Chapter 3

Introduction to cyanobacteria

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INTRODUCTION

Cyanobacteria are a very diverse group of prokaryotic organisms that thrive in almost every ecosystem on earth. In contrast to other prokaryotes (bacteria and archaea), they perform oxygenic photosynthesis and possess chlorophyll-*a*. Their closest relatives are purple bacteria (Woese et al., 1990; Cavalier-Smith, 2002) – and chloroplasts in higher plants (Moore et al., 2019). Photosynthetic activity of cyanobacteria is assumed to have changed the earth's atmosphere in the Proterozoic Era some 2.4 billion years ago during the so-called **Great Oxygenation Event** (Hamilton et al., 2016; Garcia-Pichel et al., 2019).

Historically, cyanobacteria were considered as plants or plant-like organisms and were termed "Schizophyceae", "Cyanophyta", "Cyanophyceae" or "blue-green algae". Since their prokaryotic nature has unambiguously been proven, the term "cyanobacteria" (or occasionally "cyanoprokaryotes") has been adopted in the scientific literature. A metagenomic study by Soo et al. (2017) revealed that cyanobacteria also comprise groups of

nonphotosynthetic bacteria and the taxon Oxyphotobacteria is proposed for cyanobacteria in a strict sense. However, in this volume, the term "cyanobacteria" will be used for photosynthetic, oxygenic bacteria.

3.1 CELL TYPES AND CELL CHARACTERISTICS

As prokaryotes, cyanobacteria lack a cell nucleus and other cell organelles, allowing their microscopic distinction from most other microalgae. In particular, cyanobacteria lack chloroplasts, and instead, the chlorophyll for the photosynthesis is contained in simple thylakoids, the site of the light-dependent reactions of photosynthesis (exception: *Gloeobacter* spp. not possessing thylakoids). Cyanobacteria occur as unicellular, colonial or multicellular filamentous forms. Diverse forms populate all possible environments where light and at least some water and nutrients are available – even if only in very low quantities. Examples for extreme environments in which cyanobacteria can be encountered are caves or deserts (Whitton & Potts, 2000). This volume primarily considers cyanobacteria in the aquatic environments where they may grow suspended in water (i.e., as "plankton"), attached to hard surfaces ("benthos" or "benthic", respectively), or to macrophytes or any other submerged surfaces ("periphytic" or "metaphytic").

Sexual reproduction has not been observed for cyanobacteria; therefore, their only means of reproduction is asexual, through division of vegetative cells.

The morphology of cyanobacterial cells shows a number of characteristics that can be used for microscopic examination and identification: primarily, the shape and size of cells, subcellular structures and specialised cells (Figure 3.1–3.3). Cyanobacterial cells can be spherical, ellipsoid, barrel-shaped, cylindrical, conical or disc-shaped. Some taxa include cells of different shapes. Cyanobacteria do not possess flagella, as are found in many other bacterial or phytoplankton taxa. Nevertheless, many cyanobacteria, in particular filamentous forms, show gliding motility, the mechanism of which is not yet fully understood (Hoiczyk, 2000; Read et al., 2007).

The size of cyanobacteria varies considerably between taxa: more or less spherical cells of unicellular cyanobacteria range in diameter from about 0.2 μm to over 40 μm. In consequence, cell volume may vary by a factor of at least 300 000, making simple cell counts an unreliable parameter for the determination of biomass, especially when reported without differentiation between individual taxa (see Chapter 13). Some filamentous forms have been observed to have cell diameters of up to 100 μm, but as these coin-shaped cells are generally very short, their cell volume is not necessarily much larger than that of other species (Figure 3.2; Whitton & Potts, 2000). The length of filaments (or trichomes; see below) can reach a few millimetres in certain benthic forms. Very small cells of cyanobacteria (in the size range 0.2–2 μm) have been recognised as a significant fraction of

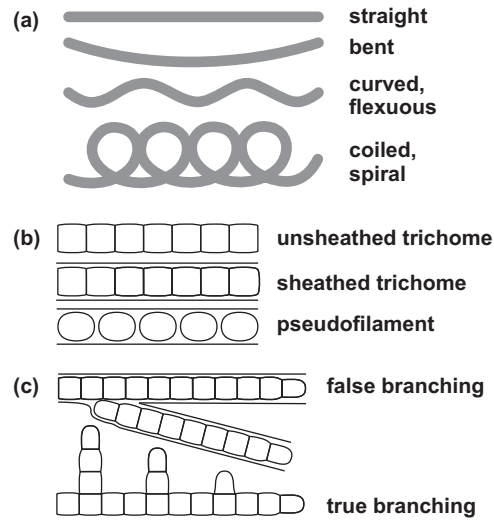

Figure 3.1 Characteristics of cyanobacteria filaments. (a) General shapes; (b) presence of sheaths; (c) branching types.

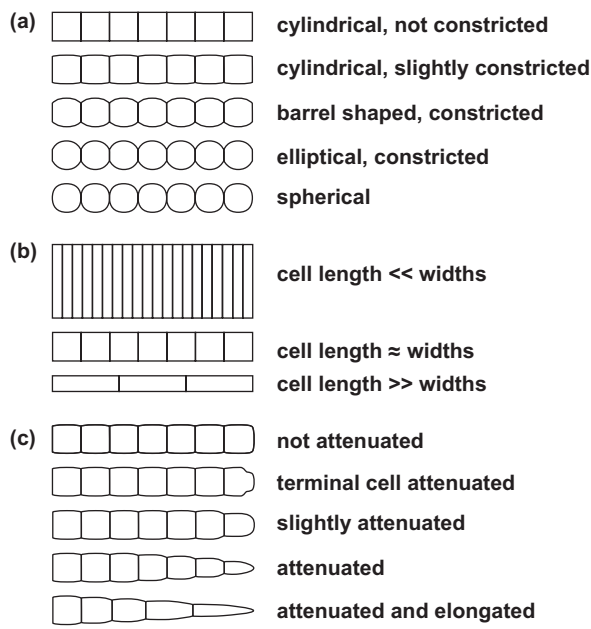

Figure 3.2 Characteristics of cyanobacteria filaments. (a) Cell shapes and arrangement in filaments; (b) cell length-to-width ratios; (c) filament terminal region.

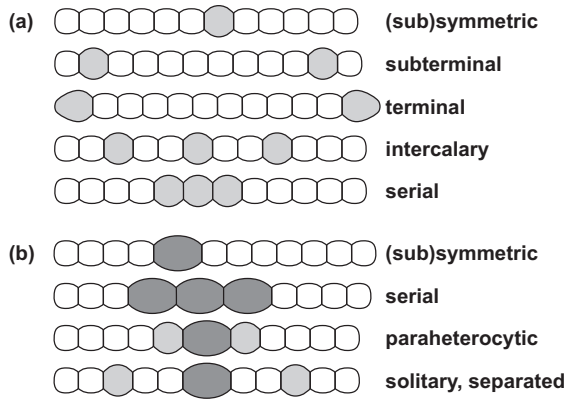

Figure 3.3 Arrangement of heterocytes (a) and akinetes (b) in filamentous cyanobacteria.

the so-called **picoplankton** in various freshwater and marine environments, such as *Prochlorococcus* that is found in huge numbers in the world's oceans (Flombaum et al., 2013). The occurrence of picocyanobacteria in freshwaters is well established (Postius & Ernst, 1999; Stomp et al., 2007) but possibly is underestimated, especially when biomass estimates are based on microscopy. With molecular tools such as metagenomics (section 13.4), our understanding of the role of picocyanobacteria in lake ecosystems may increase (Śliwińska-Wilczewska et al., 2018; Nakayama et al., 2019).

A number of cyanobacterial taxa can (facultatively) produce so-called **aerotopes** that are clearly visible in microscopy as light-refracting structures. Aerotopes (sometimes incorrectly named "gas vacuoles" – they are not vacuoles in the cytological sense) are bundles of cylindrical protein microstructures that form the **gas vesicles**. These vesicles are filled with air entering the lumen by diffusion (see Walsby (1994) for an extensive review). Gas vesicles have a density of about one-tenth of that of water and thus render the entire cells less dense than water, providing buoyancy and making them float or emerge to the water surface (see Section 3.2). The gas vesicles measure some 75 nm in diameter and up to 1.0 µm in length. The cylinders, capped by conical ends, are formed by a single wall layer of 2 nm thickness. The distribution of aerotopes within the cells is characteristic for individual taxa and can be used for identification by microscopical examination, but they can disintegrate after fixation with Lugol's solution (see Chapter 13).

Other subcellular (ultrastructural) characteristics such as the distribution of thylakoids are used in taxonomic studies (Hoffmann et al., 2005; Komárek et al., 2014). As thylakoids are not visible using light microscopy with standard equipment, other methodologies are generally applied for their examination, such as transmission electron microscopy.

In some groups of cyanobacteria (see Table 3.1), specialised cells occur, which are morphologically different from vegetative cells and which can be

Table 3.1 Major groups of cyanobacteria in the taxonomic schemes proposed by Castenholz et al. (2001) and Cavalier-Smith (2002)

Group	*Morphological characteristics*	*Genera (selection)*
Subsection I "Chroococcales"	• Unicellular • Colonies with regular or irregular cell arrangement • Embedded in extracellular mucilage	*Aphanocapsa, Gomphospheria, Merismopedia, Microcystis, Synechococcus, Synechocystis, Woronichinia*
Subsection 2 "Pleurocapsales"	• Colonial or filamentous • Reproduction through baeocytes	*Pleurocapsa, Chroococcidiopsis, Cyanocystis*
Subsection 3 "Oscillatoriales"	• Multiplication by hormogonia • Unbranched, linear filaments • No heterocytes or akinetes • Cells typically shorter than broad	*Leptolyngbya, Lyngbya, Microcoleus, Oscillatoria, Phormidium, Planktothrix, Pseudanabaena, Tychonema*
Subsection 4 "Nostocales"	• Multiplication by hormogonia • Nonbranching or false branching • Heterocytes (can be absent in individual filaments) • Akinetes	*Anabaena, Aphanizomenon, Raphidiopsis (Cylindrospermopsis), Cuspidothrix, Chrysosporum, Dolichospermum, Nostoc, Sphaerospermopsis*
Subsection 5 "Stigonematales"	• Multiplication by hormogonia • True branching • Heterocytes (can be absent in individual filaments) • Akinetes	*Chlorogloeopsis, Fischerella, Stigonema*

The morphological characteristics are based on microscopic observation. Exemplary genera are given for subsections.

generally easily recognised by light microscopy (see examples below), that is, heterocytes and akinetes.

Heterocytes are specialised cells that allow the fixation of atmospheric nitrogen, a process also called **diazotrophy** that involves nitrogenases, enzymes capable to reduce nitrogen to ammonium (Berman-Frank et al., 2003). Note that "heterocyte" is the more appropriate term than the traditionally used term "heterocyst" because a "cyst" has another, clearly defined meaning in cytology. Both terms may be seen as synonyms, while in this volume the term "heterocyte" is preferred.

Heterocytes lack the complete photosynthetic apparatus, thus avoiding the production of oxygen which would irreversibly damage nitrogenases (Bothe et al., 2010). Further, they possess a thickened cell wall, which further supports the anoxic intracellular milieu needed for diazotrophy.

Heterocytes often differ in size and shape from vegetative cells. In the microscope, they are generally easily recognised due to their different size and light refraction properties. Their number and the location of heterocytes in filaments can be used for taxonomic determination (Figure 3.3), although heterocyte formation depends on environmental

and physiological conditions and may hence vary. They may be completely absent under conditions of ample availability of inorganic nitrogen. For example, *Aphanizomenon* spp. without heterocytes may be confused with *Planktothrix agardhii* if the terminal cells of the filaments are not examined carefully. Some authors suggested that *Raphidiopsis* spp. could be a nonheterocytous stage or type of *Cylindrospermopsis* spp. as recent studies showed both taxa to be phylogenetically very close (Moustaka-Gouni et al., 2009) and should hence be combined (Aguilera et al., 2018).

Akinetes are resting stages that can be found in the same taxa that form heterocytes. They are characterised by a generally (much) larger size compared to vegetative cells and different light refraction in microscopic view. Their cell wall is multilayered, and they often contain granules of glycogen and cyanophycin but generally no polyphosphate granules. Akinete formation and germination is triggered by environmental conditions (Adams & Duggan, 1999).

The position, number and distribution of the heterocytes and akinetes are important morphological characteristics of species and genera. Heterocytes can be in an intercalary position between vegetative cells, that is, in the middle of a trichome, or terminal or subterminal. Akinetes are in an intercalary or subterminal position but generally not terminal. Because the formation of heterocytes and akinetes is triggered by environmental conditions, individual species can appear variable in natural samples or strain cultures. The distribution of these specialised cells also determines the symmetry of the trichome.

