

Cyanobacteria

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Based in part on the previous version of this *Encyclopedia of Life Sciences (ELS)* article, Cyanobacteria by Katarzyna A Palinska, William J Horgan and Wolfgang E Krumbein.

Cyanobacteria is a widely distributed group of unicellular and multicellular photosynthetic bacteria that possess chlorophyll *a* (Prochlorales additionally possess chlorophyll *b*) and perform oxygenic photosynthesis.

Introduction

The oldest known sedimentary rock formations found in Australia and Africa, approximately 3700 million years in age, bare microfossils of cyanobacteria-like organisms. Derivatives of 2-methylbacteriohopanepolyols, which occur in many modern cyanobacteria, have been found in sediments as old as 2500 million years (Summons *et al.*, 1999). It is nearly certain that cyanobacteria were the first oxygenic phototrophic organisms to evolve, and were paramount in the initial conversion of the Earth's atmosphere from anoxic (without oxygen) to oxic (with oxygen). Today this ancient group of bacteria displays an overwhelming diversity of morphological and physiological properties. Cyanobacteria, formerly known as blue-green algae, are prokaryotic microorganisms which share, with eukaryotic algae and plants, the capacity to perform oxygenic photosynthesis by employing light and water in the reduction of carbon dioxide. Approximately 2.2 billion years ago, an enormous increase in the concentration of free atmospheric oxygen can be noted in banded iron formations of the fossil record. This accumulation can only be explained by the cyanobacterial release of this potentially poisonous gas. This role in the creation of an aerobic atmosphere coupled with a continuing role in the carbon dioxide and oxygen cycling of our planet shows the intense impact of cyanobacteria on the global environment. Being capable of oxygenic photosynthesis, many cyanobacteria still may grow under low oxygen conditions and even free sulfide is tolerated by some strains at levels much higher than those tolerated by most eukaryotic algae (Padan and Cohen, 1982). Some can utilize hydrogen sulfide as a hydrogen donor in addition to water, a feature which is absent even in those eukaryotes, which can tolerate relatively high

ELS subject area: Microbiology

How to cite:

Palinska, Katarzyna A (July 2008) Cyanobacteria. In: *Encyclopedia of Life Sciences (ELS)*. John Wiley & Sons, Ltd: Chichester.
DOI: 10.1002/9780470015902.a0000454.pub2

Advanced article

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Online posting date: 15th July 2008

hydrogen sulfide concentrations. Endowed with the capacity to acclimate to a wide range of environmental conditions, including extreme ones, cyanobacteria colonize nearly all aquatic and terrestrial ecosystems. **See also:** [Earth: Changes Through Time](#); [Fossils and Fossilization](#); [Palaeoclimatology](#)

The term 'cyanobacteria' in contrary to 'blue-green algae' emerged 20 years ago (Stanier *et al.*, 1978). The oxygenic phototrophic bacteria containing chlorophyll *a* and phycobilins, and the Prochlorales containing chlorophylls *a* and *b* were later grouped together as cyanobacteria. These organisms were first classified as blue-green algae due to their superficial resemblance to eukaryotic algae. Cyanobacteria, however, like all other bacteria, lack the membrane-bounded organelles, and nuclei of true eukaryotes. Although truly prokaryotic, cyanobacteria have an elaborate and highly organized system of internal membranes which function in the photosynthetic process. Embedded in these photosynthetic lamellae, called thylakoid membranes, the macromolecules chlorophyll *a* and several accessory pigments such as phycoerythrin and phycocyanin play a major role in the functioning of the photosynthetic apparatus. It is also the high concentration of phycocyanin which leads to the bluish colour of the organisms and hence the name: blue-green algae. All cyanobacterial cell walls are found to contain peptidoglycan, and due to their cell wall structure, are furthermore Gram-negative. **See also:** [Chlorophylls](#)

Cyanobacteria may be single celled or may form colonial structures such as filaments, flat sheets or hollow balls, all of which are often surrounded by a gelatinous or mucilaginous sheath (**Figure 1**). Some filamentous cyanobacteria show the ability to differentiate into three different cell types: vegetative, climate-resistant akinets and thick-walled heterocysts. The wide span of different cyanobacterial forms include unicellular organisms reproducing by binary fission (e.g. *Synechocystis*, *Synechococcus* and *Microcystis*), unicellular organisms reproducing by specialized, small, motile or nonmotile daughter cells called baeocytes (e.g. *Dermocarpa* and *Pleurocapsa*), filamentous organisms without heterocysts (e.g. *Microcoleus* and *Oscillatoria*), filamentous organisms with heterocysts (e.g. *Anabaena* and *Nostoc*) and filamentous organisms with heterocysts and branched trichomes (e.g. *Fischerella*). Cells

