

## Taxonomic classification of cyanoprokaryotes (cyanobacterial genera) 2014, using a polyphasic approach

Taxonické hodnocení cyanoprokaryot (cyanobakteriální rody) v roce 2014 podle polyfázického přístupu

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The whole classification of cyanobacteria (species, genera, families, orders) has undergone extensive restructuring and revision in recent years with the advent of phylogenetic analyses based on molecular sequence data. Several recent revisionary and monographic works initiated a revision and it is anticipated there will be further changes in the future. However, with the completion of the monographic series on the *Cyanobacteria* in Süsswasserflora von Mitteleuropa, and the recent flurry of taxonomic papers describing new genera, it seems expedient that a summary of the modern taxonomic system for cyanobacteria should be published. In this review, we present the status of all currently used families of cyanobacteria, review the results of molecular taxonomic studies, descriptions and characteristics of new orders and new families and the elevation of a few subfamilies to family level. All recently defined cyanobacterial genera (some still invalid) are listed in the family to which they are likely to belong and an indication is given of their taxonomic validity and level of polyphasic characterization of each genus.

**Key words:** concept of genera, cyanobacteria, molecular methods, taxonomic classification, polyphasic approach

### Introduction

Taxonomic classification is the primary method used to evaluate the diversity of all biological groups of organisms. Criteria for classification have continually changed over the years since Linnaeus conceived his scientific system. Taxonomy has been transformed from a system that simply placed morphologically similar taxa into a hierarchical system of classification that ideally reflects evolutionary relationships and creates a network of hypotheses about evolutionary history. While in its initial stages systematic classification was somewhat arbitrary and artificial, it can now be argued that it reflects phylogenetic relationships. Consequently, when classification does not match phylogenetic evidence it needs to be revised.

*Cyanobacteria* (cyanoprokaryotes) are an especially challenging group to classify. They are arguably one of the most ancient groups of organisms on earth, with some fossil representatives having morphology very similar to present-day species (Schopf 1974, Knoll 2008). Their long and arguably complex evolutionary history (possibly achieved by horizontal gene transfer, as indicated by their homoplasy) is difficult to discern simply

from morphology. A number of the morphological characters used to define higher taxa (coccal vs trichal form, tapering, polarity, types of branching, dimensions, presence of akinetes, etc.) have apparently arisen and/or been lost several times during the evolution of modern species and genera (Gugger & Hoffmann 2004, Schirrmeister et al. 2011, Komárek 2013, Shih et al. 2013).

There were published several systems of higher level classification of *Cyanobacteria*. After the first classification systems (Gomont 1892, Bornet & Flahault 1886–1888), Geitler (1925) first proposed *Chroococcales*, *Entophysalidales*, *Pleurocapsales*, *Dermocarpales*, *Siphononematales*, *Nostocales* and *Stigonematales*, but seven years later he adopted the system proposed by Frémy (1929), which included only three orders: *Chroococcales*, *Chamaesiphonales*, and *Hormogonales* (Geitler 1932). Ten years later he recognized *Chroococcales*, *Dermocarpales*, *Pleurocapsales* and *Hormogonales* (Geitler 1942), a system still in use 24 years later with only a few modifications (Elenkin 1936–1949, Starmach 1966). Desikachary (1959) mainly reviewed the *Stigonematales* and followed other authors in uniting the non-branching filamentous taxa into one order (although he chose *Nostocales*). Prescott (1962) followed Frémy's (1929) system, and Bourrelly (1970) used, in principal, Desikachary's system of higher classification. Rippka et al. (1979) recommended five sections, which became the primary basis for the nomenclatural classification in Bergey's Manual of Systematic Bacteriology, which recognized five subsections instead of orders, I (= *Chroococcales*), II (= *Pleurocapsales*), III (= *Oscillatoriales*), IV (= *Nostocales*) and V (= *Stigonematales*) (Castenholz 2001).

The taxonomic system of cyanobacteria was radically changed particularly with the introduction of electron microscopy and of molecular and genetic methods for characterization of cyanobacterial taxa. *Cyanobacteria* were nearly continually being revised since the work of Francis Drouet, with radically different proposals being made simultaneously over the last fifty years. The first group of researchers, typified by Drouet, wanted to simplify the systematic classification by substantial reducing the number of taxa (Drouet & Daily 1956, Drouet 1968, 1973, 1978, 1981, Bourrelly 1970, Otsuka et al. 2001), while a second group proposed splitting both species and genera (and indeed all higher level taxa), in order to achieve monophyly in all taxonomic groups (Anagnostidis & Komárek 1985, Casamatta et al. 2005, Johansen & Casamatta 2005, Řeháková et al. 2007, Siegesmund et al. 2008, Perkerson et al. 2011). A third group advocated caution and recommended a moratorium on taxonomic revision until there was considerably more molecular evidence (Hoffmann 2005). The extreme consequence of this approach is to effectively discard the nomenclatural definition of orders, families, genera and species and replace them with subsections, “families” and “form genera” that do not reflect evolutionary history but provide a temporary, artificial, nomenclaturally invalid, but convenient and stable method of referring to cyanobacterial strains (Castenholz 2001).

While the authors of this paper recognize the merits and difficulties of these three approaches, we advocate another system of taxonomic classification that reflects evolutionary history and includes monophyletic taxa. We feel it is better to have narrowly-defined, ostensibly monophyletic genera, each containing relatively few species than large, poorly defined polyphyletic genera containing many unrelated species. This taxonomic system is not yet available. However, considerable revisionary work has been undertaken in recent years (Anagnostidis & Komárek 1985, 1988, 1990, Komárek & Anagnostidis 1986, 1989, Büdel & Kauff 2012), and many new genera and species have

been described. Consequently, while we have not yet arrived at a complete and stable revision, the classical system and indeed approach of the most important cyanobacterial researchers of the 20th century (Geitler 1925, 1932, 1942, Frémy 1929, Elenkin 1936–1949, Desikachary 1959) is so dated and incorrect that without adoption of a provisional taxonomic system that more clearly reflects modern evidence no further progress will be made. The new Süßwasserflora series on the cyanoprokaryotes (cyanobacteria) is now finally complete (Komárek & Anagnostidis 1998, 2005, Komárek 2013). The use of a more modern higher level systematics is recommended by Hoffmann et al. (2005a, b), who divide the class *Cyanophyceae* into four subclasses: *Gloeobacteriophycidae*, *Synechococcophycidae*, *Oscillatoriophycidae* and *Nostochopycidae*. This system reflects the phylogeny and is radically different to past systems in that it recognizes that coccoid lineages (formerly the *Chroococcales*) and filamentous lineages (formerly the *Oscillatoriales*) are mixed to some degree, with the *Synechococcales* and *Pseudanabaenales* representing both coccoid and filamentous orders containing cells with parietal thylakoids (and thus in *Synechococcophycidae*), and the *Chroococcales* and *Oscillatoriales* containing cells with more complicated thylakoid arrangements (and thus in the *Oscillatoriophycidae*) (cf. Komárek & Kaštovský 2003). This system has undergone some changes in the intervening several years, and this publication reflects the newest thinking and newest system. It is superior to older schemes of classification, because it more closely reflects phylogeny, but it is likely there will be further revisions in the near future as more taxa are sequenced and more genomes become available.

Since 2000, more than 50 genera of cyanobacteria have been described. At the 19th IAC symposium in Cleveland (28 July – 2 August 2013), additional 16 putative new genera were proposed along numerous species. We are in a time of fairly radical and rapid systematic and taxonomic development. The purpose of this review is threefold. First, we will present a more phylogenetically-based system of higher level taxonomy and classification of the cyanobacteria as currently exists in early 2014 (recognizing it will undoubtedly change in the coming decade). Second, we will present all the genera that have some taxonomic standing or are currently accepted and give an indication of their current standing. Third, we will discuss the nature of the taxonomic challenges cyanobacterial taxonomists face in creating a taxonomic system in which at least the genera and species will be monophyletic.

## Methods

### *Phylogenetic methods*

The phylogenetic tree (Fig. 1) was generated using 31 conserved proteins previously tested for (cyano)bacteria (Wu & Eisen 2008, Shih et al. 2013). First, BLAST queries were made from sequences of these proteins mined from the complete genome of *Synechocystis* PCC 6803 (BA000022). Each of the 31 queries was used in tblastn (cut-off value  $1.e^{-10}$ ) algorithm searches against a custom database compiled from all the complete cyanobacterial genomes available and WGS contigs downloadable from NCBI (April 2014). Hits for each protein were aligned using MAFFT v. 7 (Katoh & Standley 2013) FFT-NS-i algorithm and the alignments were manually reviewed to remove ambiguous sites, gap regions and short sequences. All alignments were then concatenated into a 5689

amino-acid long matrix containing 146 OTUs. Only OTUs with complete or nearly complete sequences for all 31 proteins were used in the phylogenetic analysis. A maximum-likelihood tree was produced using RaxML v. 7 (Stamatakis 2006), a CIPRES supercomputing facility (Miller et al. 2012) and the Dayhoff+G likelihood model. One thousand bootstrap pseudoreplications were calculated to evaluate the relative support of branches.

#### *Evaluation of the present status of cyanobacterial genera*

The system of *Cyanobacteria* presented in this study is based on traditionally, validly described and morphologically-defined genera, and provides continuity with the research of the 19th, 20th and 21st centuries. It relies on botanical binomial nomenclature. Extant taxonomic characters were accepted where possible, applying the polyphasic approach in all cases where molecular and other data (electron microscopy, biochemical analysis) are available. The modern system is in good agreement with botanical nomenclatural rules (only with few exceptions). It is not because we prefer the botanical concept of cyanobacteria to the bacteriological nature of this group, but because the nomenclatural code for bacteria is not suitable for modern cyanobacterial classification and no cyanobacterium has been satisfactorily described according to CIP. The recognized and accepted cyanobacterial genera in June 2014 are listed by orders and families (Appendix 1). We include some genera that are provisional when we know that manuscripts describing the taxa exist and will likely be published in 2014 or 2015. All presented taxa do not share the same level of characterization and taxonomic clarity, and we divide their status into several main categories:

Category 1 indicates cyanobacterial genera supported by molecular phylogeny, including 16S rRNA gene sequence of the type species. Typically, members of this group were described using a polyphasic approach, i.e. by defining monophyletic clusters of strains together with one or more unique phenotypic characters (apomorphies) that can be used to identify them using morphology and other characters (e.g. *Acaryochloris*, *Brasilonema*, *Chakia*, *Coleofasciculus*, *Mojavia*, *Oculatella*, *Phormidesmis*, *Spirirestis*, etc.). Several older genera, originally based solely on morphology, the type species of which was later supported by molecular data, are included also in this category (e.g. *Arthrospira*, *Cyanothece*, *Cylindrospermum*, *Cylindrospermopsis*, *Gloeobacter*, *Limnococcus*, *Mastigocladus*, *Microcoleus*, *Microcystis*, *Richelia*, *Starria*). The definition of some of these genera was narrowed due to taxonomic revision, usually splitting some of the species to create new genera. Genera in this category can only be considered to be certain (*sensu stricto*) when the source of molecular characterization is the type species (or holotype material). Genera for which this is true are marked as category 1\* in Appendix 1.

Some genera are relatively well studied using modern methods; however they lack a molecular analysis of the type species (category 2). It is possible that the eventual sequencing of the type species will reveal that the other species attributed to the genus are not in the same clade. However, it is equally likely that when the type species is sequenced some of the species assigned to the genus will be in the same clade as the type and assignment to existing genera or new genera will be required to achieve monophyletic taxa. Examples of genera currently in this category include *Aulosira*, *Coelosphaerium*,

*Dermocarpella, Hyella, Myxosarcina, Petalonema, Schizothrix, Solentia, Symphyonema, Symploca* and *Trichocoleus*.

Category 3 consists of traditional morphogenera that require taxonomic revision. These genera, based on sequence-based phylogeny, are either paraphyletic or polyphyletic. Even though they are not monophyletic, complete revisions have not been undertaken because either the type has not been sequenced (so we do not know what really belongs in the genus *sensu stricto*), or very incomplete taxon sampling in these typically species-rich genera, or molecular workers are hesitant to undertake the exacting, rule-bound taxonomic work. In some instances the type species has been sequenced, but the genus remains polyphyletic and unrevised; this is true, e.g. for *Anabaena*, *Calothrix*, *Leptolyngbya*, *Nodularia*, *Nostoc*, *Oscillatoria*, *Pseudanabaena*, *Synechococcus*, *Synechocystis* and *Trichormus*. There are also genera in this group for which we have limited sequence data and the morphology is confused by the absence of clear discontinuities (e.g. *Anabaena* x *Wollea* x *Hydrocoryne*; *Gloeocapsa* x *Gloeocapsopsis* x *Asterocapsa*; *Spirulina* x *Halospirulina*). These genera need to be revised and clarified in the future using polyphasic studies.

