Historically, the major groups of algae are classified into Divisions (the equivalent taxon in the zoological code was the Phylum) on the basis of:
- pigmentation,
- chemical nature of photosynthetic storage product,
- photosynthetic membrane (thylakoids) organization and other features of the chloroplasts,
- chemistry and structure of cell wall,
- number, arrangement, and ultrastructure of flagella (if any),
- occurrence of any other special features, and sexual cycles.

Recently, all the studies that compare the sequence of macromolecules genes and the 5S, 18S, and 28S ribosomal RNA sequences tend to assess the internal genetic coherence of the major divisions. This confirms that these divisions are non-artificial, even though they were originally defined on the basis of morphology alone.

Table 1.4 attempts to summarize the main characteristics of the different algal divisions.

• cyanobacteria are possibly the most widely distributed of any group of algae and inhabit marine and freshwater environments, moist soils and rocks, either as free-living or as symbiotic organisms.
• They are
  - planktonic, occasionally forming blooms in eutrophic lakes, and are an important component of the picoplankton in both marine and freshwater systems;
  - benthic, as dense mats on soil or in mudflats and hot springs, as the “black zone” just above the mean high water level on the seashore, and as relatively inconspicuous components in most soils, and
  - symbiotic in diatoms, ferns, lichens, cycads, sponges, and other systems.
• Numerically these organisms dominate the ocean ecosystems.
  - There are approximately 10^24 cyanobacterial cells in the oceans. To put that in perspective, the number of cyanobacterial cells in the oceans is two orders of magnitude more than all the stars in the sky.

Table: Predominant photosynthetic pigments, storage products and cell wall components for the major algal groups.

- Cyanophyta
  - Predominant photosynthetic pigments: Chlorophyll a
  - Storage products: Glycogen
  - Cell wall components: Amino sugars and amino acids

- Cyanobacteria
  - Predominant photosynthetic pigments: Chlorophyll a, some also have chlorophyll b
  - Storage products: Glycogen
  - Cell wall components: Amino sugars and amino acids

- Prochlorophyta
  - Predominant photosynthetic pigments: Chlorophyll b
  - Storage products: Glycogen
  - Cell wall components: Amino sugars and amino acids
Morphology

- It is possible to have more than one trichome in a filament.

- The most complex thallus is the branched filament. Such a branched filament can be uniseriate (composed of a single row of cells) or multiseriate (composed of one or more rows of cells).

- Unicells, free-living, or enclosed within a mucilaginous envelope.
- A row of cells called a trichome. When the trichome is surrounded by a sheath, it is called a filament.

Trichome of Arthrospira sp. (Bar: 20 µm.)
Cells of Prochloron sp. (Bar: 10 µm.)

Cell wall and gliding

- The peptidoglycan is an enormous polymer composed of two sugar derivatives, N-acetylglucosamine and N-acetylmuramic acid, and several different amino acids.
- Outside of the peptidoglycan is a periplasmic space (PS), probably filled with a loose network of peptidoglycan fibrils. An outer membrane (OM) surrounds the periplasmic space.
- Gliding is a slow, uniform motion at a direction parallel to the long axis of the cell and is occasionally interrupted by reversals in direction.
- Gliding is accompanied by a steady secretion of slime, which is left behind as a mucilaginous trail.
- Some cyanobacteria rotate during gliding while other cyanobacteria do not rotate.

Gliding

- The cell wall of gliding bacteria has two additional layers outside of the cell wall.
- A serrated external layer (S-layer) and a layer of hair-like fibers occur outside of the outer membrane of the cell wall of gliding cyanobacteria.
- The hair-like fibers of the outermost layer are composed of a rod-like glycoprotein called oscillin.

Cross section wall of not capable of gliding bacteria
Cross section wall of gliding bacteria

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- Some cyanobacteria rotate during gliding while other cyanobacteria do not rotate.
The cross walls of neighboring cells of gliding cyanobacteria contain junctional pores that are 15 nm in diameter and radiate outward from the cytoplasm at an angle of about 30–40° relative to the plane of each septum. The number of rows of junctional pores around each side of the septum varies from one circumferential ring to several rows of pores that glid the septum. The junctional pore is 70–80 nm long and spans the entire multilayered cell wall. The junctional pore is composed of a tube-like base and an outer pore complex. Gliding occurs by slime secretion through the circumferential junctional pores on one side of the septum. The slime passes along the surface of the oscillin fibers of the outer layer of the cell wall and onto the adjacent substrate, propelling the filament forward.

Reversal of gliding occurs when slime stops coming out of the ring of junctional pores on one side of the septum, and when slime begins coming out of the ring of junctional pores on the other side of the septum.

Sheaths

A sheath (capsule or extracellular polymeric substances (EPS)) composed of mucilage and a small amount of cellulose is commonly present in cyanobacteria. The sheath protects cells from drying. Active growth appears necessary for sheath formation, a fact that may explain its sometimes poor development around spores and akinetes. The sheath of Gloeocapsa sp. is composed of polysaccharides with neutral sugars and uronic acids including galactose, glucose, mannose, arabinose, 2-O-methyl-D-xylene, glucuronic acid and galacturonic acids. The sheath of Gloeothecae contains only 2% protein and a trace of fatty acids and phosphates. The commercial applications of cyanobacterial EPS have been reviewed by De Philippis and Vincenzini (1998). Sheaths are often colored, with – red sheaths found in algae from highly acid soils and – blue sheaths characteristic of algae from basic soils. Yellow and brown sheaths are common in specimens from habitats of high salt content, particularly after the algae dry out.

Pili and twitching

Pili are proteinaceous appendages that project from the surface of cyanobacterial cells (Fig. 2.8). There are two types of pili in the unicellular cyanobacterium Synechocystis.