3.2 MORPHOLOGY OF MULTICELLULAR FORMS

Most cyanobacterial taxa form multicellular aggregates, and the size and shape of which can be used for the identification of cyanobacteria in freshly collected field samples. In conserved samples, however, these aggregates may disintegrate, rendering identification more difficult (see Chapter 13).

One important characteristic for identification is the type of cell division and the separation of cells following division – or the lack thereof.

In unicellular forms (e.g., *Synechococcus* sp.), dividing cells separate completely and do not form (true) filaments. Some "unicellular" species, however, can form microbial mats or colonies by embedding single cells in a mucous matrix (mucilage). In cultures, species forming colonies in natural environments often grow as singular cells or form aggregates with a morphology that differs clearly from that of naturally occurring colonies. Experimental studies with *Microcystis* sp. indicate that the presence of heterotrophic bacteria triggers the production of extracellular polysaccharide (EPS), a prerequisite for colony formation, while axenic strains generally grow as single cells (Shen et al., 2011; Wang et al., 2016).

In natural populations, colony morphology may change during the seasonal cycle (Reynolds et al., 1981). The arrangement of the cells in a colony can be completely irregular as a result of multiple cell division panes

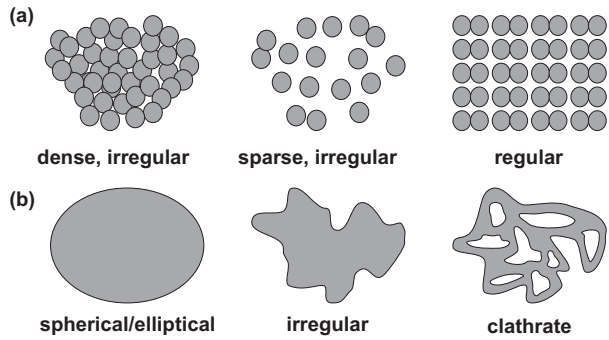

Figure 3.4 Arrangement of cells in colonies (a) and overall shapes of colonies (b).

(e.g., most *Microcystis* sp.) or through series of cell divisions in only two panes, very regular, forming two-dimensional sheets (e.g., *Merismopedia*, Figure 3.4). Colonies can be composed of hundreds or even thousands of cells and reach sizes of some hundred micrometres to a few millimetres, visible with the naked eye. A particular colony form is given when cell division occurs in a single pane, leading to so-called **pseudo-filaments**, linear colonies of singular cells in a mucilaginous sheath, for example, in *Cyanodictyon* spp.

In filamentous forms, cells remain adhered to each other after division, forming chains of connected cells termed "trichomes". Trichomes can be enveloped in a **mucous sheath** in some taxa and are then called **filaments** (Figure 3.1). The general term hence is "trichome", but the term "filament" is often used interchangeably in the literature, as in this volume. Individual cells forming a trichome can be cylindrical, barrel-shaped or nearly spherical, and the corresponding trichomes appear either like a smooth thread or like a pearl necklace, respectively. Trichomes can be completely smooth with cell walls not visible or more or less deeply constricted (Figure 3.2). The cell shape is characteristic for different taxonomic groups, which can also represent different genera (Komárek, 2013). The length-to-width ratio of vegetative cells and the type of connections between them within trichomes are often characteristic for genera. In most filamentous taxa, cell division occurs only in a single division plane, resulting in filament growth by extension in only one dimension. From a single sheath, trichomes can protrude in multiple directions appearing as branched filaments. Such a **"false" branching** combines one-dimensional filaments in a multidimensional manner (e.g., *Scytonema* sp.). Some filamentous taxa perform cell division in more than one plane leading to a **true branching** (e.g., *Fischerella* sp.). Terminal vegetative cells in trichomes often show a shape and size distinctly different from that of cells within the filament (Figure 3.2). This includes elongation, tapered or pointed ends, swelling, or the covering with a **calyptra**, a mucilaginous, cap-like structure.

Multiple filaments can aggregate, forming macroscopically visible clusters. For example, under field conditions, *Aphanizomenon flosaquae* forms

clusters (**fascicles**) with the shape and size similar to tiny conifer needles or blades of grass that can be easily recognised in water samples. In many *Nostoc* species, a large number of trichomes is embedded in a common mucilage forming large macroscopic structures of varying shapes (spheres in *Nostoc pruniforme*, sheets in *N. commune* or strings *N. flagelliforme*). Filaments of benthic cyanobacteria can aggregate to macroscopic clusters several decimetres long ("mermaids-hair" of marine *Lyngbya* spp.) or tufts that can completely cover hard surfaces (*Phormidium* spp. in streams or rivers).

Filamentous forms can form reproductive, motile units, the so-called **hormogonia**. They develop by fragmentation of trichomes and the release of short chains of cells from the immotile, unsheathed parental trichome. Hormogonial cells may or may not be different in size and shape from vegetative cells. They show active gliding motion when liberated from filaments and gradually develop into new filaments.

Baeocytes (also spelled beocytes) are small, spherical cells that arise from multiple fissions of a parental cell ("vegetative" cell) and are released after rupture of its fibrous outer wall layer. Baeocytes still contained in the parental cell wall appear as small colonies, and upon release, these reproductive cells develop into vegetative cells.

3.3 CYANOBACTERIAL PIGMENTS AND COLOURS

A key characteristic distinguishing cyanobacteria from other bacteria is that they possess **chlorophyll-*a*** like plant chloroplasts, their major photosynthetic pigment and a variety of carotenoids, the latter acting primarily as photoprotectants to reduce oxidative damage to chlorophyll-*a*. In addition, cyanobacteria possess specific accessory pigments, the **phycobilins** (Tandeau de Marsac, 2003). These pigments are bound to water-soluble proteins, the phycobiliproteins, and occur in variants with different optical properties. **Phycocyanin** is common for all cyanobacteria and appears blue, giving a blue-green colour to many cyanobacteria, hence the classic name "blue-green algae". The blueish colour is especially prominent when cyanobacterial cells have lysed and dissolved phycocyanin stains the water blue. **Phycoerythrin** appears red and is responsible for the reddish or brownish colour of many cyanobacteria, such as *Planktothrix rubescens*. Within the cells, phycocyanins and phycoerythrins absorb certain wavelengths of photosynthetically active radiation (PAR) and transfer the light energy to chlorophyll-*a* in photosystem II, thus extending the wavelength range of light available for photosynthesis (Berman-Frank et al., 2003). In some species, phycobilins are also present in the antenna of photosystem I where they are thought to serve the energy demand of nitrogen fixation (Watanabe et al., 2014).

Cyanobacterial cell colours vary from chartreuse to blue-green to violet-red, depending on the ratio between phycocyanin, phycoerythrin, carotenoids

and chlorophyll. By adapting this ratio, cyanobacteria may optimise their efficiency of exploitation of light energy (MacIntyre et al., 2002; Kehoe, 2010). Pigment ratios are often characteristic for a particular species but can also vary between clones or genotypes. They also vary in response to the light spectrum in which the cells (filaments, colonies) are growing, for example, with a higher share of red pigment (phycoerythrin) under conditions of low light intensity (Tandeau de Marsac, 1977; Acinas et al., 2009).

Cyanobacterial water blooms can have a wide variety of colours beyond the typical green or blue-green colour due to varying ratios of chlorophylls, phycocyanin, phycoerythrin and carotenoids. The latter are orange or red in colour, and they can be used to quantify phytoplankton groups, for example, by HPLC (high performance liquid chromatography) analysis of echinenone or canthaxanthin, which are specific for cyanobacteria (Frigaard et al., 1996; Takaichi, 2011). Surface blooms can appear orange, brownish, purple, and light green, among other colours, and have been occasionally reported as suspected "contamination with paint" due to their unexpected colour.

In addition to photosynthetic pigments, cyanobacteria can produce pigments that supposedly protect the cells from intense irradiation, in particular in the UV-wavelength range. These pigments can mask the colour of chlorophyll and phycocyanin, for example, scytonemin, a black pigment produced by *Scytonema* spp. (Dillon & Castenholz, 1999).

3.4 SECONDARY METABOLITES AND CYANOTOXINS

Cyanobacteria can produce a large diversity of secondary metabolites. These are compounds produced by the cells that are not required for the basic cell metabolism, including the compounds considered as cyanobacterial toxins in this volume. These metabolites include polyketides, oligopeptides, lipids, alkaloids and other types of molecules. Many of them show bioactivity in various test systems, but their function for the cyanobacterial cells is not well understood (De Philippis & Vincenzini, 1998; Burja et al., 2001; Gerwick et al., 2001; Welker & von Döhren, 2006; Pereira et al., 2009). It is possible that among the multitude of yet poorly studied metabolites (see section 2.10), further compounds with adverse effects on higher plants and animals – or with therapeutic potential – will be identified in future (Vijayakumar & Menakha, 2015).

A number of cyanobacterial metabolites are considered to serve as UV protection. Scytonemin, an aromatic indole alkaloid (Proteau et al., 1993), has been found primarily in filamentous, sheath-forming types exposed to high UV doses, such as the (semi)terrestrial *Scytonema* sp. (Dillon & Castenholz, 1999). Mycosporine-like amino acids are a diverse family of compounds produced by fungi and several groups of eukaryotic phytoplankton (Oren & Gunde-Cimerman, 2007) as well as by cyanobacteria, including *Microcystis* sp. (Liu et al., 2004; Pathak et al., 2019).

3.5 TAXONOMY OF CYANOBACTERIA

As for all organisms, the key criteria for classifying cyanobacteria in a taxonomic system are phylogenetic relationships that should reflect the grouping of organisms in hierarchical taxa. Taxa (singular: taxon) are thus groups such as orders, families, genera, species, subspecies in which organisms are grouped so that they ideally share a common evolutionary ancestor. Historically, the taxonomic classification was inferred from morphological characteristics of cells and colonies studied by microscopy. In the last few decades, biochemical and molecular methods have been increasingly used in microbial taxonomy. Based on molecular data, a number of classical cyanobacterial taxa have been revised and renamed – and there will be more revisions in future (see Table 3.2).

Table 3.2 Cyanobacterial species names that underwent revision in recent years

New name	*Old name (basionym)*	*Reference*
Chrysosporum bergii	*Anabaena bergii*	Zapomělová et al. (2012)
Chrysosporum ovalisporum	*Aphanizomenon ovalisporum*	Zapomělová et al. (2012)
Cuspidothrix issatchenkoi	*Aphanizomenon issatchenkoi*	Rajaniemi et al. (2005b)
Raphidiopsis raciborskii	*Cylindrospermopsis raciborskii*	Aguilera et al. (2018)
Dolichospermum flosaquae	*Anabaena flos-aquae*	Wacklin et al. (2009)
Dolichospermum circinale	*Anabaena circinalis*	Wacklin et al. (2009)
Dolichospermum crassum	*Anabaena crassa*	Wacklin et al. (2009)
Dolichospermum lemmermannii	*Anabaena lemmermannii*	Wacklin et al. (2009)
Dolichospermum planctonicum	*Anabaena planctonica*	Wacklin et al. (2009)
Dolichospermum smithii	*Anabaena smithii*	Wacklin et al. (2009)
Dolichospermum solitarium	*Anabaena solitaria*	Wacklin et al. (2009)
Dolichospermum spiroides	*Anabaena spiroides*	Wacklin et al. (2009)
Dolichospermum viguieri	*Anabaena viguieri*	Wacklin et al. (2009)
Kamptonema formosum	*Oscillatoria formosum*	Strunecký et al. (2014)
Moorea producens	*Lyngbya majuscula*	Engene et al. (2012)
Microcoleus autumnalis	*Phormidium autumnale*	Strunecký et al. (2013)
Microseira wollei	*Lyngbya wollei*	McGregor & Sendall (2015)
Planktothricoides raciborskii	*Planktothrix raciborskii*	Suda et al. (2002)
Sphaerospermopsis aphanizomenoides	*Aphanizomenon aphanizomenoides*	Zapomělová et al. (2011)
Sphaerospermopsis reniformis	*Anabaena reniformis*	Zapomělová et al. (2011)
Wilmottia murrayi	*Phormidium murrayi*	Strunecký et al. (2011)

The list is not complete but comprises primarily those species that are potentially toxigenic or are closely related to toxigenic species. Note that a new name not necessarily comprises all forms previously published under the old name, and therefore, a retrospective renaming may be critical.