A large percentage of cyanobacterial genera, typically those described many years ago, still await modern (molecular) characterization (category 4). Some of the genera in this category are common, but have not been sequenced because they are difficult to cultivate and there are no strains available (e.g. *Asterocapsa*, *Coelomoron*, *Cyanosarcina*, *Geitleria*, *Geitleribactron*, *Homoeothrix*, *Kyrtuthrix*, *Leibleinia*, *Lemmermanniella*, *Porphyrosiphon*, *Rhabdogloea*, *Rhabdoderma*, etc.). This group also includes validly described but taxonomically doubtful taxa (e.g. *Desmosiphon*, *Letestuinema*, *Lithomyxa*, *Loefgrenia*, *Loriella*, *Placoma*, *Rhodostichus*, *Tubiella* and others). Some of them are genera with incomplete and/or unclear diagnoses that have not been found since their description or only exceptionally.

Several genera are taxonomically invalid and have no nomenclatural standing (category 5). These are names that have appeared in recent scientific papers, usually with supporting molecular data, but do not meet the nomenclatural requirements of either the Bacteriological Code or International Code of Nomenclature for Algae, Fungi and Plants (Lapage et al. 1992, Mc Neill et al. 2012, respectively), e.g. *Crocospaera*, *Euhalothece*, *Thermosynechococcus*, *Xeronema*. This category includes also some described subgenera that are considered by modern researchers as “genera”, but without a formal nomenclatural revision that would make them valid (e.g. *Myochrotes* – part of *Scytonema*, *Godlewskia* – part of *Chamaesiphon*, *Alysophoron* – part of *Komvophoron*).

## Results

### New system of classification of the Cyanobacteria (Appendix 1)

The primary morphological characteristics that are diagnostic of the families were first given in Anagnostidis & Komárek (1988, 1990) and Komárek & Anagnostidis (1986, 1989), and updated in Komárek & Anagnostidis (1998, 2005) and Komárek (2013). A further updated version is given here, reflecting the most recent changes in higher level classification (Figs 1, 2). Hoffmann et al. (2005a, b) recommend the recognition of four subclasses (*Gloeobacteriophycidae*, *Synechococcophycidae*, *Oscillatoriophycidae* and

*Nostochophycidae*). Of these, the first and last are monophyletic groups, but *Synechococcophycidae* and *Oscillatoriophycidae* are not monophyletic in phylogenies based on multigene sequence alignments (Fig. 1). Although their thylakoid structure and type of cell division remain foundational as conservative ultrastructural characters valuable for identifying deep evolutionary divisions, there is apparently more variability in these characters than previously thought and the subclasses are likely to be further fragmented in the future when greater taxon sampling gives a clearer picture of the order and subclass level diversity. The new system we present below is as consistent as possible with our phylogenetic understanding of the many published phylogenies and the sample phylogeny we present (Figs 2, 3).

## 1. *Gloeobacterales*

This order contains only one monophyletic family with one genus (Rippka et al. 1974, Mareš et al. 2013b).

### 1.1 *Gloeobacteraceae* Komárek et Anagnostidis

The typical genus *Gloeobacter* was recently studied by Mareš et al. (2013b) and has a clear independent taxonomical position at the base of all *Cyanobacteria*. It is the only genus of cyanobacteria that lacks thylakoids (Fig. 2). The two species described form a monophyletic group and the entire genome of both species has been sequenced (category 1\*).

## 2. *Synechococcales*

A large group (over 70 genera) with both unicellular (plus colonial) and filamentous types but there is no sequence data for most taxa. A 31-gene phylogeny (Fig. 1) indicates that the group as currently defined is not monophyletic, but the families we define are at least not contradicted by present phylogenetic studies. With greater taxon sampling in the future, it is highly likely more orders will be recognized and there will be a family level revision of the *Synechococcales*. This group is united by the presence of parietal thylakoids and is presently equivalent to a subclass *Synechococcophycidae*. Even though its genera have parietal thylakoids, we have separated the *Spirulinaceae* into a new order separate from the *Synechococcales* based upon definitive molecular evidence (Fig. 1, see also Shih et al. 2013).

### 2.1 *Synechococcaceae* Komárek et Anagnostidis

Many genera from this family (12 out of a total of 17) are in category 4 (no relevant molecular data, see Appendix 1). Many of the genera in this group were described on the basis of the form of their colonies and mucilaginous envelopes, which disappear quickly in cultivation. There are only two phylogenetically unrelated sequences available for *Cyanodictyon*. The relationship of this genus with the morphologically similar genera *Cyanobium* and *Synechococcus* is also questionable. The colonial genus *Anathece* has an unclear relationship with solitary-living *Cyanobium*. The colonial habit is apparently tied to environmental conditions and the genetic basis of colony formation needs further study (Hickel 1985, Komárková-Legnerová & Cronberg 1985, Komárková-Legnerová 1991, Komárek et al. 2011, etc.). *Neosynechococcus* (Dvořák et al. 2014) is a newly described independent lineage, morphologically similar to *Synechococcus* (see in *Leptolyngbyaceae*). *Thermosynechococcus* is well defined from a molecular phylogenetic and ecological point of views, but

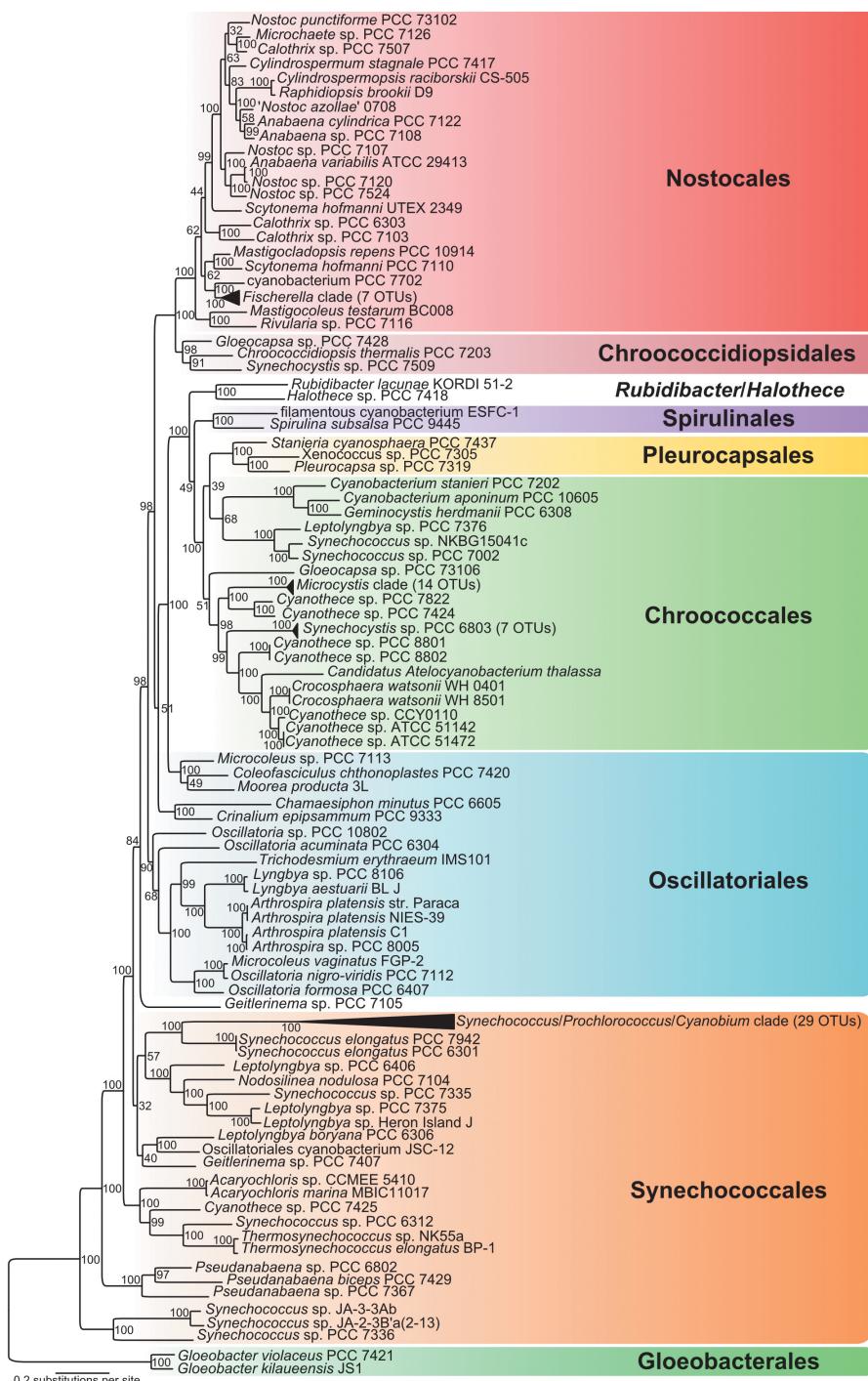


Fig. 1. – Phylogenetic tree of cyanobacteria based on 31 conserved protein sequences. All suitable complete and draft data on genomes available in April 2014 were utilized. The tree was calculated using a maximum likelihood algorithm with the bootstrap values given at the nodes. The cyanobacterial orders included in the current system are highlighted on the tree.

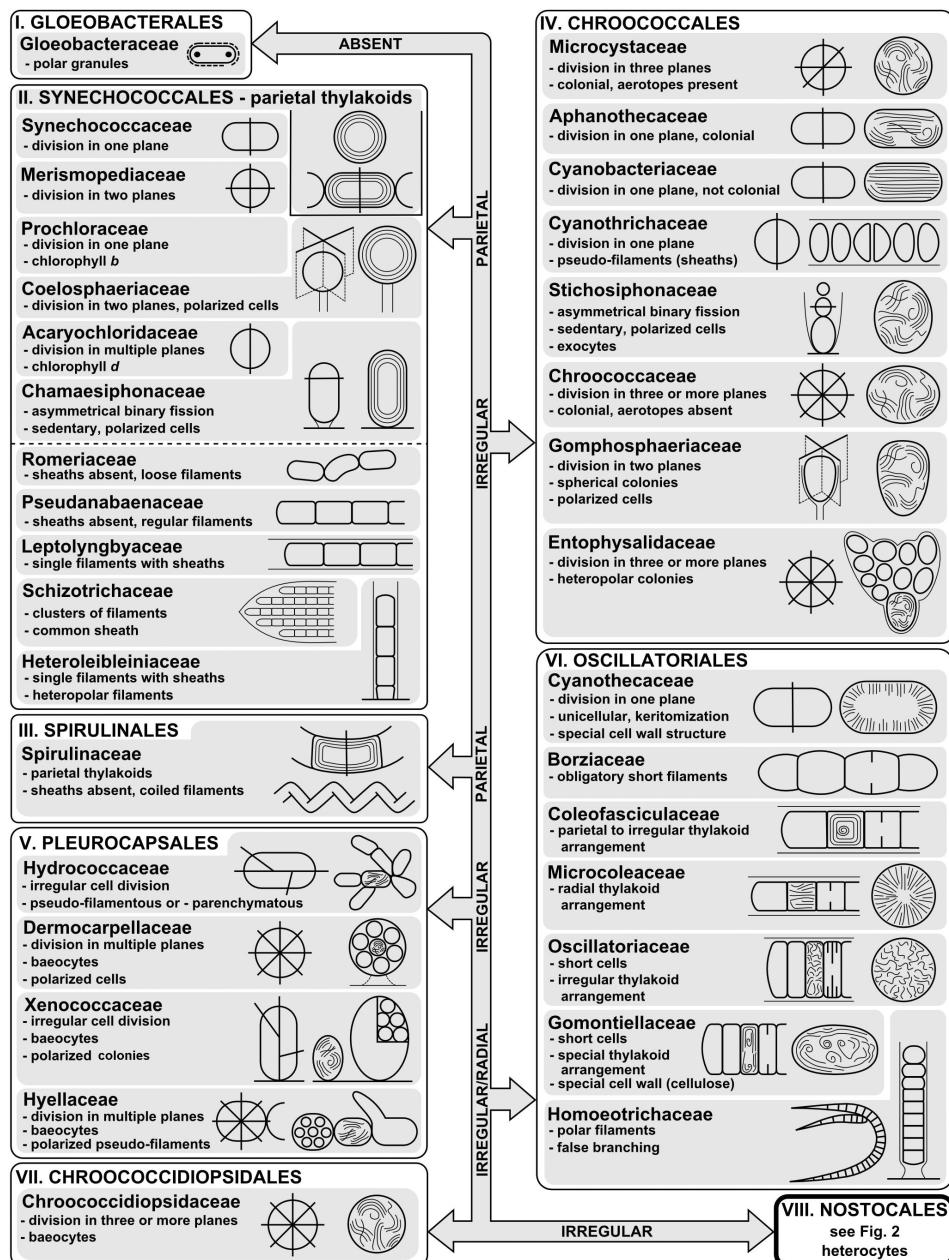


Fig. 2. – Schematic view of cyanobacterial orders and families, and the important taxonomic characters used to distinguish them. The basic separation of higher taxa is based on preliminary results of phylogenetic analyses and ultrastructural patterns of thylakoids.