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S. Synechocystis cells showing pili.
The sheath excludes India ink so the easiest way to visualize the sheath is to place a small amount of India ink in the water (Fig. 2.10).

Production of a sheath is dependent on environmental conditions.
- A shortage of CO₂ results in cessation of sheath production and release of the sheath.
- An excess of fixed carbon results in formation of a sheath.

**Protoplasmic structure**

- Many of the protoplasmic structures found in the bacteria occur in the cyanobacteria.
- In the central protoplasm are the circular fibrils of DNA which are not associated with basic proteins (histones).
- The amount of DNA in unicellular cyanobacteria varies from 1.6×10⁹ to 8.6×10⁹ daltons. This is similar to the genome size in bacteria (1.0×10⁹ to 3.6×10⁹ daltons).
- The peripheral protoplasm is composed principally of thylakoids and their associated structures, the phycobilisomes (on the thylakoids, containing the phycobiliproteins) and glycogen granules.
- The 70S ribosomes are dispersed throughout the cyanobacterial cell but are present in the highest density in the central region around the nucleoplasm.

**Carboxysomes** (polyhedral bodies) are similar to the carboxysomes in bacteria and contain the carbon dioxide-fixing enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco).

- There are two types of carboxysomes, α-carboxysomes and β-carboxysomes, which differ in their protein composition.
  - Cyanobacteria with α-carboxysomes occur in environments where dissolved carbon is not limiting (e.g., oligotrophic oceanic waters), whereas cyanobacteria with β-carboxysomes occur in environments where dissolved carbon is limiting (e.g., mats, films, estuaries, and alkaline lakes with higher densities of photosynthetic organisms).

**Polyphosphate bodies** (metachromatic or volutin granules) are spherical and appear similar to lipid bodies of eukaryotic cells in the electron microscope. Polyphosphate bodies contain stored phosphate, the bodies being absent in young growing cells or cells grown in a phosphate-deficient medium, but present in older cells.

**Polyglucan granules** (α-granules) (Fig. 2.11) are common in the space between the thylakoids in actively photosynthesizing cells. These granules contain a carbohydrate, composed of 14 to 16 glucose molecules, that is similar to amylopectin.

**Cyanophycin** is a non-ribosomally synthesized protein-like polymer that occurs in the cytoplasm in structured granules that are not surrounded by a membrane.

- Cyanophycin is a polymer that consists of equimolar amounts of arginine and aspartic acid arranged as a polyaspartate backbone and arginine side groups.
- Cyanophycin functions as a temporary nitrogen reserve in nitrogen-fixing cyanobacteria, accumulating during the transition from the exponential to the stationary phase and disappearing when balanced growth resumes (upon transfer of the maximum stationary phase culture to conditions suitable for growth).
- Nitrogen is stored in phycobilisomes in cyanobacteria that do not fix nitrogen.

Cyanophycin is composed of equimolar amounts of arginine (Arg) and aspartic acid (Asp) arranged as a polyaspartate backbone.

**Carboxysomes** contain the enzymes carbonic anhydrase and ribulose-1,5-bisphosphate carboxylase/oxygenase. Carbonic anhydrase in the carboxysome converts HCO₃⁻ into carbon dioxide, the only form of carbon that is fixed by Rubisco (Fig. 2.15) into carbohydrates.

- The amount of a cell occupied by carboxysomes increases as the inorganic carbon (HCO₃⁻, CO₂) in the medium decreases.
- Heterocysts lack ribulose-1,5-bisphosphate carboxylase/oxygenase and the ability to fix carbon dioxide. Heterocysts also lack carboxysomes.
• The membrane of the gas vesicle is quite rigid, with the gas inside it at a pressure of 1 atm.
• The membrane is permeable to gases, allowing the contained gas to equilibrate with gases in the surrounding solution.
• The membrane must, however, be able to exclude water.
• It has been postulated that the inner surface must be hydrophobic, thereby preventing condensation on it if water droplets, and restraining, by surface tension, water creeping through the pores.
• At the same time these molecules must present a hydrophilic surface at the outer (water-facing) surface in order to minimize the interfacial tension, which would otherwise result in the collapse of the gas vacuole.

Gas vacuoles
• A gas vacuole is composed of gas vesicles, or hollow cylindrical tubes with conical ends, in the cytoplasm of cyanobacteria.
• Gas vesicles do not have true protein-lipid membranes, being composed exclusively of protein ribs or spirals arranged similarly to the hoops on a barrel.
• It is possible to collapse the gas vesicles by applying pressure to the cells, the collapsed vesicles having the two halves stuck together.

Gas vesicles. These are filled with ordinary air, and are used by cyanobacteria to regulate buoyancy in water, several of these cluster together to make a gas vacuole. The gas can occupy to 9.8% of the volume of the microbe.

The loss of buoyancy, and subsequent sinking of these algae in the water column, can be due to different factors.
- the loss of gas vesicles owing to increased turgor pressure,
- cessation of gas vesicle production and an increase in cell mass,
- entrapment of whole colonies in a colloidal precipitate composed of organic material and iron salts. The colloidal precipitate is formed in certain lakes when dissolved iron in the anoxic water of the hypolimnion in stratified lakes becomes oxidized on mixing with aerated water of the epilimnion.

Cyanobacteria possessing gas vacuoles can be divided into two physiological-ecological groups.
- In the first group are those algae having vacuoles only at certain stages of their life cycle, or only in certain types of cells. In certain species, gas vesicles appear only in hormogonia. The hormogonia float when they are released, and it is possible that the buoyancy provided is of significance in dispersal of these stages.
- The second group consists of planktonic cyanobacteria. These algae derive positive buoyancy from their gas vesicles, and as a consequence form blooms floating near the water surface.