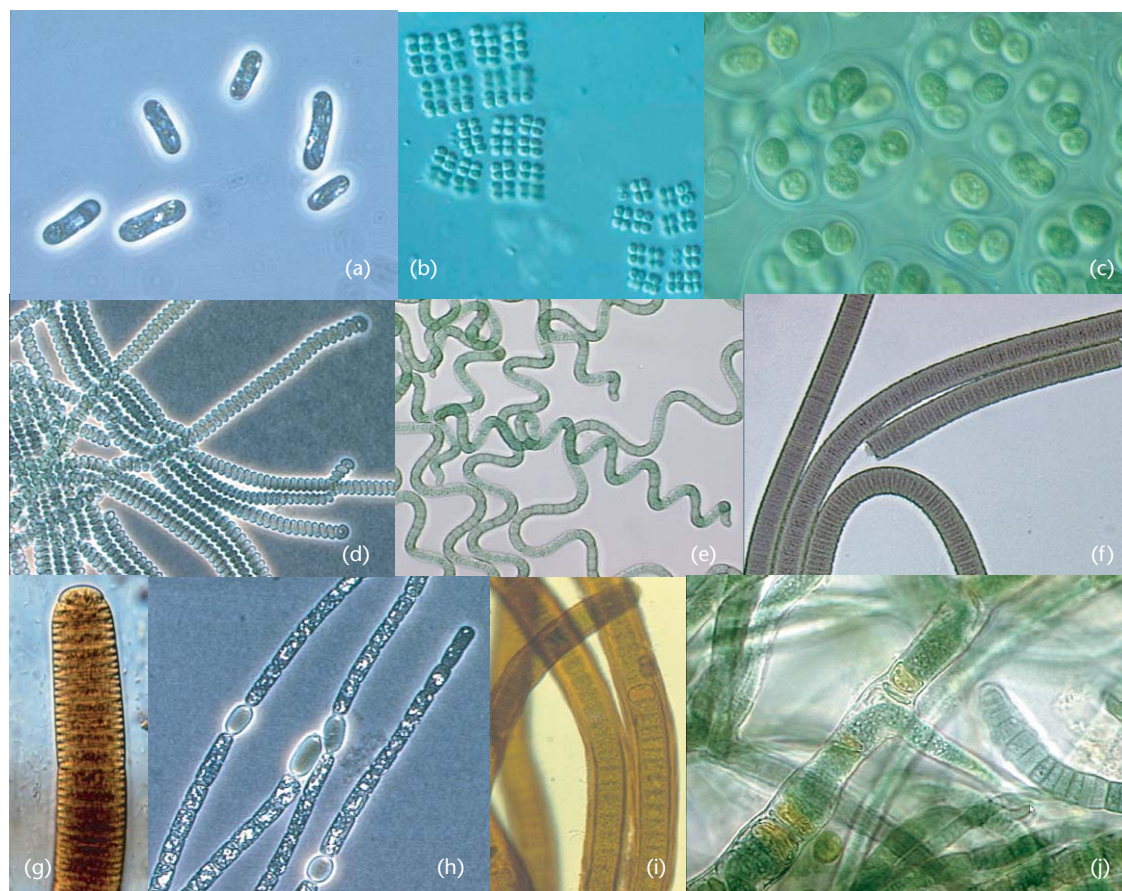


Figure 1 Morphological diversity in cyanobacteria. Unicellular: (a) single-celled *Cyanotheca* PCC 7418, (b) forming regular colonies *Merismopedia punctata* and (c) irregular colonies of *Gloeotheca* PCC 6909. Filamentous, without heterocysts: (d) *Spirulina* sp., (e) *Arthrospira* sp., (f) *Oscillatoria* sp. and (g) *Hydrocoleum cantharidosmum*. Filamentous with heterocysts: (h) *Aphanizomenon flos-aquae*, (i) *Scytonema* sp. and (j) *Stigonema* sp., filamentous cyanobacterium with heterocysts and branched trichomes.

of unicellular cyanobacteria range in diameter from approximately $0.4\ \mu\text{m}$ (*Prochlorococcus* PCC 9511) to over $40\ \mu\text{m}$ (*Chroococcus turgidus* PCC 9106). Filamentous forms belonging to the Oscillatoriaceae are reported with diameters in excess of $100\ \mu\text{m}$. The thinnest filaments of less than $1\ \mu\text{m}$ are described for the representatives of the genus *Leptolyngbya*.

All heterocyst-forming species, as well as some non-heterocystous (e.g. *Gloeotheca*, *Trichodesmium* and *Oscillatoria*), are able to 'fix' nitrogen. The most common form of nitrogen, dinitrogen (N_2) gas, can be used only by microorganisms that possess the enzyme nitrogenase and can 'fix' nitrogen into a biologically usable form. Biological dinitrogen (N_2) fixation is the dominant mechanism for introduction of nitrogen into the biosphere. It approximates the total losses from microbiological denitrification on the global scale. Filamentous, nonheterocystous and unicellular cyanobacteria capable of using dinitrogen as the source of nitrogen can be subdivided into two main groups. The first one consists of cyanobacteria that are fixing dinitrogen only under anoxic conditions. Their strategy can be characterized as avoidance of oxygenated

environments. The second group comprises cyanobacteria that are remarkable as they possess the capacity of inducing nitrogenase under fully aerobic conditions (e.g. *Trichodesmium*). The bloom-forming nonheterocystous filamentous cyanobacteria of the genus *Trichodesmium* are considered the most important nitrogen fixers in tropical oceans and may contribute *c.* 50% of global biologically fixed nitrogen (excluding the anthropogenic contribution). Surface blooms of the filamentous diazotrophic genera *Trichodesmium* and *Richelia* (endosymbiont of the diatom *Rhizosolenia*) achieve magnitudes of growth in excess of hundreds of square kilometres in what are some of the most nutrient deplete, oligotrophic waters known. As nitrogen is often a limiting factor in plant-dominated terrestrial ecosystems, plants have an obligate dependency on these microorganisms. In some plant species, the interaction of the plant and cyanobacteria is so intimate that they have co-evolved cyclical symbiotic associations such as the *Cycad–Anabaena* and the intracellular *Gunnera–Nostoc* complexes. **See also:** [Cyanobacterial Heterocysts](#)

Recent increase of scientific interest for cyanobacteria is often connected to the current environmental concerns in

conjunction with the increased incidence of cyanobacterial toxic blooms (Codd, 1999). The worldwide occurrence of toxic cyanobacterial blooms in fresh and brackish eutrophic waters creates a problem for all life forms. Most water-based poisonings by cyanobacteria occur when heavy surface growths or scums accumulate near shorelines of lakes, ponds and reservoirs where animals have free access to high concentrations of these toxic cells. Deaths attributed to cyanobacterial toxins have been reported for man, animals, birds and fish. Cyanobacterial blooms are ubiquitous, often associated with eutrophication and appear to be on the increase. These toxins fall into various categories. Some are known to attack the liver (hepatotoxins, over 60 variants of microcystins) or the nervous system (neurotoxins, e.g. anatoxin-a and saxitoxin), others simply irritate the skin.