A major challenge for cyanobacterial taxonomy is the lack of a clear concept or definition of a species. Commonly accepted species definitions generally used in bacteriology such as genomic DNA/DNA hybridisation or average nucleotide identity (ANI) are not easily applied to cyanobacteria because these methods require axenic cultures (i.e., pure, clonal cultures free of any other bacteria). For cyanobacteria, taxonomy is further complicated by the fact that two basically different systems of nomenclature have become established, the International Code of Nomenclature for algae, fungi, and plants (ICN) and the International Code of Nomenclature of Bacteria (ICNB) (see Box 3.1). As a consequence, the number of recognised species in a given sample can vary greatly, depending on the scientific background of the person identifying the species and counting them in the sample (Whitton & Potts, 2000; Nabout et al., 2013).

BOX 3.1: NOMENCLATURE OF CYANOBACTERIA: UNSOLVED ISSUES

Historically, cyanobacteria were considered as algae. When their prokaryotic nature was revealed in the mid-20th century (Stanier & Van Niel, 1941), many of the established genera had been already described following the International Code of Nomenclature for algae, fungi, and plants ("botanical code", ICN) – as it was historically the case with heterotrophic bacteria, too. While the nomenclature of heterotrophs and Archaea follows the International Code of Nomenclature of Bacteria ("bacteriological code", ICNB) from 1980 onwards, cyanobacterial nomenclature is treated by both the botanical code and the bacteriological code. Because this is a constant source of confusion, several solutions have been proposed but none found unanimous acceptance (Stanier et al., 1978). In 1985, the "Subcommittee on the Taxonomy of Phototrophic Bacteria" proposed to consider species validly published under the botanical code as valid species in the sense of the bacteriological code, but this proposal was never accepted and the debate is ongoing (Oren & Ventura, 2017). The latest proposals take extreme positions for cyanobacteria, either exclusively following the botanical code (Oren & Garrity, 2014) or exclusively following the bacteriological code (Pinevich, 2015). While taxonomic committees continue to search for a solution, the existing dual nomenclature has consequences in practice when studying toxic cyanobacteria (Komárek, 2006; Komárek, 2011; Gaget et al., 2015a; Gaget et al., 2015b; Dvořák et al., 2018).

Numbers of species: Following the bacterial code, only a very low number of cyanobacterial species are considered as valid bacterial species, while the number of species described following the botanical code is continuously

increasing. However, the botanical code is difficult to follow because (botanically) valid descriptions are published in a large variety of scientific journals and not recorded in a central registry. As a result, no comprehensive list of globally accepted species is available.

Example: For the genus *Microcystis*, Algaebase (http://www.algaebase.org/) lists 51 "taxonomically accepted" species (and additionally 62 synonyms and species of unclear status), Cyano database (http://www.cyanodb.cz/) lists 2 species (*M. aeruginosa* and *M. minutissima*), the National Center for Biotechnology Information (NCBI) taxonomy browser (https://www.ncbi.nlm.nih.gov/taxonomy) lists 19 species for which sequences are deposited – while the "list of prokaryotic names with standing in nomenclature" (LPSN, http://www.bacterio.net/index.html) lists 12 species (published under the ICN) but considers *Microcystis aeruginosa* as an illegitimate species name "in need of a replacement" (all accessed April 2020).

Type strains: Formal type strains are not required for species described following the rules of ICN, and in consequence, there are no reference genomic sequences available. This is critical especially for molecular studies that generally rely on designated type strains. Therefore, the taxonomic classification of a deposited sequence depends largely on the depositor's judgement – or misjudgement.

Example: The majority of nucleotide sequences deposited for the genus *Anabaena* in the NCBI GenBank is not assigned to a species, and among those assigned to a species, a large share is classified "cf." (from Latin "*confer*" referring to an unconfirmed classification), for example, *Anabaena* cf. *circinalis* (now *Dolichospermum* cf. *circinale*). Based on these database entries, a reliable molecular identification is not possible.

Global taxonomy: An unambiguous taxonomic scheme for ranks above genera is lacking. Higher ranks are variably labelled as order, sections or subgroups. None of the schemes is formally accepted by the International Committee on Systematics of Prokaryotes (ICSP).

Example: The order Oscillatoriales *sensu* Cavalier-Smith (2002) corresponds largely to Subsection III *sensu* Castenholz et al. (2001) and Section III *sensu* Rippka et al. (1979), each comprising a similar but not identical list of genera. It is not congruent with the order Oscillatoriales *sensu* (Komárek et al., 2014) that includes unicellular taxa like *Cyanothece* but excludes filamentous ones such as *Leptolyngbya* (see also Table 3.3).

Table 3.3 Overview on taxonomic classification systems of cyanobacteria, following either the International Code of Nomenclature for algae, fungi and plants (ICN) or the International Code of Nomenclature of Bacteria (ICNB)

Reference	*Criteria*	*Classification and morphology*	*Observations*
Komárek et al. (2014) (ICN)	*Polyphasic*, including ultrastructure, molecular, genomic	Order Gloeobacterales (U) Order Synechococcales (U/Fi,C) Order Spirulinales (coiled Fi) Order Chroococcales (U/pFi,C) Order Pleurocapsales (U/pFi,Bc) Order Oscillatoriales (U/Fi,fB) Order Chroococcidiopsidales (U/Bc) Order Nostocales (Fi,fB/tB,Ho,Hc,Ak)	New orders: Spirulinales, Chroococcidiopsidales
Hoffmann et al. (2005) (ICN)	*Polyphasic*, including morphology, ultrastructure, molecular	Order Gleobacterales (U) Order Synechococcales (U/Fi,C) Order Pseudoanabaenales (Fi) Order Chroococcales (U,C) Order Oscillatoriales (Fi,fB,Ho) Order Nostocales (Fi,fB/tB,Ho,Hc,Ak)	New orders: Pseudanabaenales, Synechococcales; Some orders with both filamentous and colonial forms; No partitioning of true and false branching in forms with heterocytes; Order Stigonematales is dispersed and former members moved to other orders
Cavalier-Smith (2002) (ICNB, not valid)	Morphology	Order Gloeobacterales (U) Order Chroococcales (U,C) Order Pleurocapsales (U,C,Bc) Order Oscillatoriales (Fi,fB,Ho) Order Nostocales (Fi,fB,Ho,Hc,Ak) Order Stigonematales (Fi,tB,Ho,Hc,Ak)	Classification of cyanobacteria in global bacterial taxonomy; Gloeobacterales (with genus *Gloeobacter*) as sister group of all other cyanobacteria; No details on classification of genera

(*Continued*)

Table 3.3 (*Continued*) Overview on taxonomic classification systems of cyanobacteria, following either the International Code of Nomenclature for algae, fungi and plants (ICN) or the International Code of Nomenclature of Bacteria (ICNB)

Reference	*Criteria*	*Classification and morphology*	*Observations*
Castenholz et al. (2001) (ICNB, not valid)	Morphology	Subsection I (U,C) Subsection 2 (U,C,Bc) Subsection 3 (Fi,fB,Ho) Subsection 4 (Fi,fB,Ho,Hc,Ak) Subsection 5 (Fi,tB,Ho,Hc,Ak)	Largely based on morphological characteristics; Genera known at the time as "form genus"; Largely in agreement with Rippka et al. (1979)
Anagnostidis & Komárek (1985) (ICN)	Morphology	Order Chroococcales (U,C,Be) Order Oscillatoriales (Fi,fB,Ho) Order Nostocales (Fi,fB,Ho,Hc,Ak) Order Stigonematales (Fi,tB,Ho,Hc,Ak)	All nonfilamentous taxa are unified in Chroococcales
Rippka et al. (1979) (ICN)	Morphology	Section I (U,C) Section II (U,C,Bc) Section III (Fi,fB,Ho) Section IV (Fi,fB,Ho,Hc,Ak) Section V (Fi,tB,Ho,Hc,Ak)	Based on morphology, cell organisation and types of cell division
Geitler (1932) (ICN)	Morphology	Order Chroococcales (U,C) Order Chamaesiphonales (U,C,Bc) Order Hormogonales (Fi,fB/tB,Ho,Hc,Ak)	

For each system, the main groups are given and a brief description of applied criteria and a summary of observations.

Morphological characteristics: U: unicellular; Fi: filaments; C: colonies; pFi: pseudofilaments; Bc: baeocytes; fB: false branching; tB: true branching; Ho: hormogonia; Hc: heterocytes; Ak: akinetes. "Not valid" refers to the fact that despite a description following the rules of ICNB, a formal recognition was not granted by taxonomic committees.

The multiple taxonomic systems are a constant source of confusion in academic discussions, albeit of less relevance for practitioners. Nevertheless, an essential understanding of the issue may help to appraise deviating views on taxonomic ratings and to understand why a particular organism is named variably in the literature.

Molecular approaches to cyanobacterial taxonomy are most promising for inferring true phylogenetic relationships. The methods applied involve sequencing of marker genes (16S rDNA, phycocyanin operon), DNA–DNA hybridisation, genome sequencing and biochemical characteristics (fatty acid profiles) or immunological procedures (Wilmotte, 1994; Whitton & Potts, 2000). Preferably, molecular results are combined with other characteristics as the basis for a so-called **polyphasic taxonomy approach** (Vandamme et al., 1996; Komárek, 2016a; Wilmotte et al., 2017).

On the genus level, evolutionary trees based on 16S rRNA gene (Tomitani et al., 2006) sequences are largely in agreement with classifications based on morphological characteristics, in particular if these were re-evaluated and include ultrastructural characteristics (Hoffmann et al., 2005; Komárek, 2006), in particular, the structure and distribution of thylakoids (Mareš et al., 2019).

Most of the species descriptions in the currently available manuals and reference books are based on morphological traits that can be recognised by optical microscopy. Section 13.2 lists taxonomic reviews and keys for the determination of cyanobacteria, focusing on potentially toxigenic taxa. Although some classification systems based on morphological features were published before biochemical and molecular characteristics became important classification criteria, they are still being used (Table 3.2) because new criteria have not sufficiently been consolidated and, particularly, because the identification by microscopy has been the most accessible method for routine analyses. However, for identifying cyanobacteria, it should be considered that their morphological appearance can vary in response to actual growth conditions (phenotypic plasticity).

Today, most species of cyanobacteria have been described following the botanical code of nomenclature based on morphological criteria. Many of the older species descriptions are based on drawings and other pictures that hence cannot be used as fully objective criteria, especially since the botanical code does not require the deposition of a type strain. Possibly the description of cyanobacterial taxa by the bacteriological code would be biologically more appropriate (see Box 3.1) as there is no doubt that cyanobacteria are a monophyletic branch in the global bacterial phylogenetic tree (Woese, 1987; Pace, 1997).

The ambiguity of the definition of cyanobacterial species and the lack of accessible reference material for many species often hamper the unambiguous assignment of cyanobacteria in field samples to a species, especially when molecular methods are applied (section 13.4). For this reason,

throughout this volume, taxonomic assignment to the genus level is given preference (e.g., *Microcystis* sp.). In some cases, a more precise identification of a dominant organism to the species level may be useful for a more accurate prediction of toxin occurrence. For example, *Planktothrix agardhii* and *P. rubescens* have both been shown to potentially contain microcystins, but may contain different analogues with different toxicity, typically occur in different types of waterbodies and usually can readily be distinguished by both their colour and cell dimensions.

Practitioners in health authorities with some experience in microscopy can easily learn to recognise the dominant cyanobacterial genera (and in some cases also species), which occur in the region they are monitoring. For a number of taxa, recent revisions have led to a renaming of common taxa, and in a few cases, changes in genus names require close attention for a certain period while old and new names may be used in parallel. Also, some taxa have been reorganised beyond simple renaming of a taxonomic entity. For example, while the organisms described as *Moorea producens* (Engene et al., 2012) formerly were named *Lyngbya majuscula*, we cannot be sure that all organisms referred to as *L. majuscula* in publications prior to 2010 would indeed be classified as *M. producens* today. In this book, we generally refer to the most recent names of species or genera as of 2019 (see Table 3.3 and Salmaso et al. (2016a)), but when referring to older literature, for which allocation of a taxon to the new name risks being wrong, we quote the former name.

In field samples, most cyanobacteria can be readily distinguished from other phytoplankton and particles under the microscope at a magnification of 100× to 400×. The following section describes and depicts the most frequently occurring taxa known to produce toxins.