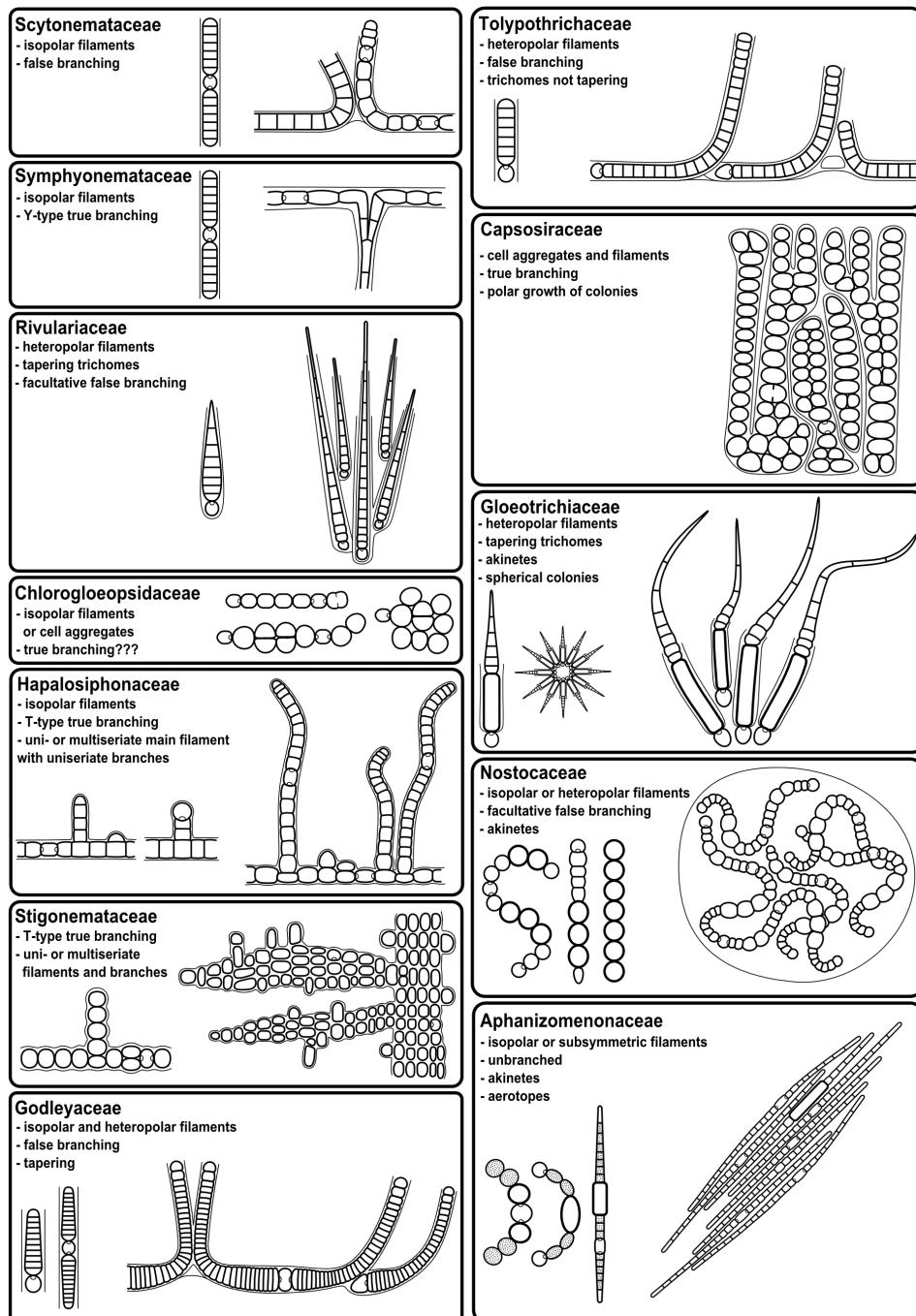


Fig. 3. – Schematic view of the families of heterocytous cyanobacteria (*Nostocales*) at the level of orders and families, and features important for their identification.

was unfortunately not validly published (Katoh et al. 2001). *Synechococcus* is a broad genus that is poorly morphologically and ecologically defined and includes many independent undescribed lineages (Waterbury et al. 1979, Willmotte 1994, Honda et al. 1999, Palenik 2001, Robertson et al. 2001 and many others). This family is in great need of study and revision at all taxonomic levels.

## 2.2 *Merismopediaceae* Elenkin

There are only a few sequences for *Aphanocapsa* and *Eucapsis*, which indicate a few unclear relationships (in particular, marine and freshwater *Aphanocapsa* are apparently different genera). There are no detailed polyphasic taxonomic publications. There are probably several small-celled types described originally within the genus *Chroococcus* belonging to the *Eucapsis* clade (Komárek & Hindák 1989, Komárková et al. 2010). The several 16S rRNA sequences that exist for *Merismopedia* (Palinska et al. 1996) and *Synechocystis* indicate they are polyphyletic, but the focus of the studies containing these sequences is on other taxa and the *Merismopediaceae* are considered only marginally (Rajaniemi-Wacklin et al. 2006, Korelusová et al. 2009). *Limnococcus* was assigned morphologically and ecologically to a separate subgenus of *Chroococcus* (Komárek & Anagnostidis 1998), but after a subsequent polyphasic study (Komárková et al. 2010) it was elevated to genus status as it is unrelated to typical *Chroococcus*, belonging to another family.

## 2.3 *Prochloraceae* R. A. Lewin

Only two marine genera are described (Lewin 1977, Chisholm et al. 1992), characterized by the presence of chlorophyll b. *Prochlorococcus* (one of the most important primary producers in the oceans of our planet) is well studied (Six et al. 2007), but the taxonomic level of two ecologically distant groups (high- and low-light adapted clusters) and the relations to some marine *Synechococcus* (Rocap et al. 2003) is still unclear. Symbiotic *Prochloron* is well studied in nature, but unresolved taxonomic problems include differences between symbiotic and non-symbiotic *Prochloron* and their relationship to *Synechocystis trididemnii* (Munchhoff et al. 2007). Finally, this family needs to be split into separate families as *Prochlorococcus* and *Prochloron* are phylogenetically separated in distantly related lineages in all phylogenies based on a sufficient sampling of taxa.

## 2.4 *Coelosphaeriaceae* Elenkin

In this family only a few strains of *Woronichinia* and *Snowella* have been studied using molecular methods (Rajaniemi-Wacklin et al. 2006), in spite of the fact that many members of this family are frequently abundant in stagnant waters throughout the world. This study supported the continued recognition of these genera. There are no sequences for *Coelomorion*, *Coelosphaeropsis* and *Siphonosphaera*, but there are two undocumented environmental sequences from New Zealand (EF638722 and EF638723) for *Coelosphaerium*. However, all data presently available show this family to be monophyletic.

## 2.5 *Acaryochloridaceae* fam. nov.

This family is an isolated lineage with one genus, *Acaryochloris*, well supported by Miyashita et al. (2003). According to the available data, there are probably more than one species in this genus.

## 2.6 *Chamaesiphonaceae* Borzì

No typical species of *Chamaesiphon* has yet been studied in detail, but sequencing of several species of various *Chamaesiphon*-types indicates that the traditional genus is polyphyletic (Turner 1997, Loza et al. 2013). The remaining genera lack polyphasic characterization. The subgenus *Godlewskia* probably belongs to another clade (*Chroococcales*, *Stichosiphonaceae*).

## 2.7 *Romeriaceae* fam. nov.

This is a small and poorly known group (Komárek 2001). A few sequences of the 16S rRNA gene are attributed to *Romeria*, but it is possible that none of these sequences are for typical *Romeria*. The rest of this family lacks polyphasic characterization. Other genera also possibly belong to this group, e.g. *Wolskyella* (Mareš et al. 2008).

## 2.8 *Pseudanabaenaceae* Anagnostidis et Komárek

A small family that contains the ecologically important genera *Limnothrix* and *Pseudanabaena*, which are both polyphyletic (Guglielmi & Cohen-Bazire 1984a, b, Anagnostidis & Komárek 1988, Komárek & Anagnostidis 2005, Turicchia et al. 2009, etc.). Strains assigned to the genus *Limnothrix* are in two (or more) distinct clades and belong to different genera (Suda et al. 2002, Gkelis et al. 2005, Zhu et al. 2012). *Limnothrix*, *Pseudanabaena* and *Arthonema gygaxiana* are intermixed in most phylogenies (Casamatta et al. 2006, Acinas et al. 2009, Johansen et al. 2011), and all three genera as currently circumscribed are polyphyletic. The sequences in the GenBank of the type species of *Arthonema*, *A. africanum*, are dissimilar (< 92%) to those of all named cyanobacteria, so it is certainly a distinct genus, but of very uncertain familial placement. There do not exist molecular data for *Yonedaella*. *Komvophoron* is apparently polyphyletic and the position of the type species is still unknown (Komárek & Anagnostidis 2005, Hašler & Pouličková 2010). The genera and species in this family are in need of polyphasic characterization and study in order to sort the taxa into monophyletic supported clades.

## 2.9 *Leptolyngbyaceae* stat. nov.

This is a large, relatively well-characterized family. *Halo Leptolyngbya* (Dadheech et al. 2012b), *Halomicronema* (Abed et al. 2002), *Nodosilinea* (Perkerson et al. 2011), *Oculatella* (Zammit et al. 2012, Johansen et al. 2013), *Phormidesmis* (Komárek et al. 2009, Turicchia et al. 2009), *Prochlorothrix* (Urbach et al. 1992) and *Neosynechococcus* (Dvořák et al. 2014) are monophyletic and the 16S rRNA gene of their holotypes has been sequenced. *Plectolyngbya* (Taton et al. 2011) is phylogenetically close to *Leptolyngbya*, whereas species of *Planktolyngbya* occur in two distant clades (Thomazeau et al. 2010). The broad definition of the widespread genus *Leptolyngbya* results in it still remaining polyphyletic (Casamatta et al. 2006, Johansen et al. 2011, Perkerson et al. 2011, Dadheech et al. 2012b, Zammit et al. 2012, etc.) The situation of the genus *Trichocoleus* is complicated due to the absence of sequence data for the type species as well as a sequence attributed to *T. sociatus* (Siegesmund et al. 2008, Mühlsteinová et al. 2014b). For this family we lack molecular data only for *Leibleinia*, which is morphologically and probably also genetically diverse (Komárek & Anagnostidis 1998).

### 2.10 *Heteroleibleiniaceae* stat. nov.

This small family is closely allied with the *Leptolyngbyaceae*, from which it is distinguished by the presence of a heteropolar attachment to the substrate; however, it grows usually without attachment organelles in cultures. There is no molecular characterization of *Heteroleibleinia*. Only one species of *Tapinothrix* has been sequenced (Bohunická et al. 2011), but its relationship to the type species has not been established. More evidence is needed to establish the family as independent from *Leptolyngbyaceae*.

### 2.11 *Schizotrichaceae* Elenkin

Only two sequences for *Schizotrichix* exist. The main problem within this wide genus is its morphologically supported polyphyly, the calcified types (=subgenus *Inactis*) versus typical *Schizotrichix* (Komárek & Anagnostidis 1998, Komárek et al. 2006). Sequences of the type species are needed. Since the sheath likely disappears in culture, it is possible that sequences exist for *Schizotrichix* but have been attributed to other genera in the Synechococcales. *Dasygloea* has not been characterized and is rarely reported.

## 3. *Spirulinales* ordo nov.

This order has a special phylogenetic position and is characterized by typical, regularly screw-like coiled trichomes without sheaths and has a characteristic cytology and ecology. *Spirulina* had an unstable position in molecular phylogenies for a long time. From a morphological point of view, the problem of open and closed helices remains unsolved. With whole genome sequencing now making phylogenetic placement easier, it appears that it is in its own special family distant from the *Synechococcophycidae* to which it was long thought to belong. We place it and its possible relatives into a new order. The commercially important “*Spirulina platensis*” is very different according to all phylogenetic and cytological criteria, does not belong in this order and must be classified in the genus *Arthrospira* (*Oscillatoriales*, *Microcoleaceae*).