Diversity of cyanobacteria is expressed by their morphological, biochemical and physiological properties which enable them to settle and persist in a wide range of habitat sometimes even near the limits for life. Cyanobacteria have developed effective protection strategies in response to extreme life conditions. Representatives of the genus *Synechococcus* and *Mastigocladus* for instance live in 73°C thermal water. *Spirulina platensis* is adapted to the high sodium carbonate concentrations of east African soda lakes. Cyanobacteria evolved different strategies to counter the effects of ultraviolet (UV)-radiation and to protect themselves from excessive solar radiation. The best understood of these includes the development of sunscreen pigments such as scytonemin or gloeocapsin that envelope the cell and function even when cells are at rest, the synthesis of compounds such as mycosporine-like amino acids, development of efficient systems for repair of damaged deoxyribonucleic acid (DNA), storing of calcium carbonate inside their slime capsule or implementation of directed gliding motility for escaping the diurnally high intensities of solar irradiance. Most of the species produce special proteins (shock proteins), in response to high salinity or heat, to stabilize other cellular proteins and enzymes. Cyanobacteria associated with rocky surfaces form 'Tintenstriche' (German for 'inky streak') on white dolomite surfaces. Owing to their abilities to both photosynthesize and fix nitrogen as well as perfect adaptation to desiccation (EPS, extracellular polymeric substances), and solar radiation (UV-protective pigments), cyanobacteria are important and widespread components of rock biofilms. Additionally to the protection mechanisms enabling life on the rocks some cyanobacteria effectively burrow into the rock surfaces in deserts where they hide in an endolithic environment. Representatives of the genus *Chroococcidiopsis* are the most frequent and widespread cryptoendolithic organisms (Büdel *et al.*, 2004). A wide range of cyanobacterial species was reported to live at salinities exceeding 200%. To be able to withstand the high osmotic pressure caused by the salt concentrations in their surrounding medium, cyanobacteria possess mechanisms allowing temporarily entry of ions (Na^+ , K^+ , Cl^-) into the cells to counteract rapid increase in medium salinity. In the long

term, organic solutes are accumulated to provide osmotic balance. Being cosmopolitan in distribution, cyanobacteria are thought to have been exposed to different levels and types of stresses during their development, thus providing a suitable system for analysing the adaptive mechanisms developed in response to changing stress conditions (Whitton and Potts, 2000).

Additionally both benthic and planktonic cyanobacteria are capable of different types of motility. Gliding motility requires contact with a solid surface and occurs in a direction parallel to the long axis of the cell or filament. This solid surface can also be the interior of the polysaccharide sheath. Trichomes may move forwards and backwards in their sheath and may move out of it, leaving an empty sheath behind (e.g. *Microcoleus chthonoplastes*). The hypotheses explaining gliding motility include the secretion of mucilage, possibly through the pores in the cell wall (propulsive force that moves the trichomes) and contractile structures that cause surface undulations (microfibrils found in the external layers; Halfen and Castenholz, 1973). Cyanobacteria possess essentially chemo- and phototaxis. Phototaxis is a movement, which orients itself to the direction of light. Both positive and negative phototaxis are important for microbial mats inhabitants allowing them to obtain an optimum position in the mat. Chemotaxis occurs when the chemical gradients control the direction of cyanobacteria in the dark (e.g. oxygen, carbon dioxide, bicarbonate and sulfide). Planktonic species adjust their position in the water column by means of gas vacuoles; they float near the surface during the day for photosynthesis and sink deeper at night to harvest nutrients. Certain marine unicellular cyanobacteria of the genus *Synechococcus* exhibit a unique and mysterious form of motility characterized by the ability to swim in liquid in the absence of flagella (Waterbury *et al.*, 1985).

It appears that cyanobacteria are the most versatile organisms of this planet, and have had a deep influence on all aspects of life and its creation (morphogenesis). They initiated the most dramatic changes in the mode of life and the atmospheric and geochemical equilibrium on Earth by the invasion of the oceans and atmosphere with their release of initially toxic, free oxygen. They allowed for, and perhaps spurred on, the evolution of plants and animals by converting the Earth's atmosphere from anaerobic to aerobic. Cyanobacteria deeply influence the metabolic and global cycles of phosphorus, carbon, oxygen, hydrogen, nitrogen and sulfur. Other elements such as sodium, calcium, magnesium, iron and even rather inert elements such as silica, gold and iridium are often found to be bound in the Earth's crust due to past and present stromatolitic cyanobacterial activities. **See also:** [Global Carbon Cycle](#); [Global Water Cycle](#)

Found in almost every conceivable habitat, from oceans to freshwater, from bare rock to soil, cyanobacteria deserve special emphasis because of their great ecological importance in the global carbon, oxygen and nitrogen cycles, as well as their evolutionary significance in relation to many eukaryotic organisms.

Stromatolites

Cyanobacteria have an extensive, well-preserved fossil record and are among the easiest microfossils to recognize. They are larger than other bacteria, and the morphologies of the group have been conserved throughout much of their evolution. Fossilized, layered cyanobacterial mounds called 'stromatolites' exhibit a continuous geologic record covering 2.7 billion years. This widely distributed sedimentary rock type, characterized by a multilaminated, partly dome-shaped pattern, was created by the interaction between cyanobacterially dominated biofilms or microbial mats and their physical and chemical environment, which resulted in the binding and depositing of mineral compounds.

Stromatolite layers are produced when cyanobacterial photosynthesis depletes carbon dioxide levels in the surrounding water, thus initiating the precipitation of calcium carbonate over the growing mat of bacterial filaments. These minerals, along with other grains of sediment precipitating from the water, are then trapped within a sticky layer of mucilage from the bacterial colonies called EPS. As sediment accumulates and blocks sunlight, the microbes migrate phototactically upwards and begin a new layer. **See also:** [Plant Gums](#)

Today, stromatolites are formed in only a few places, such as shallow, saline pools in hot-dry climates (i.e. Shark Bay in Western Australia). In the Proterozoic, stromatolites were widespread on Earth, and were ecologically important as the first true reef builders. By the close of the Proterozoic, the abundance of stromatolites decreased markedly, though cyanobacteria continued to leave a fossil record.

From the earliest periods of Earth history (3500 Mya, million years ago), such rocks are recorded and have been attributed to the activity of benthic cyanobacterial microbial mats (**Figure 2** and **3**). The early sequestration of elemental carbon in fossil rocks was dominated by these microbial mats through the transformation of their photosynthetic products into lithified organic matter.

