cyanobacteria

In essence, the cyanobacteria lead an aerobic life, and, being oxygenic phototrophs, they increase the oxygen concentration of their environment in the light. However, different types, especially species of subsection III morphology, are found in abundance in environments such as layered microbial mats and stratified lakes where they are exposed to anaerobic conditions, either on a temporal basis (anaerobiosis at night, presence of oxygen, and possibly even oxygen supersaturation during daytime) or permanently in habitats such as sulfur springs or the monimolimnion of shallow meromictic lakes. Solar Lake, Sinai, is a prime example of an environment where cyanobacteria are found in oxygen-free conditions for prolonged periods (Cohen,

Padan and Shilo, 1975; Padan, 1979a; Padan and Cohen, 1982). Another intriguing ecosystem where cyanobacteria occur at low oxygen concentrations and in the presence of sulfide is the microbial mat system recently discovered in a sinkhole at a depth of 23 m at the bottom of Lake Huron, Michigan (Voorhies *et al.*, 2012).

The first report on carbon dioxide assimilation by certain cyanobacteria in the presence of sulfide and an apparent absence of molecular oxygen dates from more than 70 years ago (Nakamura, 1938). However, the ability of some species to perform anoxygenic photosynthesis using sulfide instead of water as the electron donor for carbon dioxide photoassimilation and photoautotrophic growth was first unequivocally demonstrated in the 1970s in studies of the biota of Solar Lake (Cohen, Padan, and Shilo, 1975; Garlick, Oren, and Padan, 1977; Oren, Padan and Avron, 1977; Oren and Padan, 1978; Padan, 1979b). In the presence of sulfide, photosystem II and its water-splitting system does not function, and electrons are fed from sulfide directly to the donor site of photosystem I. This type of anoxygenic photosynthesis may be active in cyanobacteria in stratified microbial mats that are often exposed in the morning hours to high concentrations of sulfide as a result of bacterial sulfate reduction during the night. Later, when the sulfide is depleted, the cells shift to conventional oxygenic photosynthesis. A (partially) anaerobic lifestyle can also be reflected in the lipid metabolism of such cyanobacteria: polyunsaturated fatty acids, the synthesis of which is oxygen-dependent (Kenyon and Stanier, 1970), are lacking, and the "bacterial," oxygen-independent pathway can be used for the biosynthesis of monounsaturated fatty acids (Oren *et al.*, 2009).

Adaptation of such facultative anoxygenic cyanobacteria to life under anaerobic conditions is not limited to the daylight hours. When aerobic respiration is not possible in the hours of darkness, alternative ways of energy generation must be operative. At least two such modes of obtaining energy have been identified. In some cases, elemental sulfur, accumulated during daytime, for example as the oxidation product of sulfide in the process of anoxygenic photosynthesis, can serve as the electron acceptor for the oxidative breakdown of intracellular storage polymers formed during the daytime (Oren and Shilo, 1979). Another way to obtain energy in the dark when neither oxygen nor alternative electron acceptors are available is by fermentation. Intracellular glycogen-like storage material can be fermented to products such as lactate and acetate with the gain of ATP (Oren and Shilo, 1979; Heyer, Stal and Krumbein, 1989; Stal and Moezelaar, 1997). Virtually all species of cyanobacteria that grow in microbial mats are capable of fermentation (Stal and Moezelaar, 1997).

1.10 Cyanobacteria have adapted to life in extreme environments

"Patavinorum aquis calidis herbae virentes innascunutur. . . " ["Green grass grows in the hot springs of Padua. . . "]: thus wrote Pliny the Elder in Book II of his *Natural History*. The growth of cyanobacteria like "green grass" in the hot springs near Padua can still be observed today, proving that some cyanobacteria are adapted to life in extreme environments. The studies by Tom Brock and his colleagues in Yellowstone National Park, USA (Castenholz, 1969; Brock, 1978; Ward, Castenholz and Miller, 2012) and further studies of the microbial communities inhabiting hot springs all over the world have defined the upper temperature limit for photosynthesis at 73–74°C. The unicellular cyanobacterium known as *Synechococcus lividus* or *Thermosynechococcus* (a species name still without standing in the botanical and in the bacteriological nomenclature) is the most thermotolerant; the filamentous *Mastigocladus* type starts appearing at somewhat lower temperatures. Curiously, a study of the cyanobacteria of Yellowstone National Park performed in the early 1930s documented apparent cyanobacterial growth at much higher temperatures: an upper limit of 85.2°C was found for two newly described members of the Oscillatoriales: *Phormidium bijahense* and *Oscillatoria filiformis*, observed in a spring identified as "Meadow Spring." Members of the *Chroococcales* were then found at Yellowstone up to 84°C and *Chamaesiphonales* up to 80°C (Copeland, 1936).