### 3.1 *Spirulinaceae* (Gomont) Hoffmann, Komárek et Kaštovský

Syn. *Spirulinoideae* Gomont 1892. *Spirulina* and *Halospirulina* are genera primarily described using molecular data. If *Halospirulina* is retained as a separate genus, it will make *Spirulina* polyphyletic and in need of revision (Nübel et al. 2000). There are no molecular data for *Glaucospira*.

## 4. *Chroococcales*

This order has been considerably reduced in comparison to the old concept when it included coccoid forms with more complicated cytology and lacking baeocyte production (comp. Geitler 1932, Komárek & Anagnostidis 1998). It has been restricted to include only those coccoids that have a more or less irregular thylakoid arrangement than simple parietal thylakoids (i.e. excluding forms now in the *Synechococcales*). There are no modern data for numerous families in this order and their more thorough evaluation is needed.

### 4.1. *Microcystaceae* Elenkin

We only have morphological data for *Cyanocomperia*, *Planctocyanocapsa* and *Sphaerocavum*, and only limited unclear and raw molecular data for *Radiocystis*. The well-known

genus *Microcystis* is consistently monophyletic (Kato et al. 1991, Otsuka et al. 1999, Komárek & Komárková 2002, Willame et al. 2006, van Gremberghe et al. 2011, and others), but the species-level classification within the genus can be controversial (cf. Komárek & Anagnostidis 1998, Otsuka et al. 2001).

#### 4.2. *Aphanothecaceae* stat. nov.

The following genera appear to be monophyletic and there are sequence data for the type species: *Crocospaera* (Zehr et al. 2001, Webb et al. 2008), *Euhalothece* (Garcia-Pichel et al. 1998), *Halothece* (Garcia-Pichel et al. 1998, Margheri et al. 2008) and *Rippkaea* (Mareš et al. in prep.). *Aphanothece* appears to be monophyletic, but sequence data for the type species must be confirmed (Komárek et al. 2011). *Crocospaera* and *Euhalothece* are widely used names, but are invalidly published according to both nomenclatural codes. The genus *Gloeothece* after recent conservation in the modern sense (Mareš et al. 2013a) and polyphasic study (Mareš & Hauer 2013) seems to be well defined, however there are no DNA sequence data for the generitype. Only morphological data are available for the genera *Cyanoaggregatum*, *Cyanogastrum*, *Dzensia*, *Hormothece* and *Myxobactron*. Intriguingly, *Halothece* together with *Rubidibacter* (Garcia-Pichel et al. 1998, Choi et al. 2008, Margheri et al. 2008) (and very probably also the closely related *Euhalothece*) belong in an isolated lineage basal to *Chroococcales* (Fig. 1). After more data are collected, this clade will probably need to be described as a separate order.

#### 4.3. *Cyanobacteriaceae* fam. nov.

This monotypic family includes only *Cyanobacterium*, and the sequence data available on the NCBI indicate that not all strains designated as *Cyanobacterium* belong to the clade containing the type species (*C. stanieri* PCC 6308; Rippka & Cohen-Bazire 1983).

#### 4.4. *Cyanothrichaceae* Elenkin in Kiselev

This family has only one freshwater and brackish genus, *Johannesbaptistia*, which has a very characteristic morphology. The family is named after its original generic name ("*Cyanothrix*"), which was changed only at the generic level (according to priority). One sequence is available, but it is for a marine organism and consequently its identity with the type species *J. pellucida* is questionable. There are no sequences for any other species.

#### 4.5. *Stichosiphonaceae* Hoffmann, Komárek et Kaštovský

No molecular data are available for *Stichosiphon*. It is likely that *Chamaesiphon* subg. *Godlewskia* (comp. 2.6 *Chamaesiphonaceae*) belongs in this family, but revisionary work has not been completed.

#### 4.6. *Chroococcaceae* Nägeli

Electron microscopy and molecular sequence data are not available for most genera in this family, including *Asterocapsa*, *Cyanokybus*, *Cyanosarcina*, *Cyanostylon*, *Nephrococcus*, *Pseudocapsa* and *Pseudonocbyrsa*. There is one sequence for the genus *Chondrocystis* and if properly identified it is closer to *Stanieria* (*Dermocarpaceae*) than *Chroococcus*. *Chalicogloea* (Roldán et al. 2013), *Chroogloeoecystis* (Brown et al. 2005), *Chroococcus* (Komárková et al. 2010, Kováčik et al. 2011) and *Geminocystis* (Korelusová et al. 2009) are monophyletic and the type species has been characterized molecularly. There are a few

sequences for *Gloeocapsa* and *Gloeocapsopsis* (Ramos et al. 2010), but they do not form probably monophyletic clusters.

#### 4.7. *Gomphosphaeriaceae* Elenkin

Incl. *Beckiacaeae* Elenkin. This family contains only two genera (*Beckia* and *Gomphosphaeria*), both without molecular data.

#### 4.8. *Entophysalidaceae* Geitler

This is important family with eight genera. Sequence data for only one atypical representative of *Chlorogloea* are available. Several genera have only been studied morphologically (e.g. *Chlorogloea*; Komárek & Montejo 1994).

### 5. *Pleurocapsales*

Currently this group appears to be monophyletic based on the available sequences. The problem is that a large number of genera in this order lack sequence data. Members of this order are very difficult to transfer in pure cultures.

#### 5.1. *Hydrococcaceae* Kützing

All six genera in this family have not been investigated using either electron microscopy or molecular sequence data.

#### 5.2. *Dermocarpellaceae* Ginsburg-Ardré ex Christensen

*Stanieria* has been well studied with respect to molecular sequence data, including sequencing of the type species. However, not all strains designated as *Stanieria* belong to a single clade (Ishida et al. 2001). A few sequences, excluding the type species, exist for *Dermocarrella* (Fewer et al. 2002), and one for *Cyanocystis*. There is no modern taxonomic study of the whole family.

#### 5.3. *Xenococcaceae* Ercegović

We have no molecular data for *Xenotholos*. There are molecular data for *Xenococcus* (Seo & Yokota 2003, Shih et al. 2013), but not for the type species. This genus is polyphyletic based on existing data. In the future this family is likely to be combined with *Dermocarpellaceae*.

#### 5.4. *Pleurocapsaceae* Geitler

Syn. *Hyellaceae* Elenkin. All available data indicate that this family is a well-supported monophyletic group. There is only a little modern information on this important and genera-rich family. There are no molecular data for many genera (*Chamaecalyx*, *Chroococcidium*, *Cyanoderma*, *Cyanosaccus*, *Ercegovicia*, *Pascherinema*, *Podocapsa* and *Radaisia*). The best studied genus in this family, *Pleurocapsa*, is polyphyletic and this morphological type probably includes more than two genera (Ishida et al. 2001, Loza et al. 2013). For the remaining genera (*Chroococcopsis*, *Hyella*, *Myxosarcina* and *Solentia*) we only have a few sequences, but the polyphyly recorded indicates the need for revision of the reference strains (Fewer et al. 2002, Foster et al. 2009, Brito et al. 2012).

## 6. *Oscillatoriales*

This order does not now include the filamentous taxa with relatively narrow trichomes and parietal thylakoids (*Synechococcales*, *Spirulinales*), but includes those filamentous taxa with more complicated cytology (with radial, fasciculated, or irregular thylakoid arrangement), including also the coccoid, phylogenetically close genus *Cyanothece*. This genus forms a certain grade between the *Chroococcales* and other orders with a similar thylakoid arrangement and will consequently eventually require revision if monophyletic higher level taxa are to be achieved.

### 6.1 *Cyanothecaceae* fam. nov.

This monotypic family is phylogenetically related to filamentous cyanobacteria of the family *Gomontiellaceae* (Bohunická et al. in prep.). The type species, *Cyanothece aeruginosa*, has been well characterized using a polyphasic approach (Komárek et al. 2004). Other variable strains previously designated as “*Cyanothece* sp.” fall into several distinctly separate lineages. Revision of some of the phylogenetically separated *Cyanothece* strains has revealed them to be members of *Gloeothece*, *Euhalothece* and a newly established genus *Rippkaea* (Mareš et al., in prep.).

### 6.2. *Borziaceae* Borzì

This monotypic family is based only on morphological data as molecular data are not available.

### 6.3 *Coleofasciculaceae* fam. nov.

Over the last few years this group has been well studied, with the largest part of the family consisting of newly described and well supported genera (e.g. *Coleofasciculus* Siegesmund et al. 2008, *Wilmottia* Strunecký et al. 2011, *Kastovskya* Mühlsteinová et al. 2014a, *Anagnostidinema* Strunecký et al., in prep.). Taxonomical revision of *Geitlerinema* is needed as several works have shown it is polyphyletic (Willame et al. 2006, Perkerson et al. 2010, Hašler et al. 2012, 2014b).

### 6.4 *Microcoleaceae* stat. nov.

One of the largest families in the order *Oscillatoriales* is a relatively well studied group with many genera described and based on molecular characterization and modern criteria (status 1\*): *Annamia* (Nguyen et al. 2013), *Desertifilum* (Dadheech et al. 2012a), *Johanseninema* (Hašler et al. 2014a, 2014b), *Kamptonetema* (Strunecký et al. 2014), *Oxynema* (Chatthewan et al. 2012), *Planktothricoides* (Suda et al. 2002) and *Roseofilum* (Casamatta et al. 2012). Several older genera are well documented as monophyletic, e.g. *Arthrosira* (Manen & Falquet 2002, Dadheech et al. 2010), *Microcoleus* (Strunecký et al. 2013) and *Planktothrix* (Suda et al. 2002, Lin et al. 2010). There are no molecular data available for *Lyngbyopsis*, *Porphyrosiphon*, *Proterothrix Pseudoscytonema*, *Sirocoleum* and *Symplocastrum*. The genera *Oxynema* and *Kamptonetema* were derived from the traditional and polyphyletic genus *Phormidium*, where they were classified as special “groups” in this genus by Komárek & Anagnostidis (2005). Relations of one part of the traditional genus *Phormidium* (group VII – *Ph. autumnale*) to *Microcoleus* has been clearly established several times (Garcia-Pichel et al. 1996, 2013, Boyer et al. 2002, Marquardt &

Palinska 2007, Palinska & Marquardt 2008, Hašler et al. 2012, Struneký et al. 2013). Most species in *Pseudophormidium* belong in this family, but the several sequenced representatives will consequently require assignment to the *Pseudanabaenaceae* or *Leptolyngbyaceae*. There are no sequences of the type species of *Symploca* (which is terrestrial) and available data for marine species of *Symploca* indicate they are polyphyletic (Thacker & Paul 2004). The type species of the genus *Hydrocoleum* is a freshwater species and we have no available data for any freshwater members. Marine species of *Hydrocoleum* and *Trichodesmium* are very similar and maybe congeneric (Abed et al. 2006). The marine species of *Trichodesmium* are assigned to two clades and may represent two genera. *T. erythraeum* (type of the genus) is distinct from the compact clade containing *T. thiebautii*, *T. hildenbrandtii*, *T. tenue* and a cyanobacterium designated as *Katagymnene spiralis* (Orcutt et al. 2002). The freshwater *Trichodesmium*-species are molecularly evidently different from marine types. *Tychonema* also needs revision; sequences for the species *Tychonema tenue* place it in a clade separate from the rest of the genus, which forms a robust clade. The invalidly described genus *Pseudoscillatoria* Rasoulouniriana 2013 is evidently synonymous and ecologically identical with the correctly defined *Roseofilum* Casamatta et al. 2012.

#### 6.5. *Homoeotrichaceae* Elenkin

There is no molecular data available for any member of this family.