Additionally, microbially induced precipitation of calcium carbonate (aragonite and calcite) and calcium/magnesium carbonate (dolomite) forms another important sink for

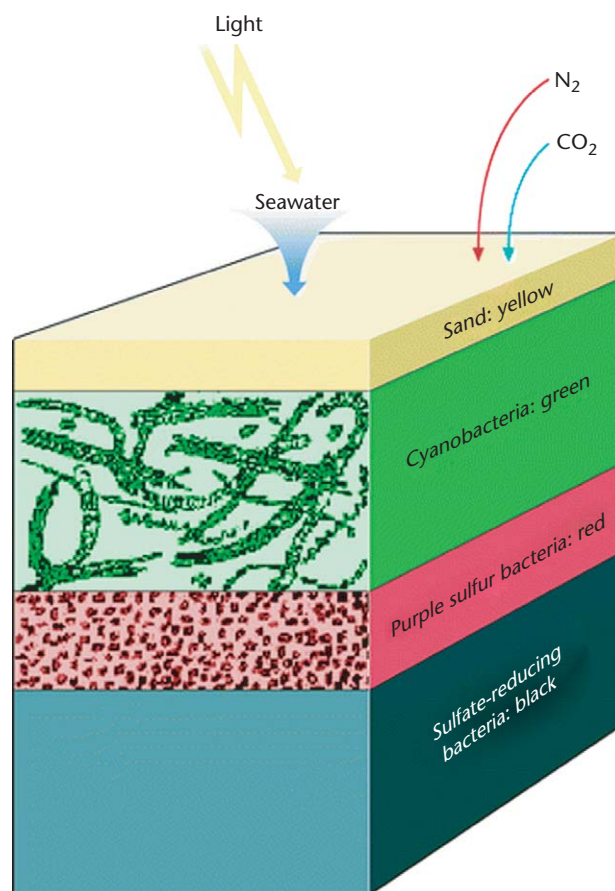


Figure 2 Schematic vertical cross-section of a typical microbial mat system.

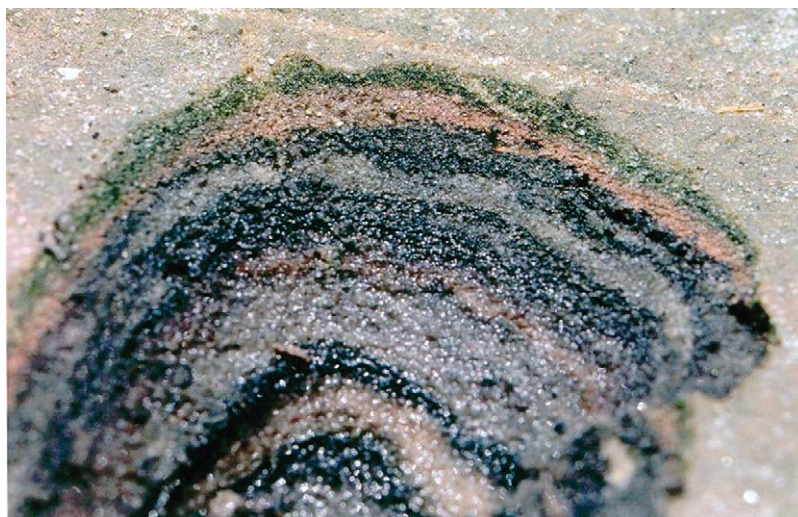


Figure 3 Laminated cross-section of microbial mats from Norderney Island (North Sea), Germany.

carbon found in the rock record. This partitioning of carbon into organic matter and carbonate rocks by cyanobacterial mats has been suggested to be the driving force of plate tectonics or global tectonics, i.e. the distribution and relief of the continents on Earth (Anderson, 1984).

The vast fossil record of cyanobacteria gives evidence of their early, widespread dominance, and their prominent role as the true media of biogeophysiology, which in this context is regarded as the science of the phenomena and processes of Earth as a living entity, deriving its energy from the sun and receiving nutrients from space and its interior.

The Photosynthetic Apparatus

All cyanobacteria are predominantly photoautotrophic organisms capable of oxygenic photosynthesis. Some of them are able to live photoheterotrophically on organic compounds in dim light (organic compounds are used only as a source of carbon, light supplies the energy for the cell) and a few are able to live heterotrophically in dark (organic compounds provide the organism with a source of carbon and energy), however photoautotrophy is their preferred mode of nutrition. They share the ability of performing oxygenic photosynthesis with the prokaryotic Prochlorales and with all photosynthetic eukaryotes. The cyanobacterial photosynthetic apparatus is clearly similar in structure, function and molecular properties with that of eukaryotic algae and plants. It consists of five complexes, four of which are common to both cyanobacteria and plants: (1) photosystem II (PS II); (2) plastoquinol-plastocyanin oxidoreductase; (3) photosystem I (PS I); (4) ATP synthase and (5) phycobilisome, light-harvesting antenna for PS I.

The interaction between these multiprotein complexes is achieved through several proteins and molecules: plastoquinone, plastocyanin, ferredoxin (flavodoxin) and protons. In cyanobacteria and Prochlorales, the photosynthetic membranes are dispersed throughout the cytoplasm, as opposed to photosynthetic eukaryotes, where they are always localized in a membrane-bound organelle, the chloroplast. **See also:** [Photosynthesis and Respiration in Cyanobacteria](#); [Photosystem I](#); [Photosystem II](#)

The cyanobacterial photosynthetic apparatus is localized in and on intracytoplasmic membranes, thylakoids, the arrangement of which varies with species, cell type and culture conditions. Until now only one cyanobacterium, *Gloeobacter violaceus*, has been found not to possess real thylakoids and its phycobilisomes (PBS) are directly attached to the plasmic membrane.