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Such conditions occur in many stagnant eutrophic lakes during the summer.
- In these lakes, rapid growth of algae has depleted the NH\textsuperscript{+4} and CO\textsubscript{2}.
- The water transmits little light because of the large standing crop of algae.
- Under these conditions, A. flosaquae and other nitrogen-fixing cyanobacteria having gas vacuoles increase their buoyancy and rise close to the surface of the water. Here they are able to out compete other algae because of their ability to fix nitrogen in water that has little available nitrogen.
- Cyanobacteria that do not fix nitrogen have reduced growth, and therefore reduced buoyancy, and sink in the water column.
- Once established, a bloom of buoyant, nitrogen-fixing, cyanobacteria tends to be self-perpetuating in that increased mass of the bloom maintains the reduced light and CO\textsubscript{2} levels required for maximum buoyancy.

• There is a direct relationship between buoyancy and light quantity in nitrogen-fixing cyanobacteria such as Anabaena flosaquae.
- The relationship is complex and also involves the concentration of ammonium ions (NH\textsuperscript{+4}) in the water.
- Buoyancy in Anabaena flosaquae increases under
  - low irradiance (less than 10 µEm\textsuperscript{2} s\textsuperscript{-1}),
  - absence of NH\textsuperscript{+4}, and
  - low CO\textsubscript{2} concentrations.
Pigments and photosynthesis

- The structures other than gas vesicles can cause significant variation in cell density, and therefore buoyancy.
  - Polyphosphate granules may have a density of 2 g cm\(^{-3}\) or greater, and
  - glycogen (which is accumulated under high light intensities) has a density of about 1.5 cm\(^{-3}\).
- Both have a higher density than water (1 g cm\(^{-3}\)) and can cause cells to sink.

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An example of this is the Solar Lake, Eilat, Palestine, where in the winter high levels of sulfide are found in the anaerobic bottom layers of water of the thermally stratified lake. Oscillatoria limnetica occurs in these highly anaerobic bottom layers, where sulfide functions as an electron donor for photosynthesis.

- In the spring, the lake overturns, with all of the water becoming aerobic, Oscillatoria limnetica activates aerobic photosystem II and carries out photosynthesis aerobically.

- Thus Oscillatoria limnetica, by utilizing combined anoxygenic and oxygenic photosynthesis, is the dominant phototroph of the Solar Lake, with its fluctuating photoaerobic and photoanaerobic conditions.

- Photosynthesis in many cyanobacteria is stimulated by lowered oxygen concentration, the oxygen competing with carbon dioxide for the enzyme ribulose-1, 5-bisphosphate carboxylase/oxygenase.

- This phenomenon probably reflects an adaptation to the absence of free oxygen in the atmosphere of Precambrian times when the cyanobacteria first evolved.

- After the evolution of the oxygen-evolving cyanobacteria, the oxygen in the atmosphere gradually built up, creating a protective ozone (O3) layer in the atmosphere at the same time. The ozone layer removed most of the harmful ultraviolet radiation from the sun and allowed the evolution of more radiation sensitive organisms.

- The cyanobacteria are relatively insensitive to radiation, having a system that repairs radiation damage.

- In Aphanizomenon, the development of akinetes from vegetative cells involves (1) an increase in cell size, (2) the gradual disappearance of gas vacuoles, and (3) an increase in cytoplasmic density and number of ribosomes and cyanophycin granules.

- Akinetes of Nostoc lose 90% of their photosynthetic and respiratory capabilities, as compared with vegetative cells. The loss occurs even though there is little change in phycocyanin and chlorophyll, the main photosynthetic pigments.

- Mature akinetes are usually considerably larger than vegetative cells; contain protoplasem full of food reserves, and have a normal cell wall surrounded by a wide three-layered coat.

- Akinetes are generally recognized by their larger size relative to vegetative cells and conspicuous granulation due to high concentrations of glycogen and cyanophycin.

- The most consistent property of akinetes is their greater resistance to cold compared with vegetative cells.

- Akinetes have often been compared to endospores in Gram-positive bacteria.

- Akinetes, however, are neither as metabolically quiescent nor as resistant to various environmental extremes.

- Akinetes only occur in cyanobacteria that form heterocysts.

- In Anabaena, the development of akinetes from vegetative cells involves (1) an increase in cell size, (2) the gradual disappearance of gas vacuoles, and (3) an increase in cytoplasmic density and number of ribosomes and cyanophycin granules.

- In akinete germination, there is a reverse of the above events (Fig. 2.24).

- A wide range of physicochemical factors have been reported to stimulate akinete differentiation; for example, phosphate deficiency, low temperature, carbon limitation and reduction in the availability of light energy.

- Loss of flotation by an increase in cytoplasmic density causes filaments with akinetes to sink and overwinter in bottom sediments.

- In akinete germination, there is a reverse of the above events (Fig. 2.24).

- A wide range of physicochemical factors have been reported to stimulate akinete differentiation; for example, phosphate deficiency, low temperature, carbon limitation and reduction in the availability of light energy.

- Heterocysts are generally recognized by their larger size relative to vegetative cells and conspicuous granulation due to high concentrations of glycogen and cyanophycin.

- The most consistent property of heterocysts is their greater resistance to cold compared with vegetative cells.

- Heterocysts can be terminal as in Gloeotrichia, or intercalary as in Anabaena.
Heterocysts have been drastically altered to provide the necessary anoxic environment which is ideal for nitrogenase, a notoriously O₂-sensitive enzyme necessary for the process of nitrogen fixation as following:

- They are photosynthetically inactive because they lose photosystem II thus they do not fix CO₂ nor do they produce O₂.
- They also exhibit a high rate of respiratory O₂ consumption.
- They are surrounded by a thick, laminated cell wall that limits ingress of atmospheric gases, including O₂.
- Heterocysts also have a form of myoglobin called cyanoglobin that scavenges oxygen, preventing inhibition of nitrogenase.

