

## Cyanobacteria: characteristics and life history

Cyanobacteria are a critical component of the Earth's biosphere and are largely responsible for life as we know it. It was cyanobacteria in the Archaean and Proterozoic Eras (2.7 billion years ago) that were responsible for creating our oxygen atmosphere through their photosynthetic activities (specifically, photosynthesis that split  $H_2O$  to release  $O_2$ ). Before that time the atmosphere had a very different chemistry, unsuitable for life as we know it. Many bacteria split  $H_2S$  instead of  $H_2O$  as a source of electrons during their photosynthesis; this is why they don't produce free  $O_2$ . Cyanobacteria split  $H_2O$ . They were among the first (or the first) organisms to utilize two photosystems (photosystems I and II).

Though cyanobacteria do not have a great diversity of form, and though they are microscopic, they are rich in chemical diversity. The autotrophic cyanobacteria were once classified as "blue green algae" because of their superficial resemblance to eukaryotic green algae. Although both groups are photosynthetic, they are only distantly related: cyanobacteria are prokaryotic and lack internal organelles, a discrete nucleus and the histone proteins associated with eukaryotic chromosomes. Like all eubacteria, their cell walls contain peptidoglycan, not cellulose (like many algae and all plants). Studies of metabolic similarities and ribosomal RNA sequence suggest that cyanobacteria form a good, monophyletic taxon.

Although they are truly prokaryotic, cyanobacteria have an elaborate and highly organized system of internal membranes which function in photosynthesis. Chlorophyll a and several accessory pigments (*phycoerythrin* and *phycocyanin*) are embedded in these photosynthetic lamellae, the analogs of the eukaryotic thylakoid membranes. Cyanobacteria were likely part of a process of *endosymbiosis* by eukaryotic cells, resulting in the chloroplasts found in plant and algal cells.

Cyanobacteria gets its common name from the blue-green pigment, *phycocyanin*, which along with chlorophyll a gives cyanobacteria a blue-green appearance. Phycocyanin is a protein that functions as the photosynthetic pigment in photosystem II, whereas in plants chlorophyll b is the pigment in photosystem II.

Cyanobacteria inhabit a wide variety of habitats that range from frozen lakes to oceans, acidic bogs, deserts and volcanoes. They are most commonly found in alkaline aquatic environments (but also in aquatic environments ranging in salinity and acidity), they can also be found in soil, on rocks, and even in the atmosphere (new studies have found evidence of cyanobacteria in rain and fog). There are a number of unique characteristics of cyanobacteria that are responsible for this wide variety of habitats.

Along with a wide variety of habitats, cyanobacteria also have a range of organization. They can range from unicellular, to filamentous, to colonial. Since cyanobacteria can inhabit some pretty extreme environments they are often the

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primary colonizers of a new area. As primary colonizers they have an important role in adding organic matter to the soil. The cells of a colony are mostly undifferentiated from each other (except for *heterocysts* and *akinetes* – see below). Some colonial forms of cyanobacteria have been known to form mats down on the surface of the soil, which helps to prevent erosion. The filamentous organization is composed of a chain of cells and their enveloping sheath; this organization can be modified or lost as the environment changes.

Most cyanobacteria are photoautotrophic organisms [some are also photoheterotrophic, which means they use light to generate ATP but they must obtain carbon in organic form] that fix CO<sub>2</sub> and release O<sub>2</sub>. Cyanobacteria have a special environmental adaptation for surviving in low CO<sub>2</sub> concentrations, the CO<sub>2</sub> concentrating mechanism (CCM). This mechanism actively transports and accumulates inorganic carbon (HCO<sub>3</sub><sup>-</sup> and CO<sub>2</sub>) within the cell, creating a high CO<sub>2</sub> concentration pool around the CO<sub>2</sub>-fixing enzyme, *Rubisco* (Ribulose-1,5-bisphosphate carboxylase oxygenase is an enzyme that helps to convert carbon dioxide into sugars). You'll see this special CCM type mechanism show up later in plants as C<sub>4</sub> photosynthesis.

Another unique characteristic of some cyanobacteria is their ability to fix elemental (gaseous) nitrogen. They do not have to rely on other combined nitrogen sources. The enzyme complex responsible for this nitrogen fixation is called nitrogenase. In low N<sub>2</sub> environments cyanobacteria will produce *heterocysts*, which are larger, thicker-walled cells that are better at fixing nitrogen. They are one of very few groups of organisms that can convert inert atmospheric nitrogen into an oxidized form, such as nitrate (NO<sub>3</sub><sup>-</sup>) or nitrite (NO<sub>2</sub><sup>-</sup>) or a reduced form as in ammonium (NH<sub>3</sub>) (rhizobium bacteria in soil and on some plant roots can do this too). Nitrification cannot occur, however, in the presence of oxygen, so heterocysts are thick walled and anaerobic. Heterocysts are present as the larger, thick-walled cells in the filaments such as in *Nostoc* or *Anabaena*. The ability of cyanobacteria to fix elemental nitrogen has made it a very important agricultural asset. They have been used as nitrogen fertilizer in the cultivation of rice and beans.