The pigments which comprise the cyanobacterial photosynthetic apparatus are chlorophyll *a*, phycobiliproteins and carotenoids (Figure 4). Most of the chlorophyll (85–90%) is associated with photosystem I. The carotenoid universally found in all cyanobacteria is β -carotene, and in most cases accompanied by zeaxanthin and echinone. Cyanobacteria also synthesize group-specific carotenoids. Phycobiliproteins are water-soluble, brilliantly coloured proteins, which may serve as nitrogen storage compounds. The unique light-harvesting complexes for PS II in cyanobacteria (with the exception of red algae and certain dinoflagellates) are multimolecular structures, primarily composed of phycobiliproteins, the PBS. PBS are attached to the stromal surface of the thylakoid membrane at regular intervals and their efficiency in light-harvesting and energy transfer of 95% is quite remarkable. Classically, two substructures are distinguished within the PBS: the



Figure 4 Different pigmentation of cyanobacteria due to their various ratios of phycocyanine and phycoerythrine as well as divergent carotenoids.

core, which is mainly composed of allophycocyanin and is in direct contact with the photosynthetic membrane; and the rods, which are attached to the core and consist of hexamers of phycocyanin and, in some species, of phycoerythrin or phycoerythrocyanin. **See also:** [Algal Pigments](#); [Dinoflagellates](#); [Light-harvesting Complex](#); [Red Algae](#)

Cyanobacteria are able to adapt their photosynthetic apparatus to light intensity as well as to changes in the light wavelength. This phenomenon occurs via a change in the ratio of PSI/PSII activity, and by changes in the number of PBS and cytochrome (cyt *c553*) per unit area of thylakoid membrane. This response is called inverse chromatic adaptation and occurs in all photoautotrophic organisms. Cyanobacteria can also perform a process known as complementary chromatic adaptation, which is the ability to change the proportions of phycoerythrin (red pigment) and phycocyanin (blue pigment) when cells are exposed to light of different spectral compositions. This adaptive response to light wavelength is unique to cyanobacteria and occurs only in certain species which are capable of phycoerythrin synthesis. In these strains, the synthesis of both phycocyanin and phycoerythrin are modulated by light wavelength.

Symbiosis: The Role of Cyanobacteria in the Evolution of Eukaryotic Photosynthesis

All photosynthetic plants and protocista contain membrane-bounded organelles referred to as chloroplasts. From the first descriptions of these cellular somes, or bodies, it was noted that they are never generated inside a cell *de novo*, i.e. chloroplasts always form from preexisting chloroplasts or prochloroplasts. This direct division of the bodies themselves, which is closely coordinated with the general division of their host cells, allows chloroplasts to maintain general genetic continuity. Modern molecular tools have shown the presence of nonnuclear DNA, messenger ribonucleic acid (mRNA) and protein synthesizing systems inside chloroplasts. The discovery of this cellular machinery combined with chloroplast's reproductive behaviour has provided unequivocal evidence to support the serial endosymbiotic theory (SET) of chloroplast origin (Margulis, 1970). This theory states that at some point, indeed at several points, in the phylogeny of algae (by definition chloroplast-containing protocista) and plants an anastomization occurred between their evolutionary branches and those of cyanobacteria-like organisms. **See also:** [Endosymbionts](#); [Margulis, Lynn](#)

The evolution of eukaryotic photosynthesis has independently occurred several times in the history of the biota. Further investigation into the nature of chloroplast DNA, which, like cyanobacteria, lacks histone complexes, has shown that chloroplasts from different species contain different genetic compositions. Although these differences occur, all the studied chloroplastic genomes bare a striking

resemblance to various extant cyanobacteria. Modern analogues exist for this type of close symbiotic relationship. In a number of systematically unrelated eukaryotes, the so-called 'cyanelles' have been described. Cyanelles are plastid-like organelles resembling cyanobacteria in overall morphology, organization of photosynthetic apparatus and presence of a peptidoglycan wall. It is clear that modern cyanelles, like chloroplasts, arose from former intracellular symbionts. *Cyanophora paradoxa*, an eukaryotic, unicellular alga is the most well-known and described example of this 'endocyanomic' phenomenon.

Even though the direct cyanobacterial ancestors of chloroplasts are not known, and indeed may never be known, the mounting evidence points uniformly to the multiple occurrences of permanent, endosymbiotic relationships between eukaryotes and cyanobacteria which led to the formation of all eukaryotic photosynthesizers.

Modern symbioses

Cyanobacteria enter into an extremely wide range of symbiotic association. Green algae, diatoms, liverworts, mosses, ferns, cycads, fungi, protoctista, sponges, bryozoa, didemnid ascidians, shrimps and mammals are known to enter into extra- or intracellular symbiotic associations with cyanobacteria. The individual relationships of these organisms range from cyclical to permanent, and from facultative to obligate. Interspecies metabolite and even genetic exchange have been observed in these various associations. In many of these cases, separate cultivation of symbiont is impossible, as in the case of *Prochloron didemni* or in some cyanobacterial lichens. The extensive ability of cyanobacteria to take part in these varied associations has levied a vast impact on the present and past morphologies of the biota and biosphere. **See also:** [Algal Symbioses](#); [Mutualistic Symbioses](#); [Protozoan Symbioses](#)

The Modern Concept of Cyanobacterial Taxonomy: Phenotypic and Genomic Support for the Phylogenetic Separateness

The unusually tumultuous taxonomy of cyanobacteria began, as for almost all algal groups, with Linnaeus in 1753. The metabolic property of oxygenic photosynthesis which characterizes cyanobacteria and their sharing of ecological niches with eukaryotic algae, prompted their treatment in the phycological circles, where they were called blue-green algae, although their prokaryotic nature, has been recognized for over a century. **See also:** [Classification](#); [History of Taxonomy](#); [Linnaeus, Carl \(Linné\)](#)

Cyanobacteria in botanical tradition have been distinguished on the basis of phenotypic properties, including colony formation, morphology of cells and extracellular envelopes, pigmentation, reproduction and, to a lesser extent, physiological and biochemical properties. Thuret

(1875), Bornet and Flahaut (1887–1888) and Gomont (1892) wrote the first comprehensive taxonomic monographs for cyanobacteria, recognized by phycologists as a later starting point in taxonomic referencing. The basic unit of that system is a species as defined in botany and zoology (e.g. Mayr, 1982). Forty years later, Geitler (1932) provided an updated taxonomic review and determination manual that recognized 1300 species, classified into 145 genera, 20 families and 3 orders. Geitler's (1932) work relied on morphology of field-collected specimens and his classification system marks the beginning of the modern era of cyanobacterial systematics, recognized both by phycologists and microbiologists. It has formed the basis of numerous revised systems proposed since then, including those of Elenkin (1938, 1949), Fritsch (1959), Starmach (1966), Kondrateva (1968), Bourrelly (1970) and Golubic (1976). These systems share in common the view that the systematics of cyanobacteria should be based on traditional botanical criteria, a view sometimes referred to as the 'Geitlerian' approach.