Fig. 2.25 Three-dimensional view of a heterocyst. The envelope has homogeneous (H), fibrous (F), and laminated (L) layers. (M) Membranes; (P) pore channel; (Pl) plasmalemma; (W) cell wall.

Commitment point 1.

- 2-oxoglutarate (α-ketoglutarate) is the substrate used for incorporation of ammonium in cyanobacteria.
- The absence of combined nitrogen leads to an increase in intracellular 2-oxoglutarate since cyanobacteria lack 2-oxoglutarate dehydrogenase and the ability to breakdown 2-oxoglutarate.
- The increase in intracellular 2-oxoglutarate activates the protein NtcA and results in a drop in the amount of the calcium-binding protein Ccbp, and a rise in Ca²⁺ in the cells.
- Heterocysts have 10 times more Ca²⁺ than vegetative cells.
- The rise in Ca²⁺ up-regulates the hetR gene that forms hetR, a serine-type protease, which induces the vegetative cell to change into a heterocyst.
- The hetR protein is considered the "master switch" in heterocyst development.
- The production of hetR protein constitutes commitment point 1.
- A lack of combined nitrogen over a period of about 10 hours results in continued production of hetR protein and the cell becoming a proheterocyst, which under the light microscope appears less granulated than vegetative cells but still lacks a thick cell wall.
- The hetR protein also induces the production of an oligopeptide called PatS.

This oligopeptide diffuses to adjacent cells where it prohibits the formation of hetR protein in the cells and assures that the adjacent cells do not transform into proheterocysts.

- This sets up the spacing seen in Anabaena where heterocysts are formed equidistant from each other.
- Commitment point 1 is reversible. A proheterocyst will revert back to a vegetative cell if combined nitrogen is added to the medium, causing a switch off of the hetR gene and formation of hetR protein.
- Differentiation of a vegetative cell to a proheterocyst also involves loss of photosystem II activity, thus eliminating photosynthetic generation of O₂ (which inhibits nitrogen fixation).

Commitment point 2.

- The second stage cannot be reversed by the addition of combined nitrogen and comprises the transformation of a proheterocyst into a mature heterocyst.
- This involves the formation of a thick cell wall containing glycolipids and polysaccharides to reduce diffusion of O₂.
- The nitrogen-fixing enzyme nitrogenase is activated when 11 and 55 kilobases are removed between repeat sequences flanking nitrogenase (nif) genes.

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- Commitment point 1 is reversible. A proheterocyst will revert back to a vegetative cell if combined nitrogen is added to the medium, causing a switch off of the hetR gene and formation of hetR protein.
- Differentiation of a vegetative cell to a proheterocyst also involves loss of photosystem II activity, thus eliminating photosynthetic generation of O₂ (which inhibits nitrogen fixation).
• It has been shown that the lack of nitrogen in the medium increases the number of heterocysts, whereas nitrogen-rich media inhibit their development.
• Since akinetes and heterocysts share a unique properties, it is hypothesized that akinetes were the evolutionary precursors of heterocysts.
• Akinetes are only seen in heterocyst-forming cyanobacteria, akinetes contain glycolipids characteristic of heterocysts, and the cell wall of heterocysts is identical to that of akinetes (and unlike that of vegetative cells).

• Rearrangement of nitrogen fixation (nif) genes in the heterocysts of Anabaena sp.
• 11 and 55 kb elements are excised and remain in heterocysts as unreplicated and untranscribed circles.
• As a consequence of the 11 kb and 55 kb elements removal from the chromosome a functional nif Operons are created and Nitrogenase proteins are then expressed from the rearranged genes in heterocysts and aerobic nitrogen fixation ensues.

• Nitrogen fixation
  - Cyanobacteria are diazotrophs (able to fix atmospheric nitrogen).
  - In nitrogen fixation, $N_2$ is fixed by the enzyme nitrogenase into ammonium using ATP as a source of energy (Fig. 2.27).
  - Nitrogenase, the nitrogen-fixing enzyme, is very sensitive to inactivation by oxygen. Cyanobacteria have evolved three different mechanisms designed to exclude oxygen from the area of the cells containing nitrogenase.

1. Heterocystous cyanobacteria: These cyanobacteria occur primarily in fresh and brackish water and fix nitrogen in heterocysts (described before).
2. Non-filamentous cyanobacteria that fix nitrogen in the dark but not in the light: These cyanobacteria fix nitrogen in the dark when photosynthesis is not producing nitrogenase-inhibiting oxygen.
3. Trichodesmium and Katagnymene: These cyanobacteria are the major bloom-forming, nitrogen-fixing, organisms in the oceans, responsible for fixing one-quarter of the total nitrogen of the oceans of the world.
   - These filamentous cyanobacteria do not have heterocysts but fix nitrogen in the light under aerobic conditions.
   - Within the filaments, 10 to 15% of the cells (called diazocytes) are specialized to fix nitrogen, while the others do not.
   - Cells that fix nitrogen are adjacent to one another and have a denser thylakoid network with fewer gas vacuoles and cyanophycin granules.
   - The tropical seas where Trichodesmium and Katagnymene live are relatively low in dissolved oxygen and this may assist the nitrogen-fixing cells in maintaining anaerobic conditions in the protoplasm where nitrogenase is present.
   - Trichodesmium and Katagnymene represent the most ancient type of nitrogen fixing cyanobacteria.

• Apart from the exceptional cases of germination, heterocysts are unable to divide.
• Heterocysts have a limited period of physiological activity and appear to have a limited life.
• Senescent heterocysts undergo vacuolation and usually break off from the filament, causing fragmentation of the filament.
• Heterocysts are dependent on a supply of substrates from adjacent vegetative cells through cytoplasmic connections (microplasmodesmata).
• These cytoplasmic connections probably convey nitrogen fixed in the form of glutamine by the heterocysts to vegetative cells.
• The vegetative cells transfer photosynthate to the heterocysts since the heterocysts are incapable of carbon fixation.