#### 6.6. *Oscillatoriaceae* (S. F. Gray) Harvey ex Kirchner

All available data indicate this group is a separate evolutionary clade. There exist several newly described genera for which we have polyphasic data of the type species: *Aerosakkonema* (Thu et al. 2012), *Limnoraphis* (Komárek et al. 2013b), *Moorea* (Engene et al. 2012) and *Okeania* (Engene et al. 2013a, b). In contrast, we have no data for *Polychlamydum*. Polyphyly has been detected in several genera (*Lyngbya*, *Oscillatoria*, *Phormidium*). In response, several taxonomic changes were made but several questions still persist (Turicchia et al. 2009, Struneký et al. 2011, 2013, Chatchawan et al. 2012, Engene et al. 2013b, Komárek et al. 2013b). Perhaps the most problematic and complicated case is the widespread genus *Phormidium*, in which the type species *Ph. lucidum* (and the whole “group VIII” sensu Komárek & Anagnostidis 2005) corresponds to the family *Oscillatoriaceae*. The typical members of this group were studied by Moro et al. (2010) and Sciuto et al. (2012). However, a large part of current *Phormidium*-species (including the most frequent species *Ph. autumnale*) belongs to the *Microcoleaceae* (Struneký et al. 2013). Almost all existing sequences designated as *Plectonema* belong to the species *P. boryanum* and *P. terebrans*, which are now classified both in *Leptolyngbya* (Komárek & Anagnostidis 2005). The type species for this family and the genus *Oscillatoria*, *Oscillatoria princeps*, has not been sequenced. The few other *Oscillatoria* that have been sequenced are unclear marine taxa. Most members of this genus lack molecular data. There are several sequences for *Blennothrix*, most of which are marine as is the type species (but molecular data for the type species are missing) and are designated under the incorrect name *Hydrocoleum* (*H. brebissonii*, *H. cantharidosmum*, *H. glutinosum*, *H. majus*). The thermal freshwater *Blennothrix* (EU586734-5) is very close to *Plectonema wollei*, both morphologically and molecularly.

### 6.7. *Gomontiellaceae* Elenkin

Incl. *Crinaliaceae* Elenkin. The molecular and ecological dataset for this family is not rich, but all data indicate this small and morphologically characteristic family is monophyletic (Bohunická et al. in prep.). This group has special morphology and cytology and has been confirmed several times (Claus 1959, Schuurmans et al. 2014). Currently, we have no molecular data for *Gomontiella*. There are sequences for the type species of *Starria* and a few species of *Crinalium*, but not the type of *Crinalium* (cf., e.g. Broady & Kibblewhite 1991). There are sequences for two freshwater strains of *Hormoscilla*. *Katagnymene* may be problematic; we have no molecular data for the type species, marine *K. pelagica*, but another marine taxon, *K. spiralis*, is very close (almost identical) to *Trichodesmium* (Orcutt et al. 2002, Lundgren et al. 2005). The freshwater *Katagnymene accurata* resembles this group morphologically, but detailed data are missing. Part of the genus *Komvophoron* probably belongs also to the family *Gomontiellaceae* (cf. Hašler & Pouličková 2010).

## 7. *Chroococcidiopsidales* ordo nov.

This group of organisms (one genus) which mostly live in extreme habitats was previously associated with the *Pleurocapsales*, but phylogenies based on genomic (Fig. 1) and 16S rRNA data of the type species *C. thermalis* indicate that it should be separated from that order. This order clusters surprisingly in the vicinity of the heterocytous cyanobacteria (*Nostocales*; Fewer et al. 2002).

### 7.1. *Chroococcidiopsidaceae* fam. nov.

Sequences are available for several strains attributed to *Chroococcidiopsis*, which lie outside of the clade with the type *C. thermalis* (more genera?). The whole genome of strain PCC 7203 was sequenced. The extremophiles (cold and hot desert types; e.g. Friedmann 1980, de los Ríos et al. 2010, Bahl et al. 2011, and others) appear to belong to *Chroococcidiopsis sensu stricto*.

## 8. *Nostocales*

This order represents a large and monophyletic cluster of filamentous cyanobacteria with diversified thallus and special prominent cells (heterocytes, akinetes). This order contains unbranched and isopolar, and falsely or true branched types, the filaments of few families have heteropolar structure.

### 8.1. *Scytonemataceae* Rabenhorst ex Bornet et Flahault

This species-rich group of isopolar, false-branching heterocytous cyanobacteria is currently being revised in a polyphasic study and taxonomic changes can be expected. Preliminary results (Fiore et al. 2007, Aguiar et al. 2008, Sant'Anna et al. 2010, Vaccarino & Johansen 2011, 2012, Becerra-Absalón et al. 2013, Komárek et al. 2013a, Komárková et al. 2013) show that at least the genera *Scytonema* and *Brasilonema* (and *Scytonema* sect. *Myochrotes*) form a monophyletic clade, probably also accompanied by *Chakia* and *Petalonema*, based on a 16S rRNA data analysis. However, numerous isolates morphologically convergent with *Scytonema* (and also *Petalonema*) fall into several separate lineages yet to be characterized in detail. On the other hand, part of the true-branching types (Y-type branching) from cave

habitats such as *Iphinoe* and one strain of *Sympytonemopsis* also seem to be closely related to *Brasilonema* (Bohunická et al. 2013), however the phylogeny is poorly supported. *Scytonematopsis* is highly polyphyletic (Kováčik & Komárek 1988, Komárek 2013), however the generitype has not yet been sequenced so it has not been possible so far to revise this genus. There are neither culture isolates nor sequences for *Ophiothrix* and *Kyrtuthrix*. The relationship of this family with the following family *Sympytonemataceae* is uncertain and needs clarification (cf. Gugger & Hoffmann 2004).

#### 8.2. *Sympytonemataceae* Hoffmann, Komárek et Kaštovský

This family contains isopolar, true-branching taxa. As inferred from 16S rRNA data for *Mastigocladopsis* and *Sympytonema*, these two genera probably form a monophyletic cluster. The position of *Iphinoe* and *Sympytonemopsis* is presently unclear as discussed above (8.1.; Lamprinou et al. 2011). The other genera have not been sequenced and are included because they have similar morphology.

#### 8.3. *Rivulariaceae* Kützing ex Bornet et Flahault

The three most important and widely occurring genera of these unbranched or falsely branched heteropolar types with tapering filaments, *Calothrix*, *Dichothrix* and *Rivularia*, form a relatively well characterized monophyletic lineage, but there are no phylogenetic data on the type species (Golubić & Campbell 1981, Obenlünenschloss 1991, Sihvonen et al. 2007, Berrendero et al. 2008, 2011, Dominguez-Escobar et al. 2011, Komárek et al. 2012, Whitton & Mateo 2012). In addition, the marine generitype of *Microchaete* possibly falls into this group (Hauer et al. 2013). Other strains designated as *Calothrix* without hairs or species of *Microchaete* (freshwater) belong to distant evolutionary lineages (Hauer et al. 2013). Sequence data for the remaining genera are unclear or lacking. The genus *Gloeotrichia* and *Calothrix* with akinetes belong in the vicinity of *Nostocaceae*.

#### 8.4. *Tolypothrichaceae* Hauer, Mareš, Bohunická, Johansen et Berrendero-Gomez

This family is a well-characterized monophyletic lineage of non-attenuated, false-branching heteropolar types with molecular data for the genera *Coleodesmium*, *Hassallia*, *Tolypothrix*, *Rexia*, *Spirirestis* and *Dactylohamnos* (cf. Flechtner et al. 2002, Fiore et al. 2013, Hauer et al. 2014). *Seguenzaea* and *Streptostemon* are morphologically similar but their phylogeny is poorly known. *Streptostemon* is more related to *Scytonemataceae* (recent sequences). The internal structure of the family is currently the subject of polyphasic revisions.

#### 8.5. *Godleyaceae* Hauer, Mareš, Bohunická, Johansen et Berrendero-Gomez

This family has only two members, the recently described *Godleya* (Novis & Visnovsky 2011) and *Toxopsis* (Lamprinou et al. 2012), both pseudo-branching filamentous types with characteristic morphology. They form a monophyletic lineage probably remotely related to the *Tolypothrichaceae*.

#### 8.6. *Chlorogloeopsidaceae* (Mitra) Mitra et Pandey

A monotypic family forming a monophyletic sister clade to the *Hapalosiphonaceae* as defined by Gugger & Hofmann 2004 and Dagan et al. 2013, with the type species sequenced under the incorrect name “*Chlorogloea*”. Morphological variability and life

cycle of the type (reference) strain has been described several times (Mitra & Pandey 1967, Rippka et al. 1979, Hindák 2008).

#### 8.7. *Hapalosiphonaceae* Elenkin

In Komárek (2013), several families are recognized based on the morphology of heterocytous, true-branching, mostly monoserial genera of the *Nostocales*, including the *Hapalosiphonaceae*, *Fischerellaceae*, *Loriellaceae*, *Mastigocladiaceae* and *Nostochopsidaceae*. Phylogenetic analysis has shown that the genera in these families are closely related and easily confused morphologically. *Fischerella*, *Westiellopsis*, *Nostochopsis*, *Hapalosiphon*, *Mastigocladius* and *Mastigocoleus* form a monophyletic lineage corresponding to one family (Gugger & Hoffmann 2004, Komárek & Mareš 2012, Dagan et al. 2013). The group is in urgent need of a polyphasic revision (cf., e.g. Jeeji-Bai 1972, Kaštovský & Johansen 2008). We have united these taxa under the *Hapalosiphonaceae* in this paper. Numerous genera with similar morphology have never been isolated or sequenced, and consequently their standing is unclear. Several groups within this family differ distinctly morphologically.

#### 8.8. *Capsosiraceae* (Geitler) Elenkin

Heterocytous cyanobacteria forming heteropolar colonies composed of loosely attached cells or pseudofilaments held together by a common mucilaginous sheath. None of the members have been sequenced, except the atypical species *Capsosira lowei* (Casamatta et al. 2006), in which a subsequent analysis has indicated that it is likely to belong to the *Nostocaceae*.

#### 8.9. *Stigonemataceae* Borzì

This family includes the typical complexly true-branched types. *Stigonema* clusters separately from the rest of the true-branching heterocytous cyanobacteria (Gugger & Hoffmann 2004). Neither the generitype of *Stigonema* nor many other members of this family have been isolated or analyzed using molecular methods, because keeping the *Stigonema* species in cultivation is extremely difficult. However, the genus *Stigonema* is very polymorphic and consists of several morphotypes (isopolar vs heteropolar, with monoserial vs polyseriate trichomes, with special type of hormogonia formation, etc.; cf. Sant'Anna et al. 2013, etc.).

#### 8.10. *Gloeotrichiaceae* fam. nov.

This family contains heteropolar tapering types with akinetes, forming spherical colonies. Up to now, only the peculiar aerotope-bearing planktic species *G. echinulata* has been sequenced and it has been found close to the *Nostocaceae* (Komárek & Mareš 2012). Interestingly, like *Nostocaceae* members, *Gloeotrichia* forms akinetes in its filaments (suprabasal). An investigation of the relationship among *G. echinulata*, the periphytic *Gloeotrichia* (two morphotypes) and akinete-forming members of the genus *Calothrix* will be of great interest. The *Gloeotrichia*-species with akinetes in rows ("Heliotrichia") are probably a special taxon.

#### 8.11. *Aphanizomenonaceae* Elenkin

An intensively studied group of predominantly planktic, isopolar and unbranched heterocytous types, usually with aerotopes in cells and hormogonia. The genera in this

group are extremely important, especially in the plankton in reservoirs, both in terms of biomass and toxic bloom-formers. Recent taxonomic revisions of this group have yielded the new well-characterized genera *Aphanizomenon*, *Umezakia*, *Dolichospermum*, *Cuspidothrix*, *Sphaerospermopsis*, *Chrysosporum* and possibly also *Cyanocohniella* (Barker et al. 1999, 2000, Li et al. 2000a, 2003, Komárek & Komárková 2003, Rajaniemi et al. 2005a,b, Komárek & Zapomělová 2007, 2008, Stüken et al. 2009, Wacklin et al. 2009, Zapomělová et al. 2009, 2010, 2012, Niiyama et al. 2011, Kaštovský et al. 2014). *Nodularia*, *Raphidiopsis*, *Cylindrospermopsis*, *Anabaenopsis* and *Cyanospira* also seem to be monophyletic genera (Florenzano et al. 1985, Komárek et al. 1993, Iteman et al. 2000, 2002, Li et al. 2000a,b, 2003, 2008, Komárek & Komárková 2003, Gugger et al. 2005, Řeháková et al. 2014), but mostly lack confirmed sequences for the generitypes. In addition, the *Raphidiopsis*/ *Cylindrospermopsis* clade and *Nodularia*/*Anabaenopsis*/*Cyanospira* clade show conserved 16S rRNA gene sequences, which indicate the separate status of the genera within these clades (but cf. Moustaka-Gouni et al. 2009, 2010).