In the period 1956–1981, an alternative system was developed by Drouet and Daily (summarized in Drouet, 1981), which drastically reduced the number of genera and species of cyanobacteria. It was based on the hypothesis that the many morphological differences seen in natural samples of cyanobacteria are ephemeral and that numeral 'species' of cyanobacteria are actually different 'ecophenes' of true taxa. However, it was shown that this system does not reflect the true genetic diversity among cyanobacteria and was never fully accepted.

A third approach, developed largely through the efforts of Roger Stanier and Rosmarie Rippka, and their colleagues is based on the recognition of the fact that the 'blue-green algae' are bacterial in nature. Stanier *et al.* (1978) proposed that the systematic treatment of cyanobacteria should be based on bacteriological criteria on the ground that they are unquestionably bacteria. The basic taxonomic unit in bacteriological treatment is an axenic cultured strain, whereas the species becomes a conceptual construct based on comparison of a number of similar strains. In revising the cyanobacterial genera the Stanier school relied largely on morphological properties and used Geitlerian designations, but altered many generic definitions in accordance with properties expressed in culture (Castenholz and Waterbury, 1989). Accordingly, cultured cyanobacteria are usually assigned the name of genus with a strain code. Moreover, bacteriological approach leads to gross underestimation of the diversity of cyanobacteria in nature. The current edition of the Bergey's Manual of Systematic Bacteriology includes compiled information from both bacteriological and phycological sources (Castenholz, 2001).

Another update and revision of cyanobacterial system, which includes ultrastructural properties is currently underway (Komarek and Anagnostidis, 1999, 2005). Konstantinos Anagnostidis and Jiri Komarek have developed a formal system being a compromise between bacteriological and botanical approaches. Its nomenclature is based on

botanical taxonomic criteria, but it also utilizes bacteriological information.

As described above, taxonomy of cyanobacteria has its roots in three separate traditions. It is derived from (a) description of taxa occurring in natural populations (phycological tradition), (b) from description of strains maintained in axenic culture (bacteriological tradition) and (c) from comparisons of DNA sequences from either of the former sources and directly from the environment. **See also:** [Prokaryote Nomenclature](#)

Traditional phenotypic properties (morphological and physiological features) such as development (type of reproduction and division pattern), structure (cell size and shape or type of trichome, arrangement of cells, cell and colony pigmentation, heterocyst and akinete formation, motility) and physiology (e.g. *in vivo* absorption spectrum, chromatic adaptations, presence of phycoerythrin as light-harvesting pigment, salinity tolerance, vitamin requirements) were proved to be variable with changing environmental and culture conditions (Castenholz and Waterbury, 1989; Rippka *et al.*, 1979). It is recognized among workers in this field that the identification of any particular species based solely on morphology is highly dubious and impractical. Apart from the nomenclatural difficulties mentioned earlier, cyanobacteria maintained in culture may also lose or no longer express certain characteristic features observed in nature (Palinska *et al.*, 1996; Garcia-Pichel *et al.*, 1996). To overcome some of these problems and to permit identification of cyanobacteria at the genetic level, different molecular tools have been applied for their distinction at different taxonomic levels, e.g. a phylogenetic analysis based on 16S-23S internal transcribed spacer (ITS) sequence comparisons (Iteman *et al.*, 2000), random amplified polymorphic DNA (Neilan *et al.*, 1995), *in situ* hybridization (Schönhuber *et al.*, 1999), DNA-DNA hybridization (Stam, 1980), 16S and 5S rDNA (ribosomal DNA) sequence data (Woese, 1987; Turner, 1997); restriction fragment length polymorphism on polymerase chain reaction (PCR) amplification products (PCR-RFLP) of the *cpcBA* intergenic spacer, 16S rDNA gen-fragments as well as intergenic transcribed spacer region (Scheldeman *et al.*, 1999), phylogeny of *nifH* genes (Zehr *et al.*, 2003). With the goal of establishing in the future taxonomy of cyanobacteria supported by phylogenetic relationships, a polyphasic approach, combining phenotypic and genotypic characterizations has been recommended (Wilmotte and Herdman, 2001). **See also:** [In Situ Hybridization](#); [Nucleic Acid: Hybridization](#); [Phylogeny Based on 16S rRNA/DNA](#)

Advances in molecular phylogeny in the past decades identified cyanobacteria as the source of oxygenic photosynthesis and through endosymbiotic incorporation with eukaryotes also the main source of planetary primary production. Yet the genetic identity and specific ecological roles are only started to be explored, although the molecular tools are now largely available.

Prochloron, *Prochlorothrix* and *Prochlorococcus*

The prochlorophytes are oxygenic photosynthetic bacteria, having chlorophylls *a* and *b*. These characteristics distinguish them from other cyanobacteria, which contain chlorophyll *a* but not chlorophyll *b*. Three prochlorophyte genera accommodated in the order Prochlorales, have been described: *Prochloron*, a unicellular bacterium which is an extracellular symbiont of marine ascidians in tropical and subtropical marine waters (Lewin, 1977); *Prochlorothrix*, a free living, filamentous, freshwater plankter, found for the first time in shallow lakes in the Netherlands (Burger-Wiersma *et al.*, 1989) and *Prochlorococcus*, an abundant unicellular picoplankton in the euphotic zone (sunlit layer) of temperate and tropical marine waters (Chisholm *et al.*, 1992). *Prochlorococcus* is phenotypically distinct from the other two oxychlorobacteria in having slightly different forms of chlorophylls *a* and *b*. **See also:** [Algal Taxonomy: Historical Overview](#)

Prochloron didemni cells have been found in symbiosis with 20 species of ascidians, chiefly didemnids and one holothurian. The ratio of chlorophyll *a* to *b* seems to be host dependent, and ranges from 3 to 20. Three morphological types of *Prochloron* are distinguished from each other by their shape and arrangement of the thylakoids, and the presence and location of gas vacuoles and polyhedral bodies. Unfortunately, to date, this genus has been impossible to cultivate under laboratory conditions, a situation which greatly limits investigations on this organism and makes it impossible to judge whether the various morphological types are phenotypically or genotypically determined. However, the DNA–DNA hybridization and 16S rRNA (ribosomal RNA) analysis of a number of ascidian samples containing *Prochloron*, showed that all strains belonged to one species.