Some nitrogen-fixing cyanobacteria that lack heterocysts.
Circadian rhythms

- The cyanobacteria have circadian rhythms in photosynthesis, nitrogen fixation, and cell division similar to those in eukaryotic organisms (Fig. 2.30).

Asexual reproduction

- Asexual reproduction occurs by the formation of hormogonia or baeocytes or fragmentation of colonies.

  (a), (b) Formation of a hormogonium in Oscillatoria. (c) Baeocyte formation in Chamaesiphon incrustans. (d) Baeocyte formation in Dermocarpa pacifica.

  • Hormogonia (or hormogones), which are characteristic of all truly filamentous cyanobacteria, are short pieces of trichome that become detached from the parent filament and move away by gliding, eventually developing into a separate filament.

  • The one common factor in initiation of hormogonium differentiation appears to be a change in some environmental parameter such as an increase or decrease of a nutrient or a change in the quantity of light.

  Fig. 2.35 Nostoc punctiforme. (a) Vegetative cells. (b) Hormogonia. The hormogonia lack heterocysts and are smaller than vegetative cells.

  • Baeocytes (endospores) which literally means "small cell" are formed by some cocccoid (spherical) cyanobacteria. The protoplasm divides several times in different planes without growth between successive divisions.

  • The resulting baeocytes are smaller than the original cell. Baeocytes are similar to bacterial endospores. In Dermocarpella, the baeocytes are released through an apical pore and enlarge to mature organisms.

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Lack of feedback control of enzyme biosynthesis

- Cyanobacteria, such as Chroococcum fritschii (Fig. 2.37), lack metabolic control of many pathways by repression and derepression of enzyme biosynthesis as occurs in many other organisms.

  • In other organisms, as an end product of a pathway builds up to excess, the end product represses an enzyme involved in its synthesis, thereby directing precursors to other parts of the cell's metabolism, where they can be better used. When the amount of end product falls, the enzyme is derepressed, allowing manufacture of the end product again.

  • Cyanobacteria often release considerable quantities of nitrogenous and organic substances into the medium, with most of the compounds being excreted as peptides. Such an excretion could be a necessary consequence of ill-controlled amino acid biosynthesis. Unable accurately to adjust the synthesis of each amino acid to the needs of protein synthesis, the cells would inevitably have to synthesize an excess of amino acids to ensure that protein synthesis would proceed smoothly. This excess would then form the basis of the extracellular peptide material associated with the cyanobacteria.

Growth and metabolism

- In the cyanobacteria there are three nutritional types:

  • (1) facultative chemoheterotrophs, or those organisms capable of growing in the dark on an organic carbon source and of growing phototrophically in the light (only a portion of the cyanobacteria exhibit this condition). Facultative chemoheterotrophs are able to grow in the dark on a very narrow range of substrates, being confined to glucose, fructose, and one or two disaccharides.

  • (2) obligate phototrophs, or organisms that can grow only in the light on an inorganic medium (some of these are actually auxotrophs, requiring a small amount of an organic compound that is not used as a source of carbon, invariably meaning a vitamin);

  • (3) photoheterotrophs, or those cells that are able to use organic compounds as a source of carbon in the light but not in the dark.
Symbiosis

- The cyanobacteria occur in basically two types of associations:
  - those in which the cyanobacterium is extracellular
  - those in which it is intracellular.

Extracellular associations

- In extracellular associations all Cyanobacteria show a decrease in growth, assimilation of CO₂, and assimilation of NH₄⁺.
- Conversely, there is an increase in the rate of N₂ fixation that accompanies the increased numbers of heterocysts.
- The heterocysts and vegetative cells of Nostoc within leaf cavities of Azolla are up to fourfold larger than the vegetative cells of free-living cyanobacteria.
- In the symbiosis, Nostoc receives hexose sugars from the host, while Nostoc provides fixed nitrogen to the host.
- There is also a five- to ten-fold increase in the production of motile hormogonia that serve as infective units in the establishment of the symbioses.

Azolla leaf with Anabaena in gas chamber

- Azolla is a symbiotic superorganism that captures all the nitrogen fertilizer it needs to grow from the air around it. Asia’s farmers have long known this, growing Azolla together with rice to provide a natural fertilizer to bolster rice productivity.

Azolla leaf with Anabaena in gas chamber

• The water fern Azolla (Fig. below) has cavities in the dorsal lobe of the leaf that are occupied by Anabaena azollae.
- This cyanobacterium fixes nitrogen, some of which is excreted into the cavity and taken up by the cells of the Azolla.
- The Anabaena is apparently unable to live outside of the host.
- Nitrogen fixation by the cyanobacterial symbionts of Azolla has for many years been utilized to advantage in the Far East; here the water fern has been used as a green manure in rice fields, where about 3 kg of atmospheric nitrogen per hectare per day is fixed by Azolla symbionts.

Azolla leaf with Anabaena in gas chamber

• The most common type of extracellular association is that with fungi to form lichens.
- In most lichens, there is a single algal component (phycobiont), which is a green alga, cyanobacterium, or, as with the fungi species Verrucaria, a member of the Xanthophyceae.
- Cyanobacteria occur in about 8% of the species of lichens (Fig. 2.38).
- Almost all of the fungal partners (mycobionts) are ascomycetes, but certain imperfect fungi and Basidiomycetes also occur in lichens.
- Because the mycobionts frequently reproduce sexually whereas the phycobionts usually do not, the lichens are classified with the fungi.
- In the symbiotic association, the phycobiont fixes carbon in photosynthesis and liberates it as glucose, which the mycobiont converts into mannitol and assimilates (Fig. 2.38).