#### 8.12. *Nostocaceae* C. A. Agardh ex Kirchner

This large and important family consists of unbranched heterocytous cyanobacteria with isopolar or heteropolar filaments, producing akinetes, often in series (apoheterocytic). The most important, mostly terrestrial colony-forming genus *Nostoc* has been intensively studied and recent taxonomic revisions have led to the identification of the core *Nostoc* clade and separation of two new genera, *Mojavia* (Řeháková et al. 2007) and *Desmonostoc* (Hrouzek et al. 2013). However, *Nostoc* is polyphyletic (Rajaniemi et al. 2005a, b) and more new taxa are expected in the near future. Other frequently occurring genera, such as *Anabaena*, *Trichormus* and *Wollea*, are also arguably polyphyletic (Rajaniemi et al. 2005a, Kozhevnikov & Kozhevnikova 2011, Zapomělová et al. 2013) and require revision and splitting. Several strains of *Aulosira*, *Hydrocoryne* and *Cylindrospermum* have been sequenced (Lukešová et al. 2009, Genuário et al. 2013, Johansen et al. 2014), but there is no molecular data for the type species. *Cronbergia*, *Hydrocoryne*, *Macrospermum* and *Richelia* are still little investigated and only partly sequenced (Janson et al. 1999, Komárek 2008, Komárek et al. 2010, Genuário et al. 2013). *Cylindrospermum* has been studied using isolates and sequence data for all five of the foundational species, identified by Bornet and Flahault, which indicates that at least these five species form a monophyletic group, but related to *Cronbergia* (Johansen et al. 2014). This genus has, however, numerous very different biological characters (development of heterocytes and akinetes). *Hydrocoryne* and *Richelia* are little explored, although their generitypes have been sequenced. Several isolates of various heteropolar types, provisionally designated as *Camptylonemopsis*, *Fortiea*, *Calothrix* or *Tolyphothrix* fall probably into this group, but their identification is unclear and they need revision (special families). It has been already started and resulted in the description of a nostocacean heteropolar genus *Calochaete* (Hauer et al. 2013). *Isocystis* and *Macrospermum* have not yet been isolated or sequenced. The generic name *Fremyella* De Toni 1936 is an alternative name for *Microchaete*, which was later accepted as *nomen conservandum*; the name “*Fremyella*” is therefore superfluous, but it is sometimes used for *Microchaete* species with trichomes with slightly narrowed ends.

### *Taxonomic descriptions and status changes*

Numerous higher level taxa required description or status change prior to inclusion in the system proposed in this manuscript. Below are the necessary nomenclatural changes, with family names in the order they appear in the text.

#### ***Chroococcidiopsidales ordo nov.***

Cells solitary or in more or less spherical or irregular groups, with thin, firm, colourless sheaths, without pseudofilamentous stages, with thylakoids distributed irregularly throughout the cytoplasm. Type family: *Chroococcidiopsidaceae* Geitler ex Büdel, Donner et Kauff in Frey, 2012, p. 28–29.

#### ***Spirulinales ordo nov.***

Filamentous cyanobacteria with trichomes regularly spirally coiled, with parietal thylakoids, lacking heterocytes. Type family: *Spirulinaceae* (Gomont) Komárek, Kaštovský, Mareš et Johansen, this paper.

#### ***Acaryochloridaceae fam. nov.***

Cells solitary, coccoid, containing chlorophyll *d*. Type genus: *Acaryochloris* Miyashita et Chihara, 2003, p. 1249.

#### ***Aphanothecaceae stat. nov.***

Basionym: *Aphanothecoideae* Komárek et Anagnostidis 1986, p. 213.

#### ***Coleofasciculaceae fam. nov.***

Filamentous cyanobacteria with radial or fasciculated thylakoid arrangement, constrictions at the cross-walls, with cell division completed before the next cell division begins. Type genus: *Coleofasciculus* Siegesmund, Johansen et Friedl 2008, p. 1575.

#### ***Cyanobacteriaceae fam. nov.***

Cells single or in pairs, with cell division only in one plane, without mucilaginous envelopes, with thylakoids situated in the cell lengthwise, giving appearance of lengthwise striation in the cytoplasm under a light microscope. Type genus: *Cyanobacterium* Rippka et Cohen-Bazire, 1983, p. 32.

#### ***Cyanothecaceae fam. nov.***

Cells solitary or in pairs, without gelatinous envelopes, with cell division only in one plane, with reticulate keritomization and irregular to radial arrangement of thylakoids. Type genus: *Cyanothece* Komárek 1976, p. 146.

#### ***Gloeotrichiaceae fam. nov.***

Thallus is spherical, hemispherical, or irregularly shaped, slimy, sometimes hollow, often becoming macroscopic, containing heteropolar trichomes with basal heterocytes and sub-terminal akinetes. Type genus: *Gloeotrichia* J. Agardh ex Bornet et Flahault 1886, p. 365.

***Heteroleibleiniaceae stat. nov.***

Basionym: *Heteroleibleinioideae* Komárek et Anagnostidis 2005, p. 243.

***Leptolyngbyaceae stat. nov.***

Basionym: *Leptolyngbyoideae* Anagnostidis et Komárek 1988, p. 439.

***Microcoleaceae stat. nov.***

Basionym: *Microcoleae* Hansgirg 1889, p. 56.

***Romeriaceae fam. nov.***

*Cyanobacteria* with rod-like cells arranged as short trichomes or dissociated cells in mucilaginous pseudofilaments, with parietal thylakoids. Type genus: *Romeria* Koczwara in Geitler, 1932, p. 915.

## Discussion

In modern cyanobacterial taxonomy genera should be monophyletic clusters, which consist of one to many species. For this reason, alpha level taxonomy in which species are well characterized using a polyphasic approach (which includes molecular data), is critical in order to construct monophyletic genera. Characterizing the genotypes of all genera as well as the numerous morphologically recognized species in these genera is a challenge waiting the current and next generation of cyanobacterial taxonomists.

The concept of more or less regular cyanobacterial genera according to modern criteria should contain (i) a unique supported phylogenetic position, with a clear discontinuity (about 95% or below similarity) to the nearest sister clade of species in another genus based on 16S rRNA gene sequences, (ii) distinct morphological separation from the nearest other generic entities, with a clear hiatus in any important cytomorphological (autapomorphic) character or with a distinct and unique biological specificity (type of division, type of heterocyte or akinete formation, etc.), and (iii) related ecological niches (marine vs freshwater, planktic vs aerophytic or soil types, extreme thermal or specific mineral springs, deserts, etc.). It is necessary to take into consideration that for cyanobacteria the same markers and features can have different taxonomic significance in different phylogenetic clades and morphotypes. The regular genus in cyanobacteria represents therefore a unique type, based on a combination of definable molecular, morphological and ecological criteria.

Modifications of the previous concept of genera are those clusters of species, in which the molecular differences between clusters are high (less than 95% similarity), but the morphological data are unclear (or restricted). For example, the complex *Dolichospermum*/*Sphaerospermopsis*/*Chrysosporum* was clearly derived from *Anabaena* based primarily on molecular data, because these genera are in distant clades and have a 16S rRNA gene sequence similarity of lower than 95% and the morphological diacritical differences are characteristic, but indistinct.

In contrast a number of other genera have relatively high genetic similarity (sometimes only about 95% or more), but with clear discontinuities in morphology, life cycles and ecology. We consider that these genera at least represent discrete lineages (*Anabaenopsis*/

*Nodularia/Cyanospira/Cyanocohniella; Dolichospermum/Sphaerospermopsis/ Chrysosporum/ Aphanizomenon/ Cuspidothrix*), or, at least are recognizable and delimited (*Scytonema/ Brasilonema/Petalonema/Myochrotes*). For these genera additional regions of the genome need to be sequenced so that multilocus phylogenies can be constructed and their evolutionary identity or distinctness verified. These genera are still more or less limited, defined by both phylogenetic and morphological criteria and it is likely that most of them will be retained and confirmed precisely in the future.

The first of the modifications resulting from our generic definitions is the existence of phylogenetically diverse lineages that are morphologically convergent and consequently sometimes difficult to separate in the absence of molecular data. Prior to phylogenetic analyses they were placed in genera based on their morphology, which appear to be well-circumscribed, but turn out to be polyphyletic when subjected to phylogenetic analysis. Often when the phylogeny is known, morphological and ecological characters can be found that are congruent with the molecular data and then it is relatively easy to recognize new genera. However, in some cases there are no clear morphological traits that can be used to separate these phylogenetically distinct lineages. We recommend that some of these traditional genera (e.g. *Anabaena*, *Nodularia*) be retained *ad interim* until sufficient numbers of strains and sequences are generated and a stable recommendation for a new classification can be made.

Several phylogenetically distinct clusters contain morphotypes that are almost identical. These genetic clusters are indistinguishable by any morphological or ecological criterion, or only differ in terms of indistinct markers (e.g. ultrastructural differences, in their ecology, unclear morphological differences – average width of thin filaments, etc.). Such lineages (species clusters) can be differentiated on genetic or molecular criteria and should be registered and designated as cryptic genera (**cryptogenera**). They should be classified as generic units for phylogenetic as well as taxonomical (practical) reasons. At present, we know of no cryptic genera, although it is very possible that they exist in many of the polyphyletic genera. It is also likely that putative cryptic genera exist in the morphologically simplest types (e.g. *Synechococcus*, *Pseudanabaena*, *Leptolyngbya*). A typical example is the case of *Spirulina* and *Halospirulina*. Cryptic genera are especially challenging in terms of taxonomic definition, because they do not meet the commonly applied criteria for description of taxa.

**Morphogenera** are more or less genera only defined on the basis of their morphology. Often these are old, traditional genera, clearly different in terms of their morphology (with hiatus between important features), but still without molecular characterization or only slightly based on molecular data. Sometimes these are polyphyletic when eventually studied and may have sequence similarities slightly over or below 95%. Many of the genera in the present system are likely to have this status. These genera can contain cryptic genera that are not yet recognized. They should be further studied and their existence at the very least should be registered in the literature. We save *ad interim* the names of such traditional taxa, accepting that they will be revised in the future.

From the present analyses we know that there are types with almost identical or related phylogenetic (molecular) markers, but distinctly different in morphology and biology (with hiatus between important morphological or biological features). It is highly likely that in such types there are genetic differences, which remain to be detected. An example is *Cylindrospermum* and *Cronbergia*, which differ quite fundamentally morphologically

in the apoheterocytic or paraheterocytic development of akinetes, the form and position of akinetes, position of heterocytes and type of initiation of polar or intercalar heterocytes. The morphologically limiting characters of these two genera are clearly definable and it is probable they will be shown to be genetically different in the future. Such clearly recognizable types should be retained.

Modernization of any system complicates its application. *Cyanobacteria* are important when working in ecology, technical hydrobiology, applied practice (agriculture, mass cultivation of algae for different purposes, toxicology, etc.) and various experimental laboratories (biochemistry, molecular biology). Therefore, the acceptance of all revisions by taxonomists is realized only slowly and with a certain delay, but the confirmed and proved changes should be continually introduced into laboratory and practical disciplines.

The same morphological character in different phylogenetic clades of cyanobacteria can have different taxonomic values. Good examples are the spherical form and position of akinetes in the genus *Sphaerospermopsis*, presence of aerotopes in *Planktothrix* and *Nodularia*, the absence of calyptas and sheaths in *Kamptonema*, etc.

Both natural populations and morphotypes developing in cultures should be evaluated in terms of morphological descriptions whenever possible. The morphology of numerous cyanobacterial populations sometimes changes substantially in laboratory culture, where they often form atypical and unusual forms under unfavourable conditions. This is important, especially for those morphotypes with complicated and functionally diversified thalli. In spite of this variability in culture, morphological appearance is characteristic, particularly for various ecologically specialized taxa.

Within taxa (clusters) based on molecular sequence data there are special groups of OTUs or types, morphologically distinctly separated from other members of the same cluster (*Dolichospermum*: *Aphanizomenon*, *Cuspidothrix*). Or, *vice versa*, those with a certain molecular difference exist, but without a distinct morphological or phylogenetic separation and isolation (*Spirulina* / *Halospirulina*). Such cases can be evaluated as special genera or included into morphogenera or cryptogenera categories according the authors' evaluation. The ability to define generic features and the morphology of such units is usually difficult.

The 95% limit to molecular similarity used to separate generic entities according to Wayne et al. (1987), Stackebrandt & Goebel (1994) and Stackebrandt & Ebers (2006) poses problems. There never sharp limits exist in biology, and this criterion is only helpful when similarity is below the limits, when it is informative. When it is above the limit, it cannot be used as clear evidence of taxonomic identity. This method has been extensively criticized (Ferris et al. 2003, Johansen & Casamatta 2005, Ward 2006, and others). However, this numerical guide can at least be part of the polyphasic evidence for evaluating a generic separation as justified in cyanobacterial taxonomy.

Ecological niche is an important criterion used to separate and define genera. This is the case for the majority of newly defined or circumscribed genera (*Microcystis* in freshwater eutrophic phytoplankton, *Oxynema* or planktic *Nodularia* in brackish and mineral water, *Halothecce* and *Euhalothecce* in saline and brackish habitats, *Moorea* in littoral zones of tropical oceans, etc.; Garcia-Pichel et al. 1998, Chatchawan et al. 2012, Engene et al. 2012, and others). However, some exceptions exist and genera with broad ecological ranges should be carefully studied.