As already mentioned above in the discussion of the stratified communities of cyanobacteria within gypsum crusts on the bottom of saltern evaporation

ponds at salinities of 200 g/l and above (Oren, Kühl, and Karsten, 1995; Oren *et al*., 2009), and in the discussion of the cyanobacterial growth in the depths of Solar Lake, Sinai, with up to 180 g/l salt (Padan, 1979a; Padan and Cohen, 1982), some members of the group are also adapted to life at high salt concentrations. The first description of cyanobacteria living in concentrated brines was probably that by Trijntje Hof and Pierre Frémy (1933). We know of unicellular as well as filamentous halophilic or highly halotolerant representatives (Brock, 1976; Garcia-Pichel, Nübel, and Muyzer, 1998; Oren, 2012). However, heterocystous types appear to be absent from high-salt environments. Halophilic cyanobacteria accumulate organic "compatible" solutes to provide osmotic equilibrium between the cytoplasm and the outside medium. Glycine betaine (trimethylglycine) is the commonly found osmotic solute in the most halotolerant types, while glucosylglycerol is accumulated by many somewhat less halophilic representatives (Oren, 2012). At the highest salt concentrations (halite saturation, >300 g/l salt) cyanobacteria are not successful, and the niche of an oxygenic phototroph–primary producer is occupied by eukaryotic unicellular green algae of the genus *Dunaliella*.

We also find cyanobacteria in abundance in cold environments such as lakes in Antarctica and in cold as well as in hot deserts, where low/high temperature stress is combined with drought stress (Vincent, 2007; Hu, Gao, and Whitton, 2012; Quesada and Vincent, 2012). Cyanobacteria also thrive in many alkaline lakes, and some tolerate both high pH and high salinity.

In view of the high degree of adaptability of the cyanobacteria as a group to different extremes of physical and chemical parameters, it is surprising to note that they are not very successful in colonizing acidic environments. The lower pH limit for their growth appears to be around 4–5, and they are seldom encountered between pH 5 and 6 (Brock, 1973). Oxygenic photosynthesis at lower pH values, combined with elevated temperatures, appears to be the specialty of the alga *Cyanidium* and related organisms. The occasional finding of planktonic picocyanobacteria of <2 μm in diameter at pH values down to 4.5 and the observation of several filamentous forms with true branching at about pH 4.0 are generally considered to set the lower pH limit for cyanobacteria. Occasionally there have been reports of cyanobacteria at even lower pH values: populations of two types of filamentous cyanobacteria resembling *Oscillatoria*/*Limnothrix* and *Spirulina* sp. were found in acidic lakes in Bavaria down to a pH of 2.9. In a survey of hundreds of lakes in Sweden and Canada cyanobacteria were generally present down to pH 3.7. *Aphanocapsa* and *Chroococcus*-like unicellular forms were found in acidified Canadian lakes (Steinberg, Schäfer, and Beisker, 1998).

1.11 Cyanobacteria can survive adverse conditions for prolonged periods

Water is essential to support all forms of life, but some cyanobacteria have a remarkable ability to survive for long periods in a desiccated state, to resume activity the moment water becomes available again (Potts, 1994, 1996). Their success as a major component of the biota of deserts, hot as well as cold ones (Wynn-Williams, 2000; Hu, Gao, and Whitton, 2012) is to a large extent due to their ability to survive desiccation. Other survival strategies against desiccation are the endolithic life of some species in protected areas below the surface of rocks (Friedmann, 1982) and the establishment of symbioses with fungi to form lichens. Most of the approximately 17,000 species of lichen known have green algae as the phycobiont, but cyanobacteria occur in about 8% of species. *Nostoc* is the most common cyanobacterium encountered in lichen symbioses, but *Stigonema*, *Scytonema*, *Calothrix*, *Dichothrix*, *Gloeocapsa*, *Chroococcus*, and *Hyella* have also been found (Ahmadjian, 1967).