Cyanobacteria may be single-celled or colonial. The single celled forms are coccoid and are among the most abundant phytoplankton in the middle of tropical oceans where nutrient levels are extremely low (small size means high surface area for more absorption). In addition, the coccoid form is prevalent among certain invertebrates, especially sponges, as symbionts. Depending upon the species and environmental conditions, colonies may be filamentous, forming individual chains or complex mats. Filamentous cyanobacteria can also form symbiotic relationships with a wide variety of plant hosts including cycads, rice, ferns, diatoms, mosses and lichens. Some filamentous colonies show the ability to differentiate into three different cell types. Vegetative cells are the normal, photosynthetic cells formed under favorable growing conditions. Climate-resistant spores may form when environmental conditions become harsh (*akinetes*). These are thick-walled cells that are able to resist desiccation (drying out) and freezing. They can remain

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dormant for long periods of time until conditions become right and they germinate. A third type of cell, a thick-walled *heterocyst* (mentioned above).

Cyanobacteria reproduce asexually by fission. Yet they do have three ways of genetic exchange. They can exchange genetic material through a conjugation pilus, which physically connects two adjacent cells. Secondly, transformation can occur, which is the absorption of free DNA, which is then expressed in the host. And the third way in which genetic exchange occurs is through transduction, in which a virus enters the blue-green algae cell and uses its DNA to replace the DNA already in the cell. Mutations are also a common occurrence in cyanobacteria cells. All of these factors help cyanobacteria to overcome its genetic recombination limitations due to asexual reproduction. The colonial and filamentous cyanobacteria reproduce by fragmentation. In fragmentation segments of the parents break off and float away (they are motile). These fragments then grow into new cells.

Cyanobacteria do not have organs for movement such as flagella, but some filamentous blue-green algae do exhibit a gliding movement. It is thought by some to be a result of slime secretion along with contractile waves on the cells.

Blooms of cyanobacteria due to nitrogen-based runoff (either from agricultural fertilizer or waste) have been responsible for killing aquatic life in the Gulf of Mexico, off the coast of North Carolina, and elsewhere. These algal blooms are responsible for the hypoxia (low oxygen) occurring in these areas due to bacterial decomposition of the algae and the Zooplankton waste. Algal blooms such as this have raised concerns over the safety of cyanobacteria in drinking water, and recreational water. It is known that certain species of cyanobacteria produce biotoxins that could be potentially harmful to animals and people in the right concentrations. Cyanobacteria are not all bad. Many are critical components of the ecosystem and serve as nitrogen fixers for other organisms.

### History and extant stromatolites:

Cyanobacteria - the earliest reef builders (>3.5 billion years ago), are still around at the present time. During the Precambrian (>80% of geological time), the only reef-building organisms were mat-forming cyanobacteria. Cyanobacterial mats trap fine-grained carbonate sediment. Each filament forms an external gelatinous sheath containing sticky organic matter (mucilage), to which sediment sticks. When the mat becomes covered in sediment, it grows another layer of filaments through and over the sediment, so it can continue to photosynthesize. Then another layer of sediment is trapped, building up in layers which are alternately organic-rich and sediment-rich. This combination of cyanobacterial mat and sediment is a *stromatolite*. Microbial mats allow fine-grained sediments to be deposited in environments whose energy would normally be too high for such deposition.

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Modern stromatolites are found mainly in warm climates and very shallow water. They occur in shallow subtidal, intertidal environments, and may extend into the supratidal environment where the climate is humid. They also occur in freshwater.

Stromatolites show a variety of forms, related to environmental conditions, such as energy level and rate of sedimentation. This is a simple example of more or less parallel-laminated stromatolites. More complex forms develop when energy and sedimentation rate are high.

Modern stromatolite reefs are very uncommon, but there are some examples

Shark Bay, Western Australia:

Shark Bay is one of only two places in the world with living marine stromatolites, or "living fossils". It also has the distinction of being World Heritage area. Stromatolites are able to survive in the area because Shark Bay's water is twice as saline as normal sea water and seagrasses and many other forms of life cannot survive there.

They look like rocky lumps strewn around the beach but are actually built by living cyanobacteria that use sediment and organic material to build stromatolites up to 1.5 meters high. Because they grow very slowly, a meter-high stromatolite could be millions of years old. When the Shark Bay stromatolites were discovered in 1956, they were the first growing examples ever recorded that accounted for the laminated reef-like mounds found in the Cambrian period. Since then another living stromatolite reef was discovered in the Exuma Islands in the Bahamas.

### Cyanobacteria and the environment

Cyanobacterial mats are common in many environments. The mats themselves are not just composed of cyanobacteria, but are complex communities that co-exist with other bacteria, both photosynthetic and non-photosynthetic. The consortium of organisms that constitutes the mats represent an important micro-community. They not only produce stromatolites (see above), but because the cyanobacteria are often motile they can move across surfaces including those of living corals. Black band disease is the result of one such mat community composed primarily of filaments of the genus *Phormidium*. It was once thought that it was the cyanobacteria that causes black band disease, but it is more likely the associated bacteria, especially the sulfate reducers that form toxic hydrogen sulfide (H<sub>2</sub>S). Cyanobacterial presence is often used an indicator of overall reef health, especially on coral reefs.