3.6 MAJOR CYANOBACTERIAL GROUPS

As outlined in Box 3.1, several taxonomic systems exist to group cyanobacteria in a taxonomic scheme as reviewed in more detail in Komárek et al. (2014). Table 3.3 summarises taxonomic schemes for cyanobacteria, starting from the early scheme proposed by Geitler (1932) to the most recent one proposed by Komárek et al. (2014). Several systems avoid the use of nomenclatural categories and instead use groups such as "sections" (Rippka et al., 1979) or "subsections" (Castenholz et al., 2001) instead of orders, discernible by the suffix "*-ales*" in order to reflect the understanding that at least some of these groups do not represent monophyletic units but are defined based on shared morphological characteristics (Ishida et al., 2001; Gugger & Hoffmann, 2004). Based on rapidly increasing genomic sequence information from axenic strains, metagenomic studies and ultrastructural analyses, the taxonomy of cyanobacteria will most probably converge to a truly

taxonomic system based on phylogenetic relationships in the near future (Shih et al., 2013).

The classification of taxa proposed by Komárek et al. (2014) is largely based on whole-genome sequences and on ultrastructural characteristics, such as the distribution of thylakoids in the cells. These characteristics are not observable with light microscopy and hence not helpful for the routine analysis of field samples. Further, in this system, classical and morphological characteristics easily observed by microscopy, such as formation of filaments or the presence of sheaths, are less important. For example, the filamentous genus *Pseudanabaena* is grouped together with the unicellular *Synechococcus* in a new order Synechococcales.

For practical purposes, such as the examination of high numbers of samples, earlier taxonomic systems appear more suitable. Therefore, in the following, the taxonomic scheme as proposed by Castenholz et al. (2001) is considered because characteristics like the arrangement of thylakoids or sequences of housekeeping genes are generally not available for monitoring purposes. It is also primarily based on morphological features observed by light microscopy and largely corresponds to the earlier scheme by Rippka et al. (1979) while including more genera. This scheme does not use the nomenclatural definition of categories such as orders and families but rather replaces these with "subsections", "families" and "form genera" that do not reflect monophyletic taxa (and thus is considered invalid in a system of nomenclature based on phylogenetic relationships). However, it provides a temporary system that has the advantage to be a practical, convenient and stable method for the microscopical identification of cyanobacterial strains and samples.

Nonetheless, for molecular methods (see section 13.4), a genome-based taxonomic scheme reflecting phylogenetic relationships may eventually prove to be more suitable, especially once designated type strains or sequences, respectively, are accessible.

3.7 DESCRIPTION OF COMMON TOXIGENIC AND BLOOM-FORMING CYANOBACTERIAL TAXA

The following brief descriptions of common toxigenic and bloom-forming cyanobacteria give an introduction which certainly cannot replace taxonomic keys for their identification (see Chapter 13). Also, the global diversity of cyanobacteria is higher by orders of magnitudes beyond the selection of taxa presented in this chapter. Also, the following section does not include a number of genera and species known to produce toxins but not to form blooms or benthic mats, for example, *Umezakia* sp. and *Fischerella* sp. For the illustration of morphological characteristics, see Figures 3.1–3.4. A regularly updated list of cyanobacterial taxa (and other algae) can be found in AlgaeBase (Guiry & Guiry, 2019) and

CyanoDB (Hauer & Komárek, 2019). The following descriptions consider only morphological characteristics that can be observed by standard light microscopy. Figure 3.5A–U gives microscopic images for most of the taxa. For a brief description of further genera and a short summary of recent taxonomy of cyanobacteria, see also Dvořák et al. (2017).

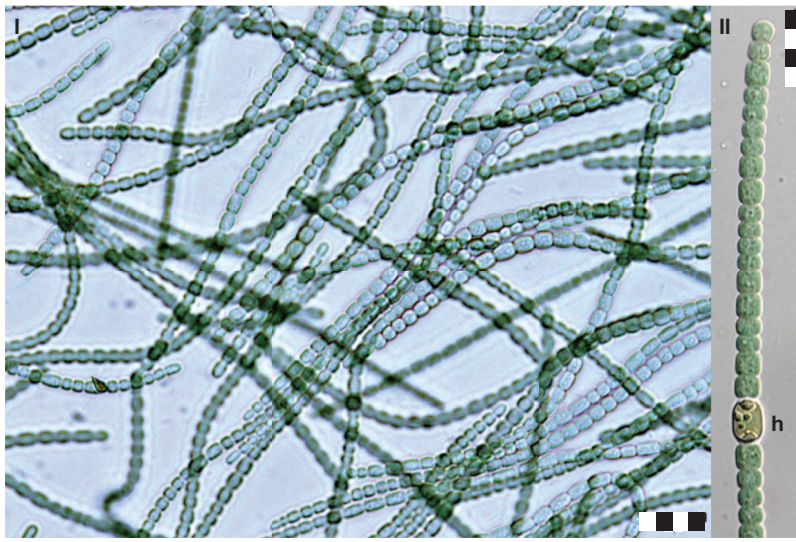

Figure 3.5A *Anabaena sensu stricto* sp. h: heterocyte. Units in scale bars correspond to 5 µm. For origin of individual photographs, see the end of this chapter.

Figure 3.5B *Anabaenopsis* sp. Short, coiled trichomes with terminal heterocytes (h) and symmetric to subsymmetric akinetes (a). Units in scale bars correspond to 5 µm. For origin of individual photographs, see the end of this chapter.

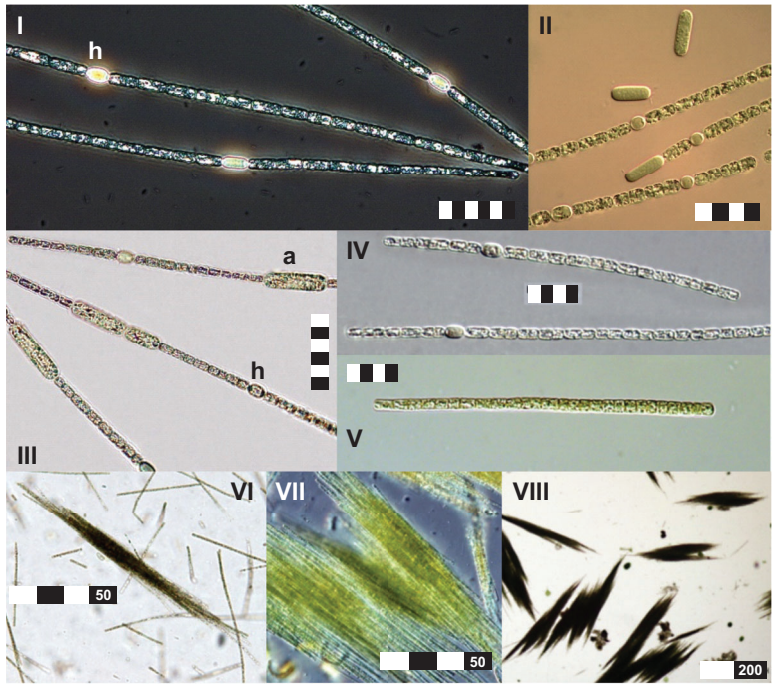

Figure 3.5C *Aphanizomenon* sp. In phase contrast, heterocytes appear highly refractory (I); aerotopes are homogeneously distributed in vegetative cells. Akinetes are much larger than vegetative cells and heterocytes (II–III) and can occur as single cells in cultures (II). Trichomes without heterocytes resemble *Planktothrix* sp. (V). Multiple trichomes of *A. flosaquae* aggregate to macroscopic fascicles (VI–VIII). Units in scale bars correspond to 5 µm if not indicated otherwise. For origin of individual photographs, see the end of this chapter.

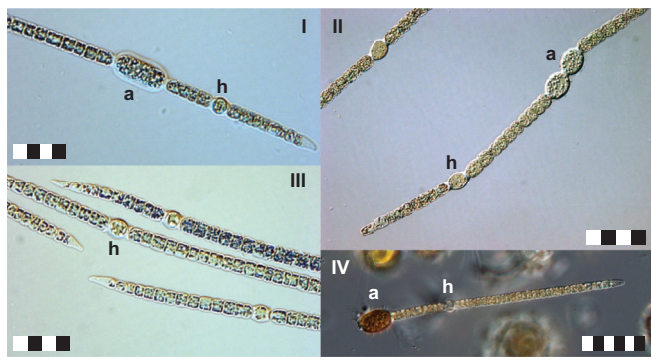

Figure 3.5D *Chrysosporum* sp. Terminal cells are pointed and appear hyaline. Akinetes (a) with distinct granulae; h: heterocytes. Units in scale bars correspond to 5 µm. For origin of individual photographs, see the end of this chapter.

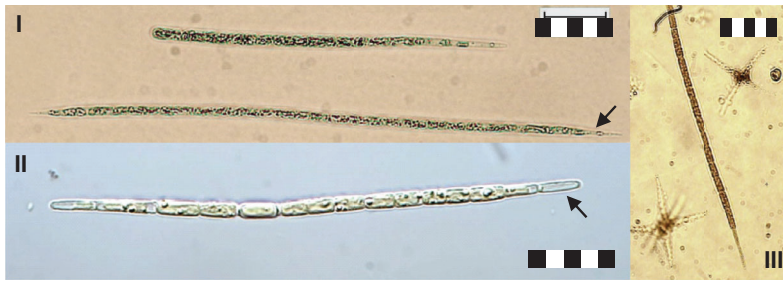

Figure 3.5E *Cuspidothrix* sp. Arrows point to attenuated and elongated terminal cells with hyaline content. Units in scale bars correspond to 5 µm. For origin of individual photographs, see the end of this chapter.

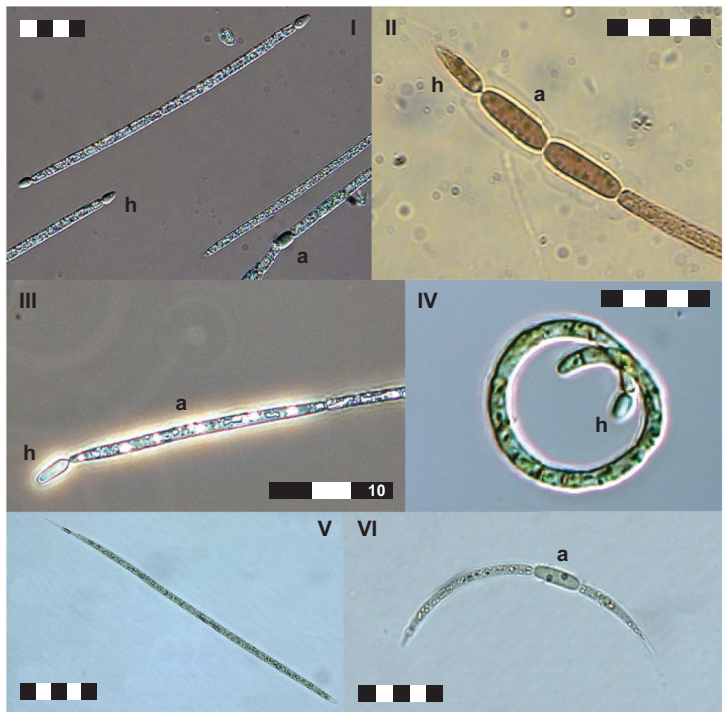

Figure 3.5F *Raphidiopsis* sp. with (*Cylindrospermopsis*; I–IV) and *without* (V–VI) heterocytes. *Raphidiopsis* has typical terminal heterocytes (h) when present. Akinetes (a) are larger than vegetative cells and often show distinct, large granulae. Units in scale bars correspond to 5 µm if not indicated otherwise. For origin of individual photographs, see the end of this chapter.

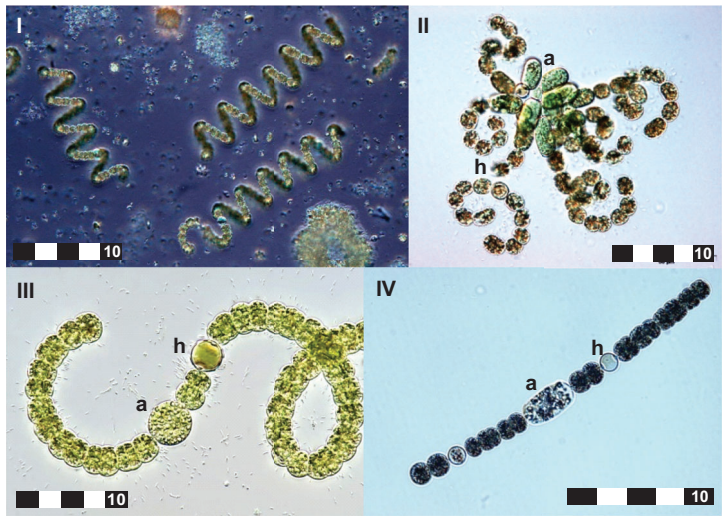

Figure 3.5G *Dolichospermum* sp. *D. crassum* (I), *D. lemmermannii* with aggregated akinetes (a) and short trichomes (II), *D. mucosum* (III) and *D. planctonicum* (IV). Heterocytes (h) with similar size than vegetative cells. Units in scale bars correspond to 10 µm. For origin of individual photographs, see the end of this chapter.