Some types of filamentous cyanobacteria can, under adverse conditions, produce specialized cells called akinetes, which can remain dormant for years, to germinate and give rise to the development of new filaments when conditions become suitable again (Nichols and Adams, 1982; Herdman, 1987). Akinetes, sometimes termed "spores," are one of the two types of differentiated cells known in the world of cyanobacteria, the second being the heterocysts that fix molecular nitrogen, as discussed above. Akinetes do not survive exposure to high temperature like endospores of e.g., *Bacillus* and *Clostridium* spp. Akinetes are usually much larger than vegetative cells, and they

are only found in heterocystous cyanobacteria. They have been reported in members of the *Nostocaceae*, the *Rivulariaceae*, and in some species of *Stigonemataceae*. Thus in *Hapalosiphon* and *Fischerella*, vegetative cells may develop into such perennating structures. Production of akinetes has been known for more than 150 years: Carter (1856) drew filaments of *Rivularia* showing a large granular cell (which he called a sporangium), which always developed next to a heterocyst; germination experiments with akinetes were already being performed nearly a century ago (Harder, 1917a).

1.12 Many cyanobacteria readily adapt to cultivation in the laboratory

Most of our knowledge of the morphological diversity of cyanobacteria is based on the study of material collected from nature. However, growth conditions may have a strong impact on the morphological attributes of cyanobacteria, and the true diversity may thus be overestimated when only morphological criteria of field-collected material are examined. Stanier and coworkers (Stanier *et al.*, 1971; Rippka *et al.*, 1979; Rippka, Waterbury, and Stanier, 1981) called for the use of pure (axenic, not only free of other types of cyanobacteria but also devoid of contaminating heterotrophic bacteria) cultures for taxonomic studies. But to bring cyanobacteria in pure culture and adapt them to life under laboratory conditions is often extremely difficult. Growth media are simple, as they are based on inorganic salts and nutrients only (Allen, 1952; Waterbury, 2006), but this does not imply that all cyanobacteria are easy to grow and to maintain in axenic culture. Many types grow very slowly, and there may also be situations in which certain species depend on the presence of "contaminating" bacteria for growth.

The first axenic cultures of cyanobacteria were probably already established nearly a century ago. A strain of *Nostoc punctiforme* was obtained from a symbiotic association with a higher plant (*Gunnera* sp.) (one of the many documented cases of symbioses between cyanobacteria and eukaryotic organisms), and was shown to grow in bacteria-free culture in the dark on various sugars and polysaccharides (Harder, 1917b). Allison, Hoover, and Morriss (1937) reported that a strain of *Nostoc muscorum* grew slowly on glucose or sucrose in the dark, both in the presence and absence of combined nitrogen. However, Stanier, in his foreword to the monograph by Carr and Whitton (1982), attributed the first pure culture studies of cyanobacteria to Emerson and Lewis (1942), who grew an axenic culture of *Chroococcus* prepared by Klara Gaffron, antedating the first axenic *Synechococcus* sp. (*Anacystis nidulans*) of Allen (1952), probably the first axenic isolate still available today.

The large collection of axenic cultures of cyanobacteria of different types established by Stanier's group forms the basis of the extensive collection of cyanobacteria maintained in the Pasteur Culture Collection in Paris.

1.13 Final comments

The paragraphs above contain no more than a few highlights, showing different aspects of the fascinating group of the cyanobacteria. The selection of the topics presented is entirely personal, but I hope that the material covered is broad enough to provide a general introduction to the nature of the cyanobacteria, whose applied aspects form the subject of most chapters in this book. In an introductory chapter of similar nature my late friend Noel Carr (1999) wrote:

> . . . my first response will be some kind of general disclaimer with respect to synoptic balance or indeed total accuracy . . . The best that one can hope for is a personal, hopeful dispassionate, version of some of the developments and constraints that have happened in our own field . . .

The same disclaimer applies to this chapter as well. More in-depth general information on the world of the cyanobacteria can be found in earlier published monographs: books such as those by Bryant (1994), Carr and Whitton (1982), Fay and Van Baalen (1987), Fogg *et al.* (1973), and Whitton (2012) provide a wealth of useful information, as do many review articles (e.g., Cohen and Gurevitz, 2006; Stal, 2007; Stanier and Cohen-Bazire, 1977).

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