Azolla leaf with Anabaena in gas chamber

• Cycad roots are frequently infected with cyanobacteria that cause distortions of the roots (cortical nodules) (Figs. a, b). In these roots the cyanobacteria occupy a clearly defined cortical zone midway between the pericycle and the epidermis. The cyanobacteria occur in the intercellular spaces and are surrounded by a sheath and a multilayered wall, whereas the adjacent cycad cells have a reduced chromosome number and secrete slime. These cyanobacteria are able to fix nitrogen and contribute a portion of the fixed nitrogen to the cycad cells.

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Azolla leaf with Anabaena in gas chamber
Approximately 40% of the photosynthetic capacity of the alga is secreted as glucose in the lichen association.

Whereas the benefits to the fungus in the association are obvious, the benefits to the alga are probably limited to some protection against desiccation.

Intracellular associations

- Intracellular associations involving cyanobacteria are usually more specialized than extracellular associations, and it is not possible to culture the cyanobacteria away from the host.
- The term cyanelle is used for intracellular cyanobacteria in symbioses, and the term cyanome for the host cell.
- It is probable that one of the endosymbiotic associations led to the development of chloroplasts in some of the algal groups.

Ecology of cyanobacteria

Marine environment

Littoral zone
- Cyanobacteria in the littoral zone occur as a black encrusting film on rocks at the upper limit of the high-tide mark. Most of the cyanobacteria in the littoral zone are nitrogen fixing, and they make a significant contribution to the productivity of rocky shores and coral reefs.

Open ocean cyanobacteria
- In the open ocean, most of the total photosynthetic capacity is made up of picophytoplankton (phytoplankton cells unable to pass through a filter with 2-µm-diameter holes), made up principally of tiny coccoid cyanobacteria at concentrations of around 10,000 cells per milliliter.
- The picophytoplanktonic cyanobacteria are more evident in nutrient-poor offshore waters where larger phytoplankton are less successful, because they are less able to utilize low concentrations of nutrients.

- Trichodesmium moves up in the water column by means of gas vesicles, and moves down in the water column by carbohydrate ballasting. The cells become progressively heavier from morning to evening as carbohydrates and polyphosphate bodies are produced.
- In the Caribbean, *Trichodesmium* cells have been found down to 200 m. The gas vesicles of this cyanobacterium are much stronger and more difficult to collapse than those found in any freshwater alga. The gas vesicles are able to stand up to 20 atm of pressure, enabling *Trichodesmium* to rise from great depths.
- Colonies of the coral *Montastraea cavernosa* contain endosymbiotic coccoid cyanobacteria in vacuoles in the epithelial cells of the coral. The cyanobacteria are capable of nitrogen fixation. Anoxic conditions (necessary for function of the nitrogen-fixing enzyme nitrogenase) are created by the Mehler reaction where glycerol provided by dinoflagellate zooxanthellae is reduced.

- Cyanobacteria larger than picophytoplankton often form a significant part of oceanic phytoplankton.
- Massive development of filaments of the nitrogen-fixing *Trichodesmium* occurs in certain tropical waters.
- Each colony of *Trichodesmium* consists of a mass of filaments that secrete a flocculent mucilage which supports bacterial colonies; these in turn are fed on by different protozoa. The large surface area produced by the algal filaments forms a miniature ecosystem.
- *Trichodesmium* produce gas vacuoles which, under calm conditions, cause the cells to accumulate at the water surface, giving rise to the phenomenon known to sailors as *sea sawdust*, or long orange or gray windrows of algae.
- One such bloom stretched 1600 km along the Queensland coast of Australia, extending from the shore to the Great Barrier Reef, and occupying an area of 52,000 km².
- *Trichodesmium* also occurs in the Red Sea, and it was probably the color produced by blooms of the alga that gave the Red Sea its name.
**Hot-spring cyanobacteria**

- Cyanobacteria are important in the colonization of non-acidic hot springs through out the world.
- Some cyanobacteria have the ability to grow at temperatures as high as 70 to 73°C, a much higher temperature tolerance than occurs in eukaryotic algae.
- In thermal environments above 56 to 60°C, both photosynthetic and nonphotosynthetic eukaryotic algae are always absent.
- In acid springs (pH less than 4), no cyanobacteria are present, and at temperatures above 56°C in these springs there are no photosynthetic organisms at all.
- The **thermophilic** cyanobacteria are especially adapted to live at elevated temperatures. Enzymes isolated from thermal algae are more stable at higher temperatures than those from other organisms.

**Freshwater environment**

- Freshwater blooms of cyanobacteria are common. Most freshwater blooms of cyanobacteria consist of *Microcystis, Anabaena, Aphanizomenon, Gloeotrichia, Lyngbya* or *Cylindrospermum*.
- Although they occur in lakes over the whole year, it is usually only in late summer and early autumn that they reach bloom proportions.

**Anhydrobiotics** are organisms that can withstand the removal of the bulk of their intracellular water for extended periods of time.

- The cosmopolitan terrestrial cyanobacterium *Nostoc commune* is able to tolerate acute water stress and can survive in the air-dry state for many years.
- Approximately 0.1 g of blackened air-dried colonies becomes an olive-green rubbery mass of more than 20 g wet weight within 30 min of rehydration.
- In *Nostoc commune*, rehydration rather than desiccation appears to be the fatal event.
- To protect the cells during rehydration, a water stress protein and large amounts of the sugar trehalose are synthesized that stabilize the phospholipid bilayers of cellular membranes.
- This because of:
  1. The superior light-capturing abilities of cyanobacteria when self-shading is the greatest.
  2. Their high affinity for nitrogen and phosphorus when nutrient limitation is most severe.
  3. Their ability to regulate their position in the water column by gas vacuoles to take advantage of areas richer in nutrients and/or light.
  4. Their higher temperature optima for growth and photosynthesis (greater than 20°C).