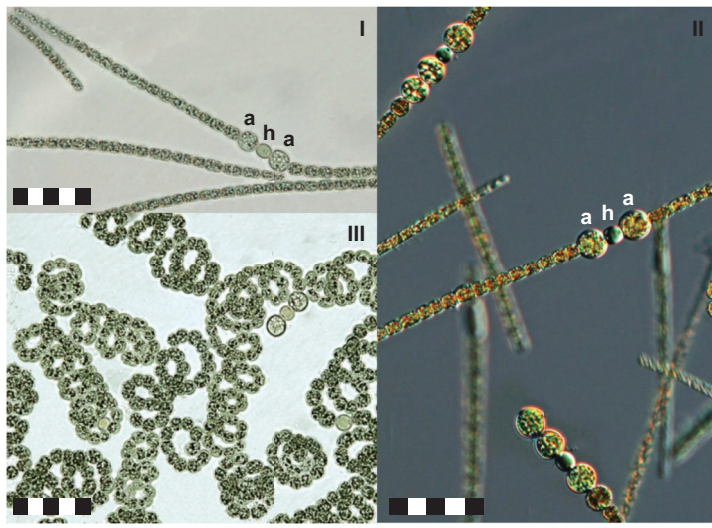

Figure 3.5H *Sphaerospermopsis aphanizomenoides* (I, II) and *S. reniformis* (III). Akinetes (a) typically next to heterocytes (h). Units in scale bars correspond to 5 µm. For origin of individual photographs, see the end of this chapter.

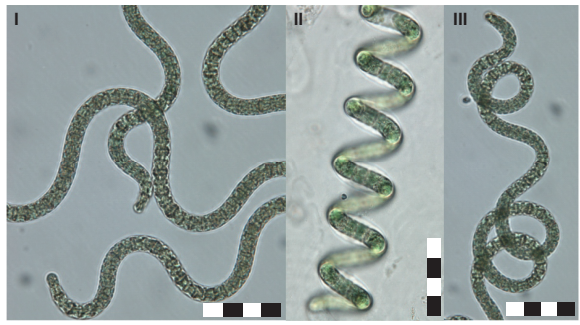

Figure 3.5I *Arthrospira* sp. with curved (I), coiled (II) or irregularly curved trichomes (III). Units in scale bars correspond to 5 µm. For origin of individual photographs, see the end of this chapter.

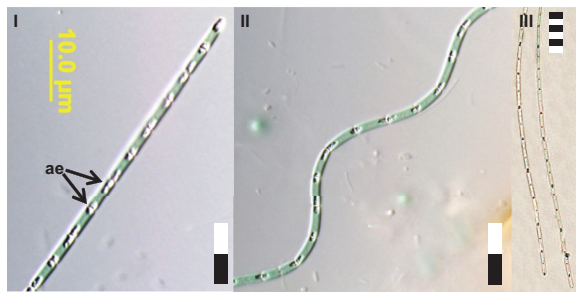

Figure 3.5J *Limnothrix* sp. Aerotopes (ae) typically at cell poles. Units in scale bars correspond to 5 µm. For origin of individual photographs, see the end of this chapter.

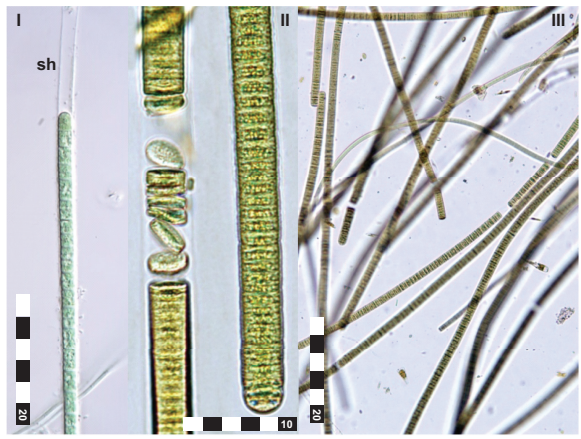

Figure 3.5K *Lyngbya* sp. Cells are enveloped in a sheath (sh) that can be partly empty. Units in scale bars correspond to 5 µm if not indicated otherwise. For origin of individual photographs, see the end of this chapter.

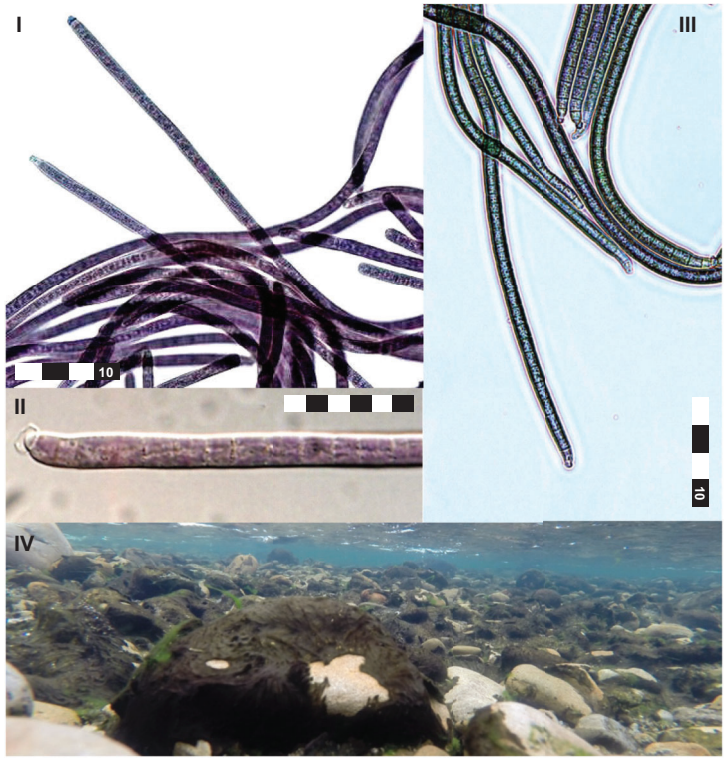

Figure 3.5L *Microcoleus*/*Phormidium* sp. Trichomes without sheath and typically pointed terminal cells (I–III). In natural habitats, *Microcoleus* (*Phormidium*) *autumnalis* can form dense mats on hard substrates covering large parts of stream beds (IV). Units in scale bars correspond to 5 µm if not indicated otherwise. For origin of individual photographs, see the end of this chapter.

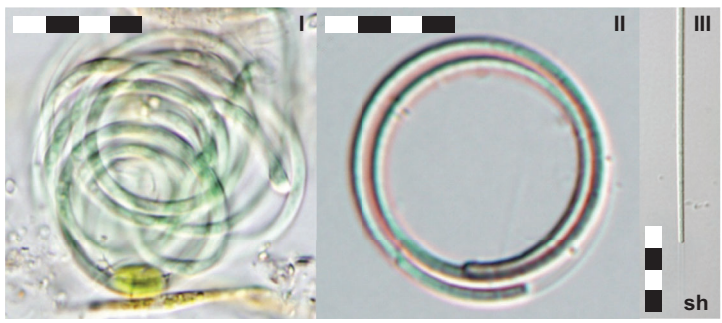

Figure 3.5M *Planktolyngbya* sp. Narrow trichomes in which individual cells can often not be distinguished, surrounded by a fine sheath (sh). Units in scale bars correspond to 5 µm. For origin of individual photographs, see the end of this chapter.

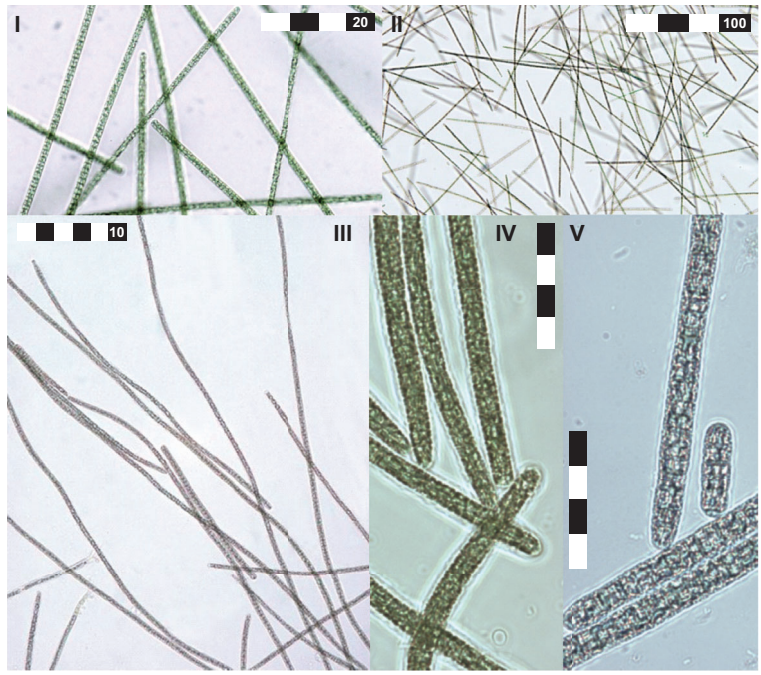

Figure 3.5N *Planktothrix* sp. Green pigmented *P. agardhii* (I, II, IV) with straight trichomes and many aerotopes. Red-pigmented *P. rubescens* (III, V) with wider and generally longer, slightly bent trichomes. Units in scale bars correspond to 5 µm if not indicated otherwise. For origin of individual photographs, see the end of this chapter.

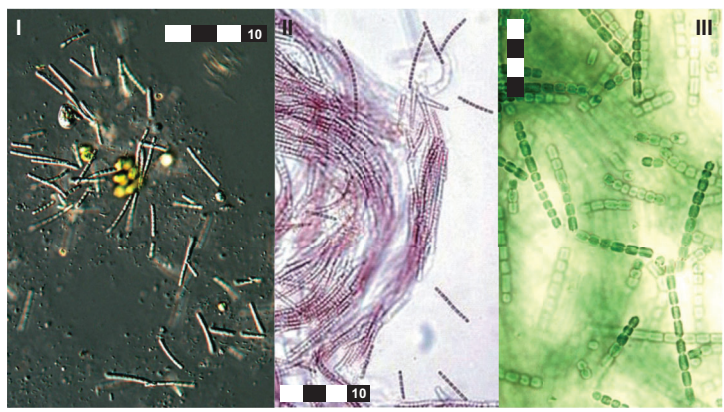

Figure 3.5O *Pseudanabaena* sp. Short trichomes associated with other phytoplankton (I). Red (II)- and green (III)-pigmented strains in culture, forming mats of long trichomes. Units in scale bars correspond to 5 µm if not indicated otherwise. For origin of individual photographs, see the end of this chapter.

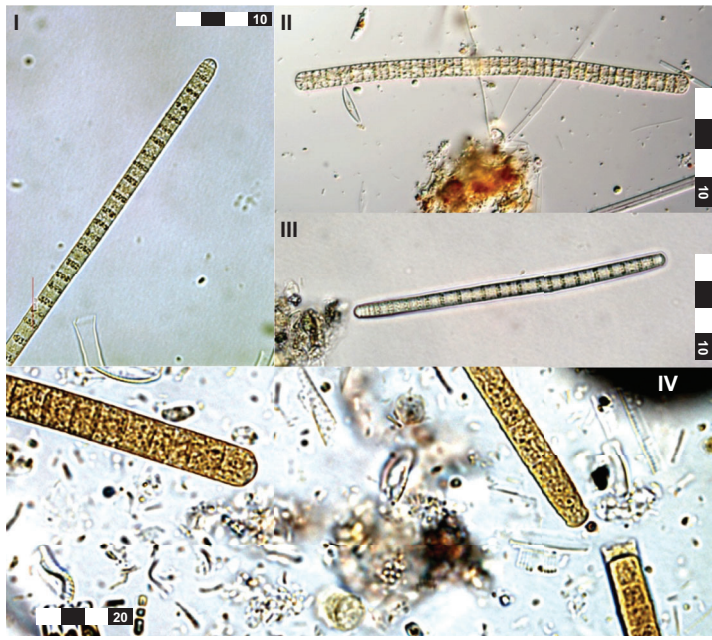

Figure 3.5P *Tychonema* sp. with partly hyaline cells (I–III). Typically, granulae accumulate at the cell walls. IV: Fragments of trichomes in a periphytic sample. Units in scale bars correspond to 10 or 20 µm as indicated. For origin of individual photographs, see the end of this chapter.