Currently, *Prochlorothrix hollandica* has only been isolated from the shallow, highly eutrophic, freshwater Loosdrecht Lake in the Netherlands. This filamentous organism is readily cultured in defined mineral media, and available in axenic culture. *Prochlorothrix hollandica* has a chlorophyll *a/b* ratio of 2.5 to 4 and attempts to induce nitrogenase activity were unsuccessful.

The genus *Prochlorococcus* consists of tiny, unicellular prochlorophytes (0.2–1.6 μm in diameter). The size makes it the smallest known photosynthetic organism (**Figure 5**). Its discovery as a major constituent of the picophytoplankton in wide areas of the world's oceans (typically 5×10^4 to 2×10^5 cells per mL^{-1}) has had profound implications for the understanding of primary productivity in the marine environment, although its real importance in terms of global production is still to be established. All isolates have so far been assigned to the same species, *Prochlorococcus marinus*. *Prochlorococcus* possesses a remarkable pigmentary complement unique to this genus, which includes divinyl derivatives of chlorophylls *a* and *b* with the chlorophyll *a/b* ratio of different strains ranging between 0.6 and 13. Other peculiarities of its photosynthetic apparatus include antenna complexes which are similar in function, but not in structure, to that of plants and green algae and, in some strains, traces of phycoerythrin, a possible remnant of the PBS present in cyanobacterial ancestors of this genus. The vertical distribution of *Prochlorococcus* often exceeds the euphotic layer (to depths that receive only 1% of the surface radiance).

Interestingly, the detailed comparison between the genomes of two *Prochlorococcus* strains isolated from different ecological niches (high- and low-light adapted) revealed many genetic foundations for the observed differences in their physiology and ecology, which helps to determine the factors that regulate species diversity in today's oceans (Rocap *et al.*, 2003). As *Prochlorococcus* strains are known

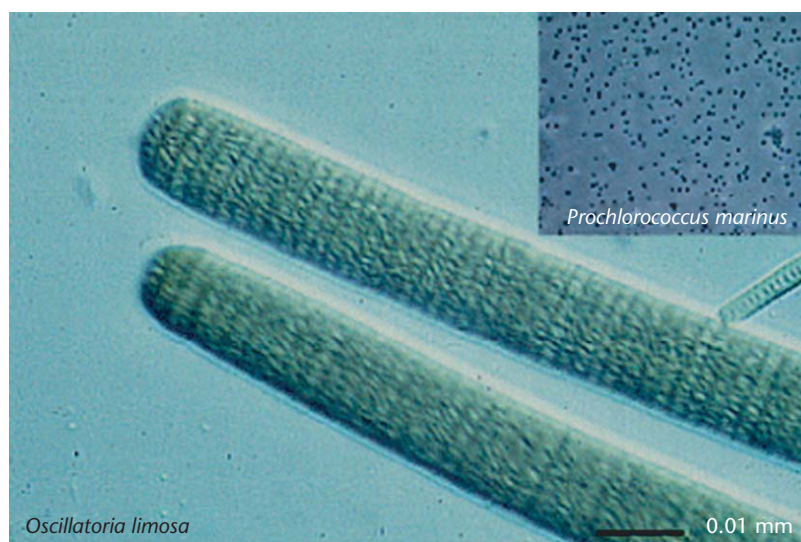


Figure 5 Size comparison of the smallest cyanobacterium *Prochlorococcus marinus* and typical microbial mat inhabitant *Oscillatoria limosa*.

to have the smallest genomes (strain PCC 9511: 1.66 Mbp; Rippka *et al.*, 2000) of any oxygenic phototroph, different *Prochlorococcus* ecotypes strictly maintain only the set of genes necessary for optimal performance at the depth at which those particular ecotypes is living. With regard to nitrogen assimilation, this would mean that when specific nitrogen sources are usually absent (i.e. nitrate in the upper ocean), the genes directly involved in its utilization (from transporters to enzymes) can be safely deleted without significant impact on the fitness of the ecotype for its habitat.

The original pigment complement found in *Prochlorococcus* cells led investigators (Chisholm *et al.*, 1992) to call it a 'prochlorophyte', which was the name given to the previously known oxyphototrophic bacteria (*Prochloron* and *Prochlorothrix*). The three known 'prochlorophytes' were originally considered to belong to a phylum distinct from the cyanobacteria; however, molecular studies using 16S rRNA or gene alignments have clearly demonstrated that this separation is not justified (Turner, 1997). It is now generally accepted that Prochlorales are not a monophyletic grouping, and that its members are not particularly related to green chloroplasts but rather are polyphyletic within the cyanobacteria. Therefore, an ancestor common to cyanobacteria and chloroplasts may have existed that possessed both phycobiliproteins and chlorophyll *a/b* protein complexes as light-harvesting antennae. Still, the evolution of *Prochlorococcus*, *Prochloron* and *Prochlorothrix*, which have evolved independently from different cyanobacterial ancestors and converged to recruit the same protein to build a novel antenna in replacement of the energy-consuming PBS, is a very new and changing topic.

The diversity of microorganisms in the marine environment and the broad spectrum of their metabolic potential, including gene expression and regulation, rapidly grow. By most accounts, we can culture fewer than 10% (by number) of the microbial inhabitants of the sea, so existing ideas of marine ecology must be flexible and accommodating to change.