**Terrestrial environment**

Terrestrial cyanobacteria play a major role as primary colonizers in the establishment of a soil flora and in the accumulation of humus.

They do this in four main ways:

1. They bind sand and soil particles and prevent erosion. They do this with their gelatinous sheaths and by their growth pattern which produces closely intertwined rope-like bundles in and among soil particles.
2. They help to maintain moisture in the soil. Booth (1941), found that soil with an algal covering had a moisture content of 8.9% compared to 1.3% in the absence of algae.
3. They are important as contributors of combined nitrogen through nitrogen fixation. In grass lands, the soil surface between crowns of grasses may support extensive zones of cyanobacteria and lichens that include cyanobacteria as their phycobiont constituting up to 20% of the ground cover.
4. It has been suggested that cyanobacteria assist higher plant growth by supplying growth substances.

**Microcoleus vaginatus** (Fig. 2.45) makes up over 90% of cryptobiotic crusts in the arid soil of the Colorado Plateau in the United States.

- Filaments of *M. vaginatus* are surrounded by thick mucilaginous sheaths that can absorb eight times their weight in water, increasing the water capacity of sandy soils.
- Clay particles and sand grains become trapped in the cyanobacterial sheaths (Fig. 2.45).
- The clay particles are negatively charged and bind positive cationic nutrients (e.g., K⁺, Ca⁺⁺) preventing them from leaching into the subsoil.
- Subsequently, lichens, fungi and moss establish themselves in the crust, enriching and stabilizing the soil.

**Cyanobacteria** comprise the dominant component of the soil photosynthetic community in hot and cold arid regions where higher plant vegetation is absent or restricted.

- Desert **cryptobiotic crusts** (also called biological soil crust) are initiated by the growth of cyanobacteria in the soil during episodic events of available moisture.
- The only cyanobacteria that are initial colonizers are those that
  - have heterocysts, and are therefore able to fix nitrogen;
  - and those cyanobacteria that produce *scytonemin*, a sunscreen that accumulates in the cyanobacterial sheaths and absorbs some of the strong sunlight in the near ultraviolet (370–384 nm).

**Calculations**

- Approximately 0.1 g of blackened air-dried colonies becomes an olive-green rubbery mass of more than 20 g wet weight within 30 min of rehydration.
- In *Nostoc commune*, rehydration rather than desiccation appears to be the fatal event.
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Adaption to silting and salinity

- In salt marshes and mud flats, Microcoleus chthonoplastes are phototactic and chemotactic, resulting in migration to the surface of the mud at a rate of about 7 mm per 24 h. The movement of the filaments is an adaption that allows the cyanobacterium to survive during silting.
- M. chthonoplastes is euryhaline, it is able to survive in a wide range of salinities in the estuarine environment by producing glycosylglycerol as an osmolyte to counteract the osmolarity of the surrounding environment.
- It also synthesizes trehalose to stabilize the phospholipid membrane bilayers of the cell.

Cyanotoxins

- Some of the cyanobacteria produce toxins (cyanotoxins).
- Physiologically, there are basically two types of cyanotoxins: neurotoxins and hepatotoxins.
- Neurotoxins – The neurotoxins are alkaloids (nitrogen-containing compounds of low molecular weight) that block transmission of the signal from neuron to neuron and neuron to muscle in animals and man. Symptoms include staggering, muscle twitching, gasping and convulsions.
- The neurotoxins can be fatal at high concentrations due to respiratory arrest caused by failure of the muscular diaphragm.
- The two neurotoxins produced by cyanobacteria are anatoxin and saxitoxin. Anatoxins are synthesized by species of Anabaena, Aphanizomenon, Oscillatoria and Trichodesmium.

- In hypersaline environments, halotolerant and halophilic cyanobacteria can adapt to the high salinity in three ways:
  1. Active export (influx) of inorganic ions that steadily diffuse along their electrochemical gradients into the cytoplasm leading to relatively unchanged internal salt concentrations.
  2. Accumulation of organic osmoprotective compounds, such as glucosylglycerol, glycine, and betaine (trimethylglycine), to maintain the osmotic equilibrium.
  3. Expression of a set of salt-stress proteins such as the protein flavodoxin.

- Hepatotoxins – The hepatotoxins are inhibitors of protein phosphatases 1 and 2A and affect the animal by causing bleeding in the liver.
- Clinical signs include weakness, vomiting, diarrhea, and cold extremities.
- Cyanobacteria produce two types of hepatotoxins, the microcystins and nodularins, that are produced along a similar pathway.
- Microcystins are synthesized by species of Microcystis, Anabaena, Nostoc, Nodularia, and Oscillatoria while the nodularins are produced by species of Nodularia.
• Another allelopathic interaction involves the zebra mussel (Dreissena polymorpha) and the cyanobacterium Microcystis.
• Zebra mussels, native to the Black and Caspian seas, were discovered in the United States near Detroit in 1988. Since then zebra mussels have spread throughout the Great Lakes of North America, displacing native shellfish. The zebra mussel has been beneficial in low-nutrient lakes (but not in lakes high in nutrients) because they graze on Microcystis, probably because the mussels have nothing else to eat (Raikow et al., 2004).
• https://www.kbs.msu.edu/images/stories/docs/hamilton/raikow.pdf