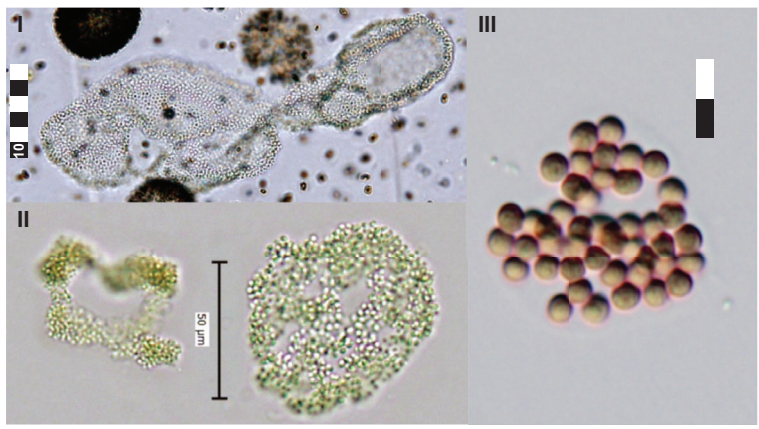

Figure 3.5Q *Aphanocapsa* sp. with small cells without aerotopes. In (I), cells and colonies of *Microcystis* sp. are shown for comparison. Units in scale bars correspond to 5 µm if not indicated otherwise. For origin of individual photographs, see the end of this chapter.

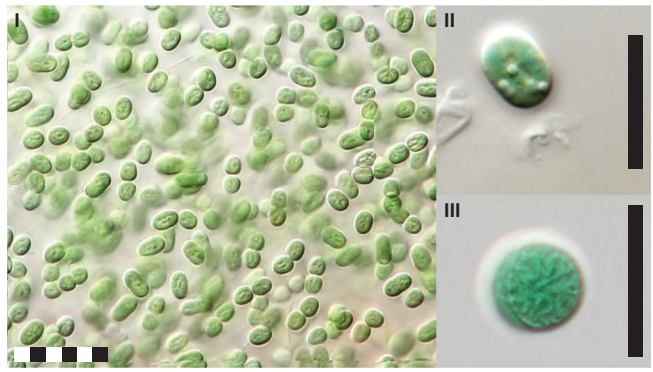

Figure 3.5R *Aphanocapsa* sp. (I), *Synechococcus* sp. (II) and *Synechocystis* sp. (III) with small cells without aerotopes. Units in scale bars correspond to 5 µm. For origin of individual photographs, see the end of this chapter.

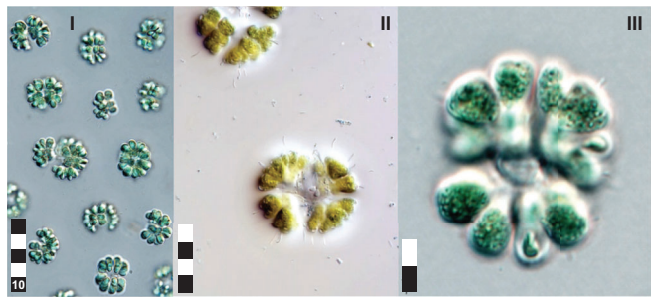

Figure 3.5S *Gomphosphaeria* sp. Small colonies of a few cells arranged radially. Units in scale bars correspond to 5 µm if not indicated otherwise. For origin of individual photographs, see the end of this chapter.

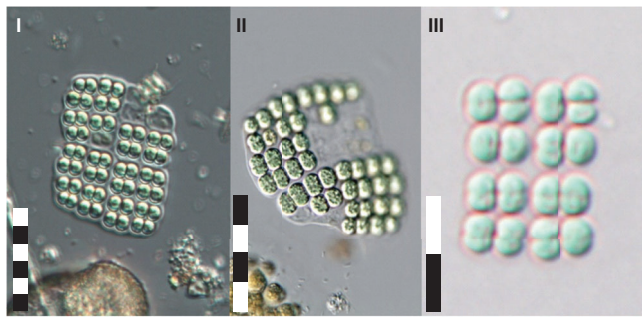

Figure 3.5T *Merismopedia* sp. with highly regular arrangement of cells in flat colonies. Units in scale bars correspond to 5 µm. For origin of individual photographs, see the end of this chapter.

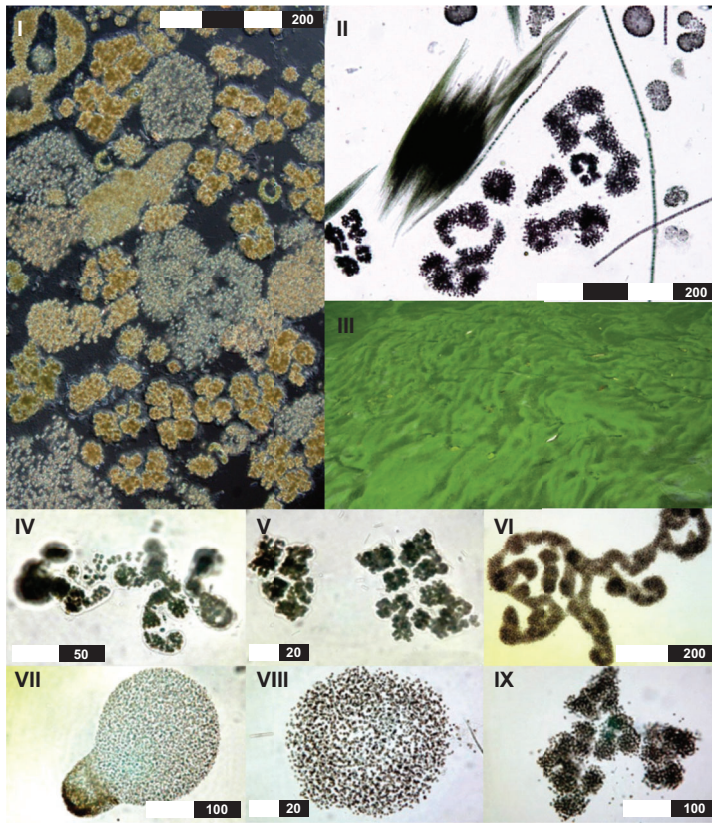

Figure 3.5U *Microcystis* sp. (I) natural sample comprising multiple *Microcystis* form species; (II) typical plankton community consisting of *Aphanizomenon flosaquae* fascicles, *Microcystis* colonies and *Dolichospermum* sp. trichomes; (III) *Microcystis* sp. surface bloom; IV–IX colonies of form species *M. wesenbergii* (IV), *M. viridis* (V), *M. aeruginosa* (VI), *M. flosaquae* (VII), *M. ichtyoblabe* (VIII) and *M. novacekii* (IX); note that the latter five form species have been proposed to be unified as *M. aeruginosa* based on molecular data (Otsuka et al., 2001). For ambiguities of *Microcystis* taxonomy, see also Box 3.1. Units in scale bars as indicated. For origin of individual photographs, see the end of this chapter.

In the following, abbreviations of genera differ occasionally from the general convention to use the initial letter to abbreviate a genus. This is done to avoid confusion, in particular if species epithets are identical. For example, *Aphanizomenon flosaquae* and *Anabaena flosaquae* are abbreviated as *Aph. flosaquae* and *Ana. flosaquae*, respectively (with the latter referred to as *Dolichospermum flosaquae* in the more recent literature). Note that the spelling of species epithets such as 'flos-aquae' has been chenged to non-hyphenated spelling 'flosaquae' in accordance with the International Code of Nomenclature for algae, fungi, and plants (Artcile 60.11; Turland et al., 2018).

The full taxonomic name includes names of those who described them, for example, '*Anabaena* Bory ex Bornet et Flahault'. The following section includes these for clarity.

3.7.1 Filamentous forms with heterocytes

These taxa correspond to subsection 4 in Table 3.2 or "Nostocales" and form filaments (trichomes) with heterocytes and akinetes.

Anabaena Bory ex Bornet et Flahault

Morphological description
The morphology of *Anabaena sensu stricto* largely corresponds to that of *Dolichospermum* except for the consistent lack of aerotopes (Figure 3.5A).

Taxonomic background
The genus *Anabaena* underwent several revisions in recent years in the course of which several new genera were proposed (see Table 3.2). *Anabaena sensu stricto* now comprises a monophyletic cluster with several species.

Ecology and distribution
Species of *Anabaena sensu stricto* are primarily benthic or epiphytic but rarely planktonic.

Anabaenopsis Miller

Morphological description
Free-floating trichomes, solitary or forming small microscopic clusters. Trichomes straight, arcuated or coiled screw-like, usually not embedded in sheaths, but sometimes with a fine sheath. Vegetative cells cylindrical or barrel-shaped, shorter than wide or up to several times longer than wide, pale blue-green, with obligatory or facultative aerotopes, without (rarely) or with constrictions at the cross-walls. Heterocytes develop intercalary in pairs with certain distances from each other. As trichomes often disintegrate after heterocyte maturation between adjacent heterocytes, this typically results in short trichomes with terminal heterocytes. Oval, cylindrical or spherical akinetes develop intercalary, normally distant from heterocytes, but exceptionally adjacent to them. Akinetes generally develop solitary or in pairs, rarely arranged in series with up to five in a row (Figure 3.5B).

Taxonomic background
The genus is clearly defined phenotypically and has been confirmed by molecular analyses. Some species have been transferred to the genera (*Cylindrospermopsis* (now *Raphidiopsis*) and *Cylindrospermum* as they

share a number of characteristics. More details are found in Komárek & Anagnostidis (1989).

Ecology and distribution
All species are planktonic and primarily found in mesotrophic to eutrophic waters, either inland or coastal, with alkaline or slightly saline conditions. Distributed mainly in tropical and subtropical regions but also during summer in temperate zones.

Aphanizomenon Morren ex Bornet et Flahault

Morphological description
Trichomes straight or slightly bent and only slightly narrowing towards the end, generally without sheaths, but sometimes with a very fine sheath. In some species, trichomes tend to form fascicules, that is, macroscopically visible aggregates of multiple trichomes. Vegetative cells cylindrical or barrel-shaped (from 2 to 5 μm in diameter) with variable length/width, often slightly constricted at the cross-wall. Cells contain aerotopes that are distributed evenly in the cells. Terminal cells larger than cells in the trichome, cylindrical with rounded ends or flattened, sometimes with hyaline (transparent) content. Generally, one heterocyte is placed intercalary (i.e., surrounded by vegetative cells) in individual trichomes, rarely 2–4 heterocytes per trichome. Heterocytes cylindrical, spherical or ellipsoidal. The akinetes develop adjacently from heterocyte (paraheterocytic, sometimes distant) forming a subsymmetric trichome. Akinetes often much larger than vegetative cells and are cylindrical, intercalary and solitary (rarely in pairs). Single trichomes of *Aphanizomenon flosaquae* without heterocytes are morphologically very similar to trichomes of *Planktothrix agardhii* (Figure 3.5C).

Taxonomic background
The traditional genus *Aphanizomenon* was recently restricted to a cluster of nine morphospecies (*A. flosaquae*, *A. gracile*, *A. klebahnii*, *A. yezoense*, *A. paraflexuosum*, *A. flexuosum*, *A. slovenicum*, *A. platense* and *A. hungaricum*) based on polyphasic analyses, while other morphotypes formerly placed in the genus were placed in other genera (*Cuspidothrix*, *Sphaerospermopsis* and *Chrysosporum*; (Rajaniemi et al., 2005a; Rajaniemi et al., 2005b; Komárek, 2013)). The main feature that separates these genera from *Aphanizomenon sensu stricto* is that *Aphanizomenon* spp. are able to form parallel fascicules that can reach macroscopic size of several millimetres visible as green, needle-like particles (Komárek, 2013). Further, the subsymmetric filaments are cylindrical, elongated with (almost) hyaline (i.e., transparent) terminal cells. Terminal cells rounded but without distinctly narrowed ends; that are typical for the proposed new genera. For a

review of *Aphanizomenon* and related genera and their toxigenicity, see Cirés & Ballot (2016).

Ecology and distribution
Aphanizomenon generally dominate eutrophic, stagnant waters, with low available nitrogen and thermal stratification. *A. gracile* is typically found in shallow lakes and reservoirs (Cirés et al., 2017). *A. flosaquae*, the most common species of the genus, occurs mainly in temperate zones. Other species occur only in isolated areas, but no tropical *Aphanizomenon* species are registered.