In modern genera, therefore, it is always necessary to determine the phylogenetic position of the corresponding entity, as well as its morphological (and ecological) characters. Registration of cryptogenera and morphogenera also has a role in advancing understanding, but are only ad interim solutions to the description of genera following polyphasic evaluation. It is also important to abide by nomenclatural rules in arriving at a satisfactory classification of any organism in a system, but that aspect of the problem is not discussed in this article and needs to be resolved in special forum.

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## Souhrn

Jedinou metodou registrace diversity jakýchkoliv organismů je taxonomická klasifikace. Taxonomická kritéria se vyvíjejí v závislosti na ostatních vědních disciplínách a procházejí tedy určitými změnami. Systematický přehled sinic (cyanobakterií) byl změněn a opraven velmi podstatně v uplynulých 30 letech, zejména po aplikaci poznatků z elektronové mikroskopie a na základě molekulárních metod. Vědecká komunita a zejména pracovníci v aplikovaných ekologických a experimentálních, laboratorních disciplínách by měli akceptovat urgentně nejnovější informace o hlavních výsledcích modernizace systému, založeného nově na zjištěných fylogenetických závislostech. V předloženém článku jsou shrnutý výsledky a opravy cyanobakteriální klasifikace, publikované a ověřené do konce roku 2013 (s několika nejnovějšími ověřenými novinkami z roku 2014) a jsou v něm definovány hlavní směry další problematiky a dalšího studia v této vědní disciplíně. Rovněž je přiloženo schéma nejmodernějšího systému sinic, založeném na preferovaném, tzv. polyfázickém přístupu.

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Appendix 1. – Names of the cyanobacterial genera that had been published by the end of 2013 (several invalidly published). 1 – genera supported by a molecular phylogeny, including a 16S rRNA gene sequence of the type species; 2 – genera, from which only one or a few species were studied using molecular methods and for which there is no 16S rRNA gene data for the type species; 3 – genera studied using molecular methods and found to be poly/paraphyletic or with no clear relationship with other genera; 4 – genera not yet studied using molecular methods; 5 – genera not yet validly described; \* genera for which there is a 16S rRNA sequence for the type material; [?] genera, problematic from the taxonomic point of view.

Taxon	status	Taxon	status
<i>Gloeobacterales</i>		<i>Acaryochloridaceae</i>	
<i>Gloeobacteraceae</i>		<i>Acaryochloris</i> Miyashita et Chihara 2003	1*
<i>Gloeobacter</i> Rippka et al. 1974 ex Mareš et al. 2013	1*	<i>Chamaesiphonaceae</i>	
<i>Synechoccales</i>		<i>Chamaesiphon</i> A. Braun et Grunow 1865	3
<i>Synechococcaceae</i>		<i>Chamaesiphonopsis</i> Fritsch 1929	4
<i>Anathete</i> Komárek et al. 2011	1.3	<i>Clastidium</i> Kirchner 1880	4
<i>Bacularia</i> Borzí 1905	4	<i>Cyanophanon</i> Geitler 1956	4
<i>Cyanobium</i> Rippka et Cohen-Bazire 1983	1, 3	<i>Geitleribactron</i> Komárek 1975	2
<i>Cyanocatena</i> Hindák 1975	4	<i>Romeriaceae</i>	
<i>Cyanodictyon</i> Pascher 1914	3	<i>Cyanocatenula</i> Joosten 2006	4
<i>Cyanogranis</i> Hindák 1982	4	<i>Romeria</i> Koczwara in Geitler 1932	2
<i>Cyanonephron</i> Hickel 1985	4	<i>Tubiella</i> Hollerbach 1935	4, [?]
<i>Cyanothamnos</i> Cronberg 1991	4	<i>Wolskyella</i> Claus 1963	4
<i>Epigloeoospaera</i> Komárková 1991	4	<i>Pseudanabaenaceae</i>	
<i>Lemmermanniella</i> Geitler 1942	4	<i>Arthonema</i> Komárek et Lukavský 1988	1
<i>Lithococcus</i> Ercegović 1925	4, [?]	<i>Jaaginema</i> Anagnostidis et Komárek 1988	1.3
<i>Lithomyxa</i> Howe 1931	4, [?]	<i>Komvophoron</i> subg. <i>Alyssophoron</i> Anagnostidis et Komárek 1988	5
<i>Rhabdoderma</i> Schmidle et Lauterborn 1900	4	<i>Limnothrix</i> Meffert 1988	1.3
<i>Rhabdogloea</i> Schröder 1917	4	<i>Prochlorothrix</i> Burger-Wiersma et al. 1989	1
<i>Rhodostichus</i> Geitler et Pascher 1931	4, [?]	<i>Pseudanabaena</i> Lauterborn 1915	1.3
<i>Synechococcus</i> Nägeli 1849	1.3	<i>Yonedaella</i> Umezaki 1962	4
<i>Thermosynechococcus</i> Katoh et al. 2001	1*, 5	<i>Leptolyngbyaceae</i>	
<i>Merismopediaceae</i>		<i>Haleolyngbya</i> Dadheech et al. 2012	1*
<i>Aphanocapsa</i> Nägeli 1849	3	<i>Halomicronema</i> Abed et al. 2002	1*
<i>Coccopedia</i> Troickaja 1922	4, [?]	<i>Leibleinia</i> (Gomont) Hoffmann 1985	4
<i>Cyanotetras</i> Hindák 1988	4, [?]	<i>Leptolyngbya</i> Anagnostidis et Komárek 1988	1.3
<i>Eucapsis</i> Clements et Shantz 1909	3	<i>Myxocorys</i> Petrasík et al. 2015 provis.	1*
<i>Limnococcus</i> Komárková et al. 2010	1*	<i>Neosynechococcus</i> Dvořák et al. 2013	1*
<i>Mantellum</i> Dangeard 1941	4	<i>Nodosilinea</i> Perkerson et Casamatta 2011	1*
<i>Merismopedia</i> Meyen 1839	1.3	<i>Oculatella</i> Zammit et al. 2012	1*
<i>Microcrocis</i> Richter 1882	4	<i>Phormidesmis</i> Turicchia et al. 2009	1*
<i>Pannus</i> Hickel 1991	4	<i>Planktolyngbya</i> Agagnostidis et Komárek 1988	1
<i>Synechocystis</i> Sauvageau 1892	1.3	<i>Plectolyngbya</i> Taton et al. 2011	1*
<i>Prochloraceae</i>		<i>Stenomitos</i> Miscoe et Johansen 2015 provis.	1*
<i>Prochlorococcus</i> Chisholm et al. 1992	1*, 3	<i>Trichocoleus</i> Agagnostidis 2001	2
<i>Prochloron</i> Lewin 1977	1*, 3	<i>Trichotorquatus</i> Petrasík et Johansen 2015 provis.	1*, 5
<i>Coelosphaeriaceae</i>		<i>Heteroleibleiniaceae</i>	
<i>Coelomorion</i> Buell 1938	4	<i>Heteroleibleinia</i> (Geitler) Hoffmann 1985	4
<i>Coelosphaeropsis</i> Lemmermann 1900	4	<i>Tapinothrix</i> Sauvageau 1892	3
<i>Coelosphaerium</i> Nägeli 1849	2	<i>Schizotrichaceae</i>	
<i>Siphonosphaera</i> Hindák 1988	4	<i>Dasygloea</i> Thwaites ex Gomont 1892	4
<i>Snowella</i> Elenkin 1938	1	<i>Schizothrix</i> Kützing ex Gomont 1892	2
<i>Woronichinia</i> Elenkin 1933	1		

Taxon	status	Taxon	status
<i>Spirulinales</i>		<i>Stichosiphonaceae</i>	
<i>Spirulinaceae</i>		<i>Godlewskia</i> Janczewski 1883	5
<i>Glaucospira</i> Lagerheim 1892	4, [?]	<i>Stichosiphon</i> Geitler 1932	4
<i>Halospirulina</i> Nübel et al. 2000	1*	<i>Entophysalidaceae</i>	
<i>Spirulina</i> Turpin ex Gomont 1892	3	<i>Chlorogloea</i> Wille 1900	2, (4)
<i>Chroococcales</i>		<i>Cyanoarbor</i> Wang 1989	4
<i>Microcystaceae</i>		<i>Cyanodermatium</i> Geitler 1933	4
<i>Cyanocomperia</i> Hindák 2002	4	<i>Entophysalis</i> Kützing 1843	4
<i>Microcystis</i> Kützing ex Lemmermann 1907	1	<i>Lithocapsa</i> Ercegović 1925	4
<i>Planctocyanocapsa</i> Hindák 2002	4	<i>Paracapsa</i> Naumann 1924	4, [?]
<i>Radiocystis</i> Skuja 1948	2	<i>Placoma</i> Schousboe ex Bornet et Thuret 1876	4
<i>Sphaerocavum</i> Azevedo et Sant'Anna 2003	4	<i>Siphononema</i> Geitler 1925	4
<i>Aphanothecaceae</i>		<i>Pleurocapsales</i>	
<i>Aphanothece</i> Nägeli 1849	1	<i>Hydrococcaceae</i>	
<i>Crocospaera</i> Zehr et al. 2001	1*, 5	<i>Dalmatella</i> Ercegović 1929	4
<i>Cyanoagggregatum</i> Werner et al. 2008	4	<i>Hormathonema</i> Ercegović 1929	4
<i>Cyanogastrum</i> Schiller 1956	4	<i>Hydrococcus</i> Kützing 1833	4
<i>Dzensia</i> Voronichin 1929	4	<i>Myxohyella</i> Geitler 1925	4
"Euhalothece" Garcia-Pichel 2000 provis.	1*, 5	<i>Onkonema</i> Geitler 1933	4
<i>Gloeothece</i> Nägeli 1849	2	<i>Tryponema</i> Ercegović 1929	4
<i>Halothece</i> Margheri et al. 2008	1*	<i>Dermocarpellaceae</i>	
<i>Hormothece</i> Jao 1944	4	<i>Cyanocystis</i> Borzì 1882	2, (4)
<i>Myxobactron</i> Schmidle 1904	4	<i>Dermocarrella</i> Lemmermann 1907	2
<i>Rippkaea</i> Mareš et al. 2015 provis.	1*, 5	<i>Stanieria</i> Komárek et Anagnostidis 1986	1, 3
<i>Rubidibacter</i> Choi et al. 2008	1	<i>Xenococcaceae</i>	
<i>Cyanobacteriaceae</i>		<i>Xenococcus</i> Thuret 1880	2, 3
<i>Cyanobacterium</i> Rippka et Cohen-Bazire 1983	1, 3	<i>Xenotholos</i> Gold-Morgan et al. 1994	4
<i>Cyanothrichaceae</i>		<i>Hyellaceae</i>	
<i>Johannesbaptistia</i> DeToni 1934	2	<i>Chamaecalyx</i> Komárek et Anagnostidis 1986	4
<i>Gomphosphaeriaceae</i>		<i>Chroococcidiopsis</i> Geitler 1933	4
<i>Beckia</i> Richter 1882	4, [?]	<i>Chroococcopsis</i> Geitler 1925	2
<i>Gomphosphaeria</i> Kützing 1836	4	<i>Cyanoderma</i> Weber van Bosse 1887	4
<i>Chroococcaceae</i>		<i>Cyanosaccus</i> Lukas et Golubić 1981	4
<i>Asterocapsa</i> Chu 1952	4	<i>Ercegovicia</i> DeToni 1936	4
<i>Chalicogloea</i> Roldán et al. 2013	1	<i>Hyella</i> Bornet et Flahault 1888	2
<i>Chondrocysts</i> Lemmermann 1899	4, [?]	<i>Myxosarcina</i> Printz 1921	2
<i>Chroogloeocysts</i> Brown et al. 2005	1*	<i>Pascherinema</i> DeToni 1936	4, [?]
<i>Chroococcus</i> Nägeli 1849	1	<i>Pleurocapsa</i> Thuret in Hauck 1885	3
<i>Cyanokybus</i> Schiller 1956	4	<i>Podocapsa</i> Ercegović 1931	4
<i>Cyanosarcina</i> Kováčik 1988	4	<i>Radaisia</i> Sauvageau 1895	4
<i>Cyanostylon</i> Geitler 1928	4	<i>Solentia</i> Ercegović 1927	2
<i>Geminocysts</i> Korelusová et al. 2009	1*	<i>Chroococcidiopsidales</i>	
<i>Gloeocapsa</i> Kützing 1843	1, 3	<i>Chroococcidiopsidaceae</i>	
<i>Gloeocapsopsis</i> Geitler ex Komárek 1993	1, 3	<i>Chroococcidiopsis</i> Geitler 1933	1, 3
<i>Nephrococcus</i> Li 1984	4	<i>Oscillatoriales</i>	
<i>Pseudocapsa</i> Ercegović 1925	4	<i>Cyanothecaceae</i>	
<i>Pseudonocobyrsa</i> Geitler 1925	4, [?]	<i>Cyanothece</i> Komárek 1976	1