Cyanobacteria and the quality of drinking water

• Geosmin (E-1,10-dimethyl-E-9-decalol) and MIB (2-methylisoborneol) are two terpenoids (isoprenoids) that are produced by some cyanobacteria.
• These terpenoids are called volatile organic compounds (VOCs), have a highly potent earthy, musty or muddy aroma and account for most of the odors in drinking water. They have odor threshold concentrations of ~10 ng l⁻¹.
• Terpenoids as a class have extensive olfactory properties, which are exploited commercially in the food, beverage, and perfume industries. Both geosmin and MIB resist conventional water treatment, and their bioaccumulation in fish and shellfish causes off-flavor in farmed and wild stocks.
• Neither geosmin nor MIB are toxic to vertebrates (including humans).
• The low incidence of human poisonings by cyanotoxins has been attributed to the avoidance of water containing cyanobacteria because of the odors produced by geosmin and MIB.
• Both compounds are commonly found in freshwater and solid habitats, but are rare in offshore marine environments, and can be used as landmass indicators.
• These volatile organic compounds produced by cyanobacteria act as infochemicals by attracting nematodes to cyanobacterial colonies where the nematodes feed and deposit eggs.

Utilization of cyanobacteria as food

• Cyanobacteria are used as human food and animal food supplements. In China, the Spirulina industry is supported by the State Science and Technology Commission as a natural strategic program. In 1996 there were more than 90 Spirulina factories with a total production of 400 tons of Spirulina dry powder and a total production area of 1 million square meters.
• Besides Spirulina pills and capsules, there are also pastries, blocks, and Spirulina-filled chocolate blocks.
• Nostoc is a cyanobacterium that has been gathered for food for over two thousand years in China. It is called “hair vegetable” because of its hair-like appearance. The Chinese word for “hair vegetable” (Facai) sounds like another Chinese word that means fortunate and get rich, adding a spiritual value to the cyanobacterial food.
• In Japan, Aphanothece sacrum, Nostoc verrucosum, N. commune, and Brachytrichia have been used as side dishes since ancient time.
Cyanophages

- Cyanophages are viruses that infect and commonly kill cyanobacteria.

- Most cyanobacteria are actually resistant to attack by cyanophages with the cyanophage population being maintained by infection of the relatively rare cyanobacteria that are susceptible to infection.

- Cyanobacteria in the open ocean are more susceptible to infection than cyanobacteria from inshore waters.

- High temperature and phosphate limitation increase the probably of cyanobacterial infection by cyanophages.

Secretion of siderophores

- The obligate requirement for iron, coupled with the low solubility of iron in many aquatic habitats, has led to the evolution of a mechanism for iron acquisition, at the cost of cellular energy and nutritional stores.

- A number of cyanobacteria release extracellular ferric-specific chelating agents (“siderophores”) during periods of low iron availability.

- Siderophores function as extracellular ligands that complex with iron ions Fe³⁺ in the medium. The siderophore complexed iron ions are absorbed by the cell (Fig. 2.52).

Secretion of antibiotics and siderophores

- Some cyanobacteria, such as Nostoc, secrete antibiotics called bacteriocins, which kill related strains of the alga.

- A bacteriocin is a proteinaceous antibiotic that is active against prokaryotic strains closely related to the organism that produces the antibiotic.

- Other cyanobacteria secrete antibiotics that are active against a wide range of cyanobacteria and eukaryotic algae.

- Scytonema hofmanni (Fig. 2.46(e)) produces such an antibiotic. This antibiotic, called cyanobacterin, is a chlorine-containing \( \lambda \)-lactone.

- All of these antibiotics probably play an active role in the survival of the producing organism by inhibiting growth of competing organisms.

Calcium carbonate deposition and fossil record

- Many species of cyanobacteria have calcium carbonate in the enveloping mucilage of the cells.

- In fresh water these algae usually grow in water where carbonate crystallizes out by non-biological physicochemical mechanisms, and the crystals of calcite become trapped in the mucilage of the algae. Normally only 1% to 2% of the calcium carbonate is actively precipitated by the cells.

- There are a large number of different forms of carbonate deposits attributed to the Cyanophyceae.

- During the night, growth ceases, and sediments accumulate on the surface of the head, forming sediment-rich laminae up to 100 µm thick.

- In the early part of the day, the algae penetrate through this deposited sediment, and grow a hyaline layer, 200 µm thick, with a low concentration of entrapped sediment.

- These alternating periods of growth and deposition give a laminated structure to the stromatolite.
• In addition, stromatolites are heliotropic and grow toward sunlight. This heliotropism allows the calculation of the extent of a day’s deposition in a stromatolite.
• The yearly cycle of movement of the sun causes the sun to be higher in the sky in the summer and lower in the winter.
• The heliotropism of the stromatolites causes the stromatolites to grow in a sine waveform over the course of a year (Fig. 2.55).
• Counting the number of laminae in one sine wave has allowed paleontologists to calculate the number of days in a year for a geological period.
• Such studies have shown that the solar year has varied considerably. For example, approximately 1000 million years ago, the solar year consisted of approximately 435 days.

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Fig. 2.55 Diagrammatic representation of the growth of a stromatolite over the period of a year. A year’s growth is represented by an S-shaped curve.

Classification

• Cyanobacteria are divided into three orders:
  • Order 1 Chroococcales: single cells or cells loosely bound into gelatinous irregular colonies i.e. palmelloid colonies. Prochlorococcus marinus is the dominant photosynthetic organism in tropical and temperate oceans.
  • Order 2 Oscillatoriales: These are filamentous cyanobacteria without heterocysts.
  • Order 3 Nostocales: filamentous cyanobacteria with heterocysts.
• http://www.dr-ralf-wagner.de/Blaualgen-englisch.html

• The production of laminae in stromatolites depends on fluctuations ultimately derived from the physical movements of the earth, sun, and moon, and requires some kind of rhythmicity that causes discontinuity in the accretionary process.
• The periodicity of laminae is due primarily to the daily photosynthetic cycle of the organisms in the stromatolites.

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