Chrysosporum Zapomělová et al., 2012

Morphological description
Solitary, straight or slightly bent trichomes with clear constrictions at the cell walls. Vegetative cells vary from nearly cylindrical to barrel-shaped or ellipsoidal. Terminal cells rounded and slightly pointed and partially hyaline (transparent). Solitary and cylindrical heterocytes formed intercalary (i.e., surrounded by vegetative cells). Akinetes characteristically oval with distinct granular contents, and distant from heterocytes, often situated nearly equidistant between two heterocytes (Figure 3.5D).

Taxonomic background
Only two species to date: *Chrysosporum ovalisporum* that has been renamed from *Aphanizomenon ovalisporum* and *Chrysosporum bergii* from *Anabaena bergii* (Zapomělová et al., 2012).

Ecology and distribution
Only limited data on the distribution of both species is available, indicating that these species may occur primarily in temperate to subtropical climates (Cirés & Ballot, 2016).

Cuspidothrix Rajaniemi et al.

Morphological description
Solitary and free-floating trichomes forming heterocytes. Trichomes straight or coiled and characteristically clearly narrowed towards the ends. Cells slightly constricted or nonconstricted at the cross-walls, up to 6 μm wide. Vegetative cells cylindrical with facultative aerotopes, generally much longer than wide. Typical apical (terminal) cells elongated up to several tens of μm, attenuated and acuminate, and mainly hyaline (i.e., transparent). Heterocytes appear only intercalary (i.e., surrounded by vegetative cells), always solitary, cylindrical or elliptical. Akinetes elongated, more or less cylindrical intercalary, solitary or rarely in pairs, close or at a short distance to heterocytes. Trichomes subsymmetric with

paraheterocytic akinetes situated on both sides or slightly distant from heterocytes (Figure 3.5E).

Taxonomic background
Cuspidothrix issatschenkoi was renamed from *A. issatschenkoi* based on polyphasic analyses (Rajaniemi et al., 2005a). Other species in the genus have formerly been assigned to *Aphanizomenon*, for example, *Cuspidothrix capricornii* and *Cuspidothrix elenkinii*.
Ecology and distribution
These species are planktonic in mesotrophic to eutrophic stagnant waters. They are rarely found in running waters. They are also present from freshwater to oligohaline and brackish waters.

Raphidiopsis (Fritsch et Rich) Aguilera et al., including ***Cylindrospermopsis*** Seenayya et Subba Raju

Morphological description
Aguilera et al. (2018) proposed to unify the genera *Cylindrospermopsis* and *Raphidiopsis* and to give preference to the latter respecting the principle of priority. Because the scientific community is increasingly accepting this revision, in this volume the genus *Raphidiopsis* refers to the combination of the former genera *Cylindrospermopsis* and *Raphidiopsis*. However, since the study of Aguilera et al. (2018) is restricted to only a limited number of species, the taxonomic opinion may change again in the future.

The genus *Raphidiopsis* comprises solitary, free-floating trichomes forming heterocytes, except for species of *Rhaphidiopsis sensu* Fritsch et Rich, for example *R. mediterranea*. Trichomes straight, bent or screw-like coiled, but in several species narrowed towards ends and without sheaths. The main characteristic is the terminal position of heterocytes, one or two at each end of the trichome (when not absent). Heterocytes ovoid, conical or drop-like. Trichomes subsymmetric, isopolar but heteropolar when only one heterocyte is present, generally without constrictions at crosswalls. Vegetative cells cylindrical or barrel-shaped, usually distinctly longer than wide, pale blue-green, yellowish or olive-green, facultatively with aerotopes. Terminal cells conical, blunt or sharply pointed. Ellipsoidal or cylindrical akinetes (2–4× longer and about 2× wider than the vegetative cells) develop usually distant from heterocytes, rarely adjacent to apical heterocytes (Figure 3.5F).

Taxonomic background
At present, 18 (morpho)species have been described of which, *Raphidiopsis* (*Cylindrospermopsis*) *raciborskii* appears to be the most important one with respect to cyanotoxin production.

Ecology and distribution
In eutrophic, turbid, warm and polymictic waters. In tropics, the appearance is often connected with nitrogen limitation of phytoplankton. All species are planktonic in lakes of the pantropical region except *Raphidiopsis raciborskii* that dispersed into the temperate region during the last 100–150 years (Padisák et al., 2016) where it can form dense, suspended water blooms.

Dolichospermum (Ralfs ex Bornet & Flahault) Wacklin, Hoffman et Komárek

Morphological description
Free-floating trichomes forming heterocytes, straight, slightly curved or flexuous, irregularly or more or less screw-like coiled. Solitary trichomes, rarely joined in irregular clusters (very rarely in fascicules). Trichomes not attenuated towards the ends, without sheaths, sometimes with fine diffluent mucilaginous envelope. Vegetative cells usually clearly constricted at the cross-walls and with many aerotopes distributed throughout the cells. Cylindrical trichomes are isopolar, metameric with respect to heterocytes. Apical cells morphologically similar to other vegetative cells in the filament. Heterocytes form intercalarly, solitary or exceptionally in pairs. They develop from vegetative cells in metameric position. Akinetes are elongated and wider than vegetative cells; they develop paraheterocytically, that is, connected with heterocytes, rarely aside heterocytes from both sides or (more commonly) separated from them by several cells, solitary or up to six in a row (Figure 3.5G).

Taxonomic background
The species of the genus *Dolichospermum* have been recently separated from the genus *Anabaena*. The main criterion for separating these genera is the absence of aerotopes in *Anabaena s. str.*, which is consistent with analyses of genomic sequences (Wacklin et al., 2009). Besides the known toxigenic species such as *D. flosaquae* or *D. circinale*, more than 30 species are given in Wacklin et al. (2009), however, without an individual taxonomic evaluation.

Ecology and distribution
All species planktonic in vegetative state, rarely associated with macrophytes (metaphytic). *Dolichospermum* is found in mesotrophic to eutrophic, both stratified and shallow lakes, generally with low nitrogen concentrations, where it can form blooms and surface scums. Several species are considered to be tropical.

Sphaerospermopsis Zapomělová et al.

Morphological description
Solitary trichomes straight, slightly bent or coiled with constrictions at cell walls. Vegetative cells cylindrical- to barrel-shaped with slightly elongated but not pointed terminal cells, often resembling cells within the trichome. Cylindrical to ellipsoidal heterocytes formed solitary and intercalary (i.e., surrounded by vegetative cells). Akinetes characteristically nearly spherical or ellipsoidal and often occur in groups of two or three, but also singularly. Akinetes are frequently formed adjacently to heterocytes, sometimes on both sides. Fragmentation of trichomes at the akinetes yields trichomes with terminal akinetes (Figure 3.5H).

Taxonomic background
Sphaerospermopsis includes species formerly belonging to *Anabaena* as well as *Aphanizomenon* (Zapomělová et al., 2011; Table 3.2).

Ecology and distribution
Sphaerospermopsis occurs primarily in temperate, subtropical and tropical shallow lakes.

3.7.2 Filamentous forms without heterocytes and akinetes

These taxa correspond to subsection 3 in Table 3.1 or "Oscillatoriales" and form filaments (trichomes) without heterocytes and akinetes. Following more recent taxonomic schemes, the genera *Planktolyngbya* and *Pseudanabaena* are placed in the order Synechococcales (Komárek, 2016b).

Arthrospira Stitzenberger ex Gomont

Morphological description
Solitary trichomes always without heterocytes, free floating or in mats covering hard substrate (microscopic or macroscopic). Trichomes more or less regularly coiled screw-like along their entire length. Generally without sheaths; however, if a sheath is present, it is colourless, tube-like with open ends enclosing single trichomes. Trichomes isopolar, 3–10 μm wide. Cells cylindrical, more or less isodiametric or shorter than wide, pale or bright blue-green or olive-green, in planktonic forms with aerotopes and in benthic forms without aerotopes. Not or only slightly constricted at the visible cross-walls. Trichomes not attenuated or only slightly attenuated towards the ends, with motility due to a rotational movement. Terminal cells widely rounded, usually with thickened outer cell walls or with calyptra (Figure 3.5I).

Taxonomic background
Arthrospira may be confused with *Spirulina*; the main difference is that *Arthrospira* has clearly delimited and visible cells, while in *Spirulina* cross-walls are not clearly visible. Further, *Arthrospira* has wider cells, and the trichomes are coiled in wider spirals compared to *Spirulina* trichomes that are tightly coiled. Eight species of *Arthrospira* are described, of which *A. platensis* seems to be the most frequently occurring one. However, in many reports, a species assignment is not made. Nowicka-Krawczyk et al. (2019) proposed to rename *A. fusiformis* to be renamed to *Limnospira fusiformis*.

Ecology and distribution
Arthrospira is generally found in shallow, turbid environments primarily in tropical and subtropical climates, in brackish or saline (alkaline) waters but occasionally also in freshwater.

Limnothrix Meffert

Morphological description
Trichomes solitary, always without heterocytes, free floating, isopolar. Straight or slightly curved or coiled irregularly screw-like, isopolar, without sheath or with an only very fine, colourless sheath. Trichomes cylindrical and from 1 to 6 μm wide, without or with reduced motility. Cells isodiametrical or longer than wide, unconstricted or slightly constricted at the cross-walls. Colour can range from pale blue-green to brown and orange. Aerotopes characteristically located close to the cross-walls. Apical cells are usually cylindrical, but sometimes conical (Figure 3.5J).

Taxonomic background
Most species of *Limnothrix* were originally placed in the genus *Oscillatoria*. The genus was amended by Meffert (1988) and confirmed by more recent studies (Suda et al., 2002; Komárek et al., 2014). The genus *Limnothrix* includes strains closely related to *Pseudanabaena* (Nishizawa et al., 2010) and is classified in the order Synechococcales by Komárek et al. (2014).

Ecology and distribution
Planktonic or tychoplanktonic, in fresh, mesotrophic to eutrophic, turbid and mixed waterbodies. *Limnothrix redekei* is distributed widely in the temperate zones but does not frequently form blooms.

Lyngbya Agardh ex Gomont, ***Moorea*** Engene et al., ***Microseira*** McGregor and Sendall and **related taxa**

Morphological description
Unbranched trichomes not constricted at cross-walls, enclosed in a firm sheath that is often protruding from trichomes. Cells short, cylindrical or, more often, coin-like (cell width ≫ cell length). Often strongly pigmented

with a brown-green or blue-green colour, making cell walls difficult to recognise. *Lyngbya/Moorea* forms benthic mats on hard substrates or occurs epiphytic, forming macroscopic structures sometimes described as "mermaid's hair" (Figure 3.5K).

Taxonomic background
Two of the most studied species with respect to cyanotoxins are *Lyngbya majuscula* and *L. wollei*. Toxigenic strains of both species have been studied taxonomically and are proposed to be renamed: one cluster of *L. majuscula* is proposed to be renamed to *Moorea producens* (Engene et al., 2012) and a cluster of *L. wollei* to *Microseira wollei* (McGregor & Sendall, 2015). Further new genera separated from the *Lyngbya* species complex are *Okeania* (Engene et al., 2013) and *Dapis* (Engene et al., 2018). More than 500 species of *Lyngbya* are listed in AlgaeBase, with descriptions of a large share dating from before 1950, that is, without support from molecular data. Expectedly, this group of mainly marine filamentous cyanobacteria forming macroscopic aggregates will be subject to taxonomic revision once molecular and polyphasic analyses are conducted systematically (Engene et al., 2010).

Ecology and distribution
L. majuscula (*Moorea producens*) occurs primarily in brackish or marine habitats in tropical and subtropical zones. *L.* (*Microseira*) *wollei* is found in rivers and streams in temperate to subtropical zones where it forms. Other species of *Lyngbya sensu stricto* are found mostly in freshwaters.

Phormidium Kützing ex Gomont, ***Microcoleus*** Desmazières ex Gomont **and related taxa**

Morphological description
Unbranched trichomes generally form fine or thick mats (microscopic to macroscopic) and are rarely solitary. Trichomes isopolar, straight, coiled or waved, usually <10–12 μm wide, facultatively with tube-like, firm, colourless sheaths with open ends. Vegetative cells cylindrical to slightly barrel-shaped, more or less isodiametrical or slightly shorter or longer than wide, constricted or unconstricted at the cross-walls, generally without aerotopes but with refractive granules. Trichomes not attenuated at the ends, sometimes bent or twisted screw-like towards the ends, motile within and outside of sheaths (Figure 3.5L).