Taxon	status	Taxon	status
<b>Borziaceae</b>		<b>Katagymnemata</b>	
<i>Borzia</i> Cohn ex Gomont 1892	4	<i>Katagymneme</i> Lemmermann 1899	3, 4
<b>Coleofasciculaceae</b>		<i>Komvophoron</i> Anagnostidis et Komárek 1988	3
<i>Anagnostidinema</i> Struneczký et al. in prep.	1*, 5	<i>Starria</i> Lang 1977	1*
<i>Coleofasciculus</i> Siegesmund et al. 2008	1*	<b>Nostocales</b>	
<i>Desertifilum</i> Dadheech et al. 2012	1*	<b>Scytonemataceae</b>	
<i>Geitlerinema</i> Anagnostidis 1989	1, 3	<i>Brasilonema</i> Fiore et al. 2007	1*
<i>Kastovskya</i> Mühlsteinová et al. 2014	1*	<i>Chakia</i> Komárková et al. 2013	1*
<i>Roseofilum</i> Casamatta et al. 2012	1*	<i>Kyrtuthrix</i> Ercegović 1929	4
<i>Wilmottia</i> Struneczký et al. 2011	1*	<i>Ophiothrix</i> Sant'Anna et al. 2010	4
<b>Microcoleaceae</b>		<i>Petalonema</i> Berkeley ex Correns 1889	2
<i>Annamia</i> Nguyen et al. 2013	1*	<i>Scytonema</i> Agardh ex Bornet et Flahault 1887	1, 3
<i>Arthrosira</i> Stizenberger ex Gomont 1892	2	<i>Scytonema</i> sect. <i>Mychorites</i> Bornet et Flahault 1887	5
<i>Hydrocoleum</i> Kützing ex Gomont 1892	2, 3, [?]	<i>Scytonematopsis</i> Kiseleva 1930	2, 3
<i>Johanseninema</i> Hašler et al. 2014	1*	<b>Sympyonemataceae</b>	
<i>Kamptonetema</i> Struneczký et al. 2014	1*	<i>Adrianema</i> DeToni 1936	4
<i>Lyngbyopsis</i> Gardner 1927	4	<i>Brachytrichia</i> Zanardini ex Bornet et Flahault 1887	4
<i>Microcoleus</i> Desmazières ex Gomont 1892	2	<i>Herpyzonema</i> Weber van Bosse 1913	4
<i>Oxynema</i> Chatchawan et al. 2012	1*	<i>Ifinoe</i> Lamprinou and Pantazidou 2011	1*
<i>Planktothricoides</i> Suda et M. M. Watanabe 2002	1*	<i>Iyengariella</i> Desikachary 1953	4
<i>Planktothrix</i> Anagnostidis et Komárek 1988	1	<i>Loriellopsis</i> Hernández Mariné et Canals 2011	1*, [?]
<i>Porphyrosiphon</i> Kützing ex Gomont 1892	4	<i>Mastigocladospis</i> Iyengar et Desikachary 1946	2
<i>Proterendothrix</i> W. et G.S.West 1897	4, [?]	<i>Parenchymorpha</i> Tseng et Hua 1984	4
<i>Pseudohormidium</i> (Forti)	2	<i>Sympyonema</i> Jao 1944	2
Anagnostidis et Komárek 1988		<i>Sympyonemopsis</i> Gugger et Hoffmann 2004	2, (3)
<i>Pseudoscytonema</i> Elenkin 1949	4	<i>Voukiella</i> Ercegović 1925	4
<i>Sirocoleum</i> Kützing ex Gomont 1892	4, [?]	<b>Rivulariaceae</b>	
<i>Symploca</i> Kützing ex Gomont 1892	3	<i>Calothrix</i> Agardh ex Bornet et Flahault 1886	3
<i>Symplocastrum</i> (Gomont) Kirchner 1898	2	<i>Dichothrix</i> Zanardini ex Bornet et Flahault 1886	(2), 4
<i>Trichodesmium</i> Ehrenberg ex Gomont 1892	1, 3	<i>Gardnerula</i> DeToni 1936	4
<i>Tychonema</i> Anagnostidis et Komárek 1988	1, 3	<i>Isactis</i> Thuret ex Bornet et Flahault 1886	4
<b>Homoeotrichaceae</b>		<i>Microchaete</i> Thuret ex Bornet et Flahault 1886	1, 3
<i>Ammatoidea</i> W. et G. S. West 1897	4	<i>Rivularia</i> C. A. Agardh ex Bornet et Flahault 1886	3
<i>Homoeothrix</i> (Thuret) Kirchner 1898	4	<i>Sacconema</i> Borzì ex Bornet et Flahault 1886	4
<i>Phormidiochaete</i> Komárek in Anagnostidis 2001	4	<b>Tolyphothrichaceae</b>	
<i>Tildenia</i> Kosinskaja 1926	4, [?]	<i>Borzinema</i> DeToni 1936	4
<b>Oscillatoriaceae</b>		<i>Coleodesmium</i> Borzì ex Geitler 1942	1, 3
<i>Aerosakkonema</i> Thu et M. M. Watanabe 2012	1*	<i>Dactylothamnos</i> Fiore et al. 2013 provis.	1*, 5
<i>Blennothrix</i> Kützing ex Anagnostidis et Komárek 1988	3	<i>Hassallia</i> Berkeley ex Bornet et Flahault 1888	1, 3
<i>Limnorphis</i> Komárek et al. 2013	1*	<i>Rexia</i> Casamatta et al. 2006	1* [?]
<i>Lyngbya</i> C. Agardh ex Gomont 1892	1, 3	<i>Seguenzaea</i> Borzì 1907	4
<i>Moorea</i> Engene et al. 2012	1*	<i>Spirirestis</i> Flechtner et Johansen 2002	1*
<i>Okeania</i> Engene et al. 2013	1*	<i>Streptostemon</i> Sant'Anna et al. 2010	4
<i>Oscillatoria</i> Vaucher ex Gomont 1892	1, 3	<i>Tolyphothrix</i> Kützing ex Bornet et Flahault 1887	1, 3
<i>Phormidium</i> Kützing ex Gomont 1892	1, 3	<b>Godleyaceae</b>	
<i>Plectonema</i> Thuret ex Gomont 1892	2	<i>Godleya</i> Novis et Visnovsky 2011	1*
<i>Polychlamydum</i> W. et G.S.West 1897	4	<i>Toxopsis</i> Lamprinou et al. 2012	1*
<b>Gomontiellaceae</b>		<b>Chlorogloeopsidaceae</b>	
<i>Crinalium</i> Crow 1927	2	<i>Chlorogloeopsis</i> Mitra et Pandey 1967	1, 3
<i>Gomontiella</i> Teoderesco 1901	4		
<i>Hormoscilla</i> Anagnostidis et Komárek 1988	2		

Taxon	status	Taxon	status
<b>Capsosiraceae</b>		<b>Aphanizomenonaceae</b>	
<i>Capsosira</i> Kützing ex Bornet et Flahault 1887	2	<i>Anabaenopsis</i> (Wołoszyńska) Miller 1923	1, 3
<i>Desmosiphon</i> Borzì 1907	4	<i>Aphanizomenon</i> Morren ex Bornet et Flahault 1888	1, 3
<i>Nematoplaca</i> Geitler 1933	4	<i>Chrysosporum</i> Zapomělová et al. 2012	1*
<i>Stauromatonema</i> Frémy 1930	4	<i>Cuspidothrix</i> Rajaniemi et al. 2005	1*
<b>Stigonemataceae</b>		<i>Cyanospira</i> Florenzano et al. 1985	1*
<i>Cyanobotrys</i> Hoffmann 1991	4	<i>Cylindrospermopsis</i> Seenayya et Subba Raju 1972	1
<i>Doliocatella</i> Geitler 1933	4	<i>Dolichospermum</i> (Ralfs) Wacklin et al. 2009	1
<i>Homoeoptyche</i> Skuja 1944	4	<i>Nodularia</i> Mertens in Jürgens ex Bornet et Flahault 1888	1, 3
<i>Pulvinularia</i> Borzì 1916	4	<i>Raphidiopsis</i> Fritsch et Rich 1929	1, 3, [?]
<i>Stigonema</i> C. Agardh ex Bornet et Flahault 1886	2	<i>Sphaerospermopsis</i> Zapomělová et al. 2010	1*
<b>Hapalosiphonaceae</b>		<i>Umezakia</i> M. Watanabe 1987	1
<i>Aetokthonos</i> Wilde et al. 2014	1	<b>Nostocaceae</b>	
<i>Albrightia</i> Copeland 1936	4	<i>Anabaena</i> Bory ex Bornet et Flahault 1886	(1), 3
<i>Baradlaia</i> Palik 1960	4, [?]	<i>Camptylonemopsis</i> Desikachary 1948	2
<i>Brachytrichiopsis</i> Jao 1944	4	<i>Coleospermopsis</i> Hauer et al. 2015 provis.	1*, 5
<i>Chondrogloea</i> Schmidle 1902	4	<i>Cronbergia</i> Komárek et al. 2010	1*
<i>Colteronema</i> Copeland 1936	4	<i>Cyanocohniella</i> Kaštovský et al. 2014	1*
<i>Fischerella</i> (Bornet et Flahault) Gomont 1895	3	<i>Cylindrospermum</i> Kützing ex Bornet et Flahault 1888	(1), 2
<i>Fischerellopsis</i> Fritsch 1932	4	<i>Desmonostoc</i> Hrouzek et Ventura 2013	1 *
<i>Geitleria</i> Friedmann 1955	4	<i>Galeter</i> Miscoe et al. 2015	1 *, 5
<i>Handeliella</i> Skuja 1937	4	<i>Hydrocoryne</i> Schwabe ex Bornet et Flahault 1888	1, 3
<i>Hapalosiphon</i> Nägeli in Kützing ex Bornet et Flahault 1887	3	<i>Isocystis</i> Borzì ex Bornet et Flahault 1888	4
<i>Hyphomorpha</i> Borzì 1916	4	<i>Macrospermum</i> Komárek 2008	4
<i>Leptopogon</i> Borzì 1917	4	<i>Mojavia</i> Řeháková et Johansen 2007	1*
<i>Letestuinema</i> Frémy 1930	4	<i>Nostoc</i> Vaucher ex Bornet & Flahault 1888	1, 3
<i>Loefgrenia</i> Gomont 1896	4	<i>Richelia</i> J. Schmidt in Ostenfeld et J. Schmidt 1901	1
<i>Loriella</i> Borzì 1892	4	<i>Spelaea</i> Miscoe et al. 2013 provis.	1 *, 5
<i>Mastigocladus</i> Cohn ex Kirchner 1898	1	<i>Tolyphothrichopsis</i> Hauer et al. 2015 provis.	1 *, 5
<i>Mastigocoelopsis</i> Geitler 1925	4	<i>Trichormus</i> (Ralfs ex Bornet et Flahault Komárek et Anagnostidis 1989	1, 3
<i>Mastigocoelus</i> Lagerheim ex Bornet et Flahault 1887	1	<i>Wollea</i> Bornet et Flahault 1888	1, 3
<i>Matteia</i> Borzì 1907	4		
<i>Nostochopsis</i> Wood ex Bornet & Flahault 1886	3		
<i>Schmidleinema</i> DeToni 1936	4, [?]		
<i>Spelaeopogon</i> Borzì 1917	4		
<i>Thalpophila</i> Borzì 1907	4		
<i>Westiella</i> Borzì 1907	4		
<i>Westiellopsis</i> Janet 1941	1.3		
<b>Fortieaceae</b>			
<i>Aulosira</i> Kirchner ex Bornet et Flahault 1886	2		
<i>Calochaete</i> Hauer et al. 2013	1*		
<i>Coleospermum</i> Kirchner in Cohn 1878	3		
<i>Fortiea</i> De-Toni 1936	2		
<i>Roholtiella</i> Bohunická et al. 2015	1*, 5		
<b>Gloeotrichiaceae</b>			
“ <i>Calothrix</i> ” (with akinetes)	5		
<i>Gloeotrichia</i> J. Agardh ex Bornet et Flahault 1886	3		