Cyanobacteria continue to surprise and discoveries about cyanobacteria continue, however. Eight years later after the identification of *Prochlorococcus*, Miyashita *et al.* (1996) has reported on a discovery of a new type of oxygenic prokaryote *Acaryochloris marina* that contains chlorophyll *d* as a major pigment along with minor contents of chlorophyll *a* and phycobiliproteins. In 1999, a free-living member of this group has been isolated from a eutrophic hypersaline lake (Miller *et al.*, 2005).

Clearly, cyanobacteria, which have been so central to life on Earth, will continue to provide many new surprises, as scientists learn more about them as they explore the world's oceans.

Biotechnological Aspects

The growth and metabolism diversity represented by the huge number of varied strains allows for cyanobacteria to

contribute greatly in biotechnologically based products and services.

Cyanobacterial molecular biology has rapidly advanced over the past two decades, and it is now possible to introduce foreign genes into a few cyanobacteria. Additionally, some of the enzymes that have been discovered in cyanobacteria are commonly used as restriction enzymes (*AflI*, *AvaI*, *AvaII*, *AvrII*, *AcyI*, *AflIII*). Present interest and studies are focused on the search for high temperature-resistant enzymes, which are of great interest in the biotechnological industry. Cyanobacteria have also been used, due to their tightly controlled, photoautotrophic growth conditions, to stable isotopically labelled biochemicals in enclosed photobioreactors. These reagents, including isotopically labelled amino acids, nucleic acids and sugars, are used in medicinal diagnostics (e.g. breath tests for utilization studies), metabolism studies (protein metabolism) and basic research into protein structure (Apt and Behrens, 1999; Lee *et al.*, 2000). **See also:** [Protein Production for Biotechnology](#); [Restriction Enzymes](#)

Many substances isolated from cyanobacteria have been used in biotechnology. Phycobiliproteins are used both as tools for basic research, and as medical diagnostics. Therapeutic uses of phycobiliproteins, as well as growth stimulation activities of allophycocyanin or c-phycocyanin have also been reported. In addition, other cyanobacterially extracted compounds are being targeted for their effects on appetite suppression, high cholesterol depletion, acquired immune deficiency syndrome (AIDS), cancer and for their use as antibacterial, antifungal and antiviral substances. Considering the wide range of growth conditions under which cyanobacteria survive, the pursuit of specialized cyanobacterial compounds may yield powerful tools for the future of medical biotechnology. **See also:** [Antibacterial agents: susceptibility *In Vitro* and *In Vivo*](#); [Antifungal Agents](#); [Antimicrobial, Host Defence Peptides and Proteins](#); [Antiviral Drugs](#)

In agricultural biotechnology, cyanobacteria have very new and very old uses. The nitrogen fixation properties of the cyanobacteria *Anabaena* have been in use for thousands of years by Asian rice farmers. This bacteria's symbiotic association with the water fern *Azolla*, which floats in the intermittent troughs of rice fields, supplies nearly all of the nitrogen necessary for the rice's growth. Currently, *Spirulina platensis* (otherwise known as *Arthrospira platensis*) has been studied as a rich source of protein and essential nutrients (γ -linolenic acid, carotenoids, iodine, protein and vitamins such as B₁₂). Cyanobacteria are also employed as aquacultural feed, e.g. oyster larvae feed mixtures.

The use of cyanobacteria for ecological purposes is just now beginning to develop. Throughout the history of the Earth, these bacteria have played a major role in modifying the environment to suit the current homeostatic parameters of life. This ancient biotechnological property of cyanobacteria is now being harvested, and used for our modern anthropocentric housekeeping. Most gaseous and liquid pollutants are metabolized by cyanobacteria, thereby removing toxic levels of these compounds in the atmosphere

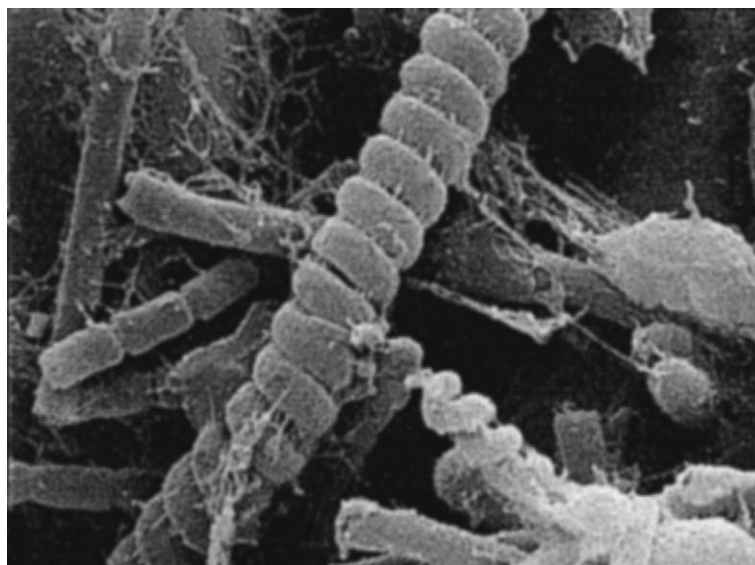


Figure 6 Scanning electron microscope (SEM) micrograph of a microbial mat community. Two different species of *Spirulina* and nonsheeted forms of the *Phormidium* sp. covered by EPS are visible.

and effluents. A number of toxic compounds such as phenolics, pesticides and antibiotics, as well as recalcitrant chemicals such as lignin, can be degraded and detoxified by these bacteria. Biofiltration using *Oscillatoria anaae* cells mixed with sand in a column format has been successfully applied in removing industrial oil wastes. *Anabaena* has been tested for removal of nickel from an electroplating effluent and *Phormidium*, a major component of microbial mats, was used to remove cadmium, lead, chromium, selenium and arsenic from the environment. Additionally, in marine and terrestrial aquatic environments, cyanobacterial biofilms and mats may be employed to fight coastal erosion via their ability to stabilize sediments against hydrodynamic erosional forces (**Figure 6**). **See also:** [Bioremediation](#)

The future development of cyanobacterial biotechnology lies in the application of molecular biological techniques to the varied phenomena represented by the biological diversity in cyanobacteria. The challenge that cyanobacterial biotechnology must meet in future is to fuse basic research with potential applications.

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