Taxonomic background
This genus comprises a large number of species (>400; e.g., *P. nigrum*, *P. autumnale*, *P. fragile*), and the taxonomic status of many has been challenged (Palinska et al., 2011). As a consequence, a number of *Phormidium* species have been assigned to new genera, for example, *Wilmottia* (Strunecký et al., 2011), *Oxynema* (Chatchawan et al., 2012; Strunecký et al., 2014) or to

existing genera such as *Microcoleus* (*Phormidium*) *autumnalis* (Strunecký et al., 2013) based on molecular analyses. *Microcoleus anatoxicus* has been reported to produce primarily dihydroanatoxin a (Conklin et al. 2020). For this reason, specimens of this taxon are often reported as *Phormidium* sp. and species assignment in elder publication may be no longer valid from a today's point of view. *Phormidium* may be confused with *Geitlerinema*, *Lyngbya* (*Moorea, Microseira*) and others.

Ecology and distribution
Epiphytic or epilithic in shallow rivers or streams but also in shallow areas in eutrophic standing waters. Due to the uncertain taxonomy and the resulting difficulties for unambiguous species determination, the knowledge on geographic distribution of individual *Phormidium* species is incomplete (Marquardt & Palinska, 2007). Specimens of the genus were found in a variety of latitudes, including extreme cold environments (Strunecký et al., 2012).

Planktolyngbya Anagnostidis et Komárek

Morphological description
Trichomes without heterocytes, solitary, with thin, simple, colourless, but firm sheaths. Isopolar, cylindrical trichomes, narrow, up to 3 μm wide, straight, waved or coiled, generally not narrowed to the ends. Slightly constricted or unconstricted at the cross-walls, and always immotile. Cylindrical cells usually longer than wide (rarely shorter than wide), without aerotopes, pale grey-blue, blue-green, yellowish or olive-green. Terminal cells rounded or narrowed-rounded without a calyptra (Figure 3.5M).

Taxonomic background
The genus was separated from *Lyngbya* by Anagnostidis and Komárek (1988) and confirmed by polyphasic analysis (Komárek et al., 2014) who placed the genus to the order Synechococcales (family Leptolyngbyaceae).

Ecology and distribution
Planktonic species are typical in large, mesotrophic reservoirs. Some species are limited to tropical and warm areas of temperate zones, while several species are presumably nordic.

Planktothrix Anagnostidis et Komárek

Morphological description
Trichomes always solitary, free floating, more or less straight or slightly irregularly waved or curved. In culture, trichomes may form irregular

clusters. Sheaths generally absent; if present, they are fine, colourless and diffluent. Trichomes isopolar, cylindrical, not constricted or slightly constricted at cross-walls. Length of trichomes up to 4 mm, width 3–12 µm. Immotile or sometimes slightly motile (trembling, gliding), slightly attenuated or not attenuated towards the ends, sometimes capitated or with terminal calyptra. Most species with prominent aerotopes take a large share of the cells' volume. Vegetative cells cylindrical or (rarely) slightly barrel-shaped, shorter than wide, up to ±isodiametric or rarely little longer than wide (Figure 3.5N).

Taxonomic background
Planktothrix was originally placed in the genus *Oscillatoria*, from which it was separated due to ecological traits and the formation of large numbers of aerotopes (Anagnostidis & Komárek, 1988).

Several species are described, of which *Planktothrix agardhii* and *P. rubescens* are the most relevant with respect to cyanotoxins. Other species (e.g., *P. mougeotii*, *P. pseudagardhii* and *P. spiroides*) are morphologically similar but have not been reported to form blooms. Some species produce only few aerotopes (*P. paucivesiculata*, *P. serta*; Gaget et al., 2015a).

Ecology and distribution
Generally, planktonic and evenly distributed in the water column in non-stratified, shallow lakes (*P. agardhii*) or cumulated at the thermocline of deep, stratified lakes (*P. rubescens* or, more rarely, *P. mougeotii*), occasionally forming blooms. In the case of blooms of *P. rubescens*, these may accumulate at the metalimnion and not be visible at the surface (see Chapter 4). Both species tolerate low light intensities. The genus is widely distributed in temperate climates, but individual species may show more restricted distribution patterns.

Pseudanabaena Lauterborn

Morphological description
Trichomes without branching and without firm sheaths, sometimes with fine, colourless, diffluent envelopes. Trichomes solitary or agglomerated in very fine mucilaginous mats. Individual trichomes straight, slightly waved or bent, usually not very long, 0.8-3 µm wide, not attenuated at the ends, usually with slight constrictions at the distinct cross-walls. Cells cylindrical, usually longer than wide (sometimes barrel shaped or nearly spherical). The apical cell is cylindrical and rounded at the end or more or less conical up to bluntly or sharply pointed. Generally without aerotopes, but sometimes with aerotopes at the ends of cells. Trichomes may have motility (trembling). Pigmentation often reddish (Figure 3.5O).

Taxonomic background
Pseudanabaena is closely related to *Limnothrix* (Acinas et al., 2009), and some authors refer to this as "*Pseudanabaena/Limnothrix*" group (e.g., Zwart et al., 2005). Both genera have been assigned to the order Synechococcales *sensu* (Komárek et al., 2014); these genera are close to single-cell forms such as *Synechococcus* sp.

Ecology and distribution
Mostly planktonic species, tychoplanktonic or benthic in oligotrophic, mesotrophic up to slightly eutrophic water reservoirs and turbid mixed waters. Short trichomes of *Pseudanabaena endophytica* can often be found attached to colonies of *Microcystis*.

Tychonema Anagnostidis et Komárek

Morphological description
Unbranched, cylindrical trichomes lack a visible sheath of 7–12 μm width not constricted at cross-walls. Cells generally slightly shorter than wide or isodiametrical and appear almost empty except for granulae at the cross-walls or the cell periphery. Trichomes mostly solitarily and lacking motility as observed in *Geitlerinema* or *Phormidium* (Figure 3.5P).

Taxonomic background
Tychonema is a currently recognised distinct genus within Oscillatoriales (Anagnostidis & Komárek, 1988) and has been confirmed by polyphasic analyses (Suda et al., 2002). Four species are described, the distinction of which may be difficult (*Tychonema bornetii*, *T. bourrellyi*, *T. decoloratum* and *T. tenue*).

Ecology and distribution
As the name already indicates, *Tychonema* typically is tychoplanktonic: the trichomes are loosely attached to macrophytes or hard substrate but can be detached due to water movement and become planktonic.

Tychonema is primarily found in mesotrophic lakes of temperate zones where macrophyte stands exist, for example, in assemblages of water moss (Fastner et al., 2018). *T. bourrellyi* is considered as truly planktonic (Salmaso et al., 2016b).

3.7.3 Colonial forms

These taxa correspond to subsection 1 in Table 3.1 or "Chroococcales" and are unicellular with cells embedded in a common mucilage. Following more recent taxonomic schemes, the genera *Aphanocapsa* and *Merismopedia* are placed in the order Synechococcales (Komárek, 2016b).

Aphanocapsa Nägeli

Morphological description
Cells form microscopic (sometimes macroscopic) more or less spherical or irregular colonies with irregularly, loosely or densely distributed cells. Mucilage fine and diffluent, generally colourless but macroscopically colonies appear as firm sheaths. Cells spherical from 1.5 to 6 μm of diameter (hemispherical after division), without own mucilaginous envelopes, generally without aerotopes, sometimes with granular content. Cell division always in two perpendicular planes in successive generations. Some species are morphologically similar to *Microcystis*, except for the lack of aerotopes in *Aphanocapsa* (Figure 3.5Q).

Taxonomic background
It is suggested that planktonic species need revision as the relationship to other form genera like *Microcystis* is not clear.

Ecology and distribution
Periphytic, benthic or metaphytic in stagnant and running freshwater systems, usually with clear water, common in lakes. Often found in late summer in the epilimnion of oligotrophic, deep lakes. Registered worldwide, but several species are ecologically sharply limited and occur in geographically limited areas.

Similar small coccoid taxa are the colony-forming *Aphanothece* and single-celled *Synechococcus* and *Synechocystis* (Figure 3.5R).

Gomphosphaeria Kützing

Morphological description
Cells embedded in a mucilage forming spherical or irregularly oval colonies, sometimes composed of multiple subcolonies. Mucilage with gelatinous stalks that radiate from the centre of the colony to the periphery. The stalks are widened at the ends and envelope individual cells with a thin mucilage layer. Cells elongate (6–12×2–8 μm), radially oriented at the end of stalks. Pigmentation pale or bright blue-green, olive-green or red (Figure 3.5S).

Taxonomic background
At first sight, the genus can be confused with *Snowella* or *Coelosphaerium*; see taxonomic update in Komárek and Anagnostidis (1999).

Ecology and distribution
Generally, found in eutrophic to hypertrophic, small- to medium-sized lakes.

Merismopedia Meyen

Morphological description
Free-floating microscopic colonies, square or rectangular with one layer of cells densely or loosely arranged in a single plane. Larger colonies may be contorted or composed of several subcolonies. Colonies of a few to several cells that divide in two alternating planes, forming groups of 4 or 16 cells that collectively form distinctive, flat colonies with hyaline (transparent), fine envelopes, some species with envelopes surrounding each cell. Cells spherical or elliptical (hemispherical after division), generally pale or bright blue-green content; in a few species in central parts of cells with refractive granulae or aerotopes (Figure 3.5T).

Taxonomic background
Some 20 morphospecies of *Merismopedia* are described, for example, *M. glauca*, *M. punctata* or *M. elegans*. In most ecological studies, only *Merismopedia* sp. is reported.

Ecology and distribution
Planktonic or metaphytic, usually in biotopes with submerged macrophyte vegetation. Temperate habitats: deep and shallow, oligotrophic to eutrophic, medium to large lakes. Common in the epilimnion of mesotrophic lakes in summer.

Cosmopolitan distribution, but several species have clearly ecologically and geographically limited areas of distribution.

Microcystis Kützing ex Lemmermann

Morphological description
Free-floating microscopic or macroscopic colonies, spherical, oval or elongated, in several species clathrate. A large number of species have been described based mainly on cell size and colony morphology. The latter is, however, not available in cultured strains that generally grow as single cells or atypical colonies (Otsuka et al., 2000). The same is true for samples fixed with Lugol's solution in which colonies disintegrate to small clusters or single cells, allowing a differentiation only by cell size. In some species, colonies are composed of subcolonies or multiple more or less separated clusters of cells. All cells densely or sparsely arranged in a common mucilage with the density of cells highly variable in particular species. Mucilage fine, colourless, diffluent or distinct and delimited (e.g., *Microcystis wesenbergii*). Gelatinous envelopes around individual cells are never present. Cells spherical or hemispherical shortly after division, ranging from 2 to 7 μm in diameter or slightly elongated, with many, irregularly arranged aerotopes. Differentiation of morphospecies in samples of natural populations is often uncertain as many colonies show characteristics of more than one morphospecies (Figure 3.5U).

Taxonomic background

The number of described morphospecies varies depending on the reference source chosen (see Box 3.1). Due to phenotypic variability, the status of individual morphospecies and their relationships is largely unclear. The genus *Microcystis* is one of the few cyanobacterial genera that underwent systematic taxonomic revision based on molecular data. As a result, based on genomic DNA homologies, Otsuka et al. (2001) proposed to unify the species *M. aeruginosa*, *M. ichthyoblabe*, *M. novacekii*, *M. viridis* and *M. wesenbergii* in a single species. This is also supported by Harke et al. (2016), but nonetheless, this proposal has not been validated, primarily for formal reasons (Oren & Ventura, 2017).

A particular morphotype occurring in tropical waters has been described as *Radiocystis*. This genus is characterised by cells more or less arranged in radial series protruding from the centre embedded in a mucilage also showing radial structures (Komárek & Komárková-Legnerová, 1993). Genomic sequences such as 16S rRNA or phycocyanin operon are, however, identical to those of *Microcystis* (Vieira et al., 2003). Similarly, *Sphaerocarvum* sp. has been split from the genus *Microcystis* based on a particular colony morphology *in situ* (Azevedo & Sant'Anna, 2003), but has genomic sequences identical to *Microcystis* (Rigonato et al., 2018).

Ecology and distribution

Planktonic, in mesotrophic to eutrophic standing waters that are at least temporally stratified, preferably in shallow or medium depth lakes. Mostly absent or restricted to the shallow basins or to the littoral region in deep, stratified lakes where they can, however, form large blooms like in the North American great lakes. *Microcystis* frequently forms blooms in eutrophic systems, and under conditions of stable thermal stratification, it can form surface blooms and massive scums. Colonies can sink to the bottom and overwinter in the sediment.

Many species with a cosmopolitan distribution, except in subpolar regions but several taxa are restricted geographically due to ecological preferences (van Gremberghe et al., 2011; Harke et al., 2016).

PICTURE CREDITS

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