

Modern taxonomic revision of planktic nostocacean cyanobacteria: a short review of genera

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Abstract The taxonomy of cyanobacteria has been substantially modified in the last few decades, particularly after application of modern ultrastructural and molecular methods. The group of heterocytous cyanobacteria (Nostocales) was found to be monophyletic, but the concept and content of different genera must be continually corrected and revised. The widespread introduction of the molecular approach (especially 16S rRNA gene sequencing) has confirmed almost all traditional genera based on distinct and morphologically recognizable type species, but indicated also broader diversity resulting in separation of more genetic and generic entities in several genera. The combination of molecular and phenotype analyses enables also a better and more objective definition of criteria for describing newly researched generic

units, discovered from various habitats in the biosphere. Here, the nostocacean generic taxa are reviewed after recent necessary taxonomic corrections. Nostocacean cyanobacteria are filamentous, heterocytous, not branched and not polarized morphotypes, classified traditionally into one family (Nostocaceae). The main part of the review focuses on the genera containing planktic species.

Keywords Cyanobacteria · Taxonomy · Ecology · Molecular evaluation · Phenotype characteristics · Plankton · Generic concept

Introduction

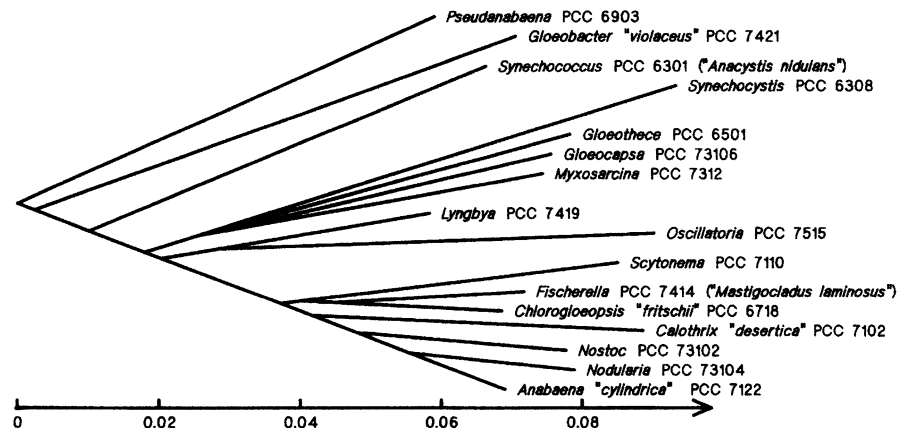
All heterocytous cyanobacteria represent a monophyletic clade according to molecular evaluation (Fig. 1; Giovannoni et al., 1988; Wilmotte & Golubić, 1991; Turner, 1997, 2001; Castenholz, 2001; Rajaniemi et al., 2005a, b, etc.). The only exceptions are several non-heterocytous types, which were earlier classified as coccoid types with a complicated and differentiated thallus (e.g. several strains of *Chroococidiopsis*). Their phylogenetic position among heterocytous types must be studied and explained in the future. Molecular sequencing appeared to be particularly important for determining phylogenetic relations among various genera, which represent distinct taxonomic units in the spectrum of cyanobacterial diversity.

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Fig. 1 Example of phylogenetic evaluation of Cyanobacteria with clearly separated group of heterocytous genera. After Giovannoni et al. (1988)



Subclusters inside the clade of Nostocales (e.g. on the level of taxonomic families) were re-defined according to the genetic investigations and, subsequently, re-evaluated morphological features. The nostocalean cyanobacteria form more or less complicated filaments. They are very unique bacteria, where the individuals have a multicellular, diversified thallus with prominent cells of different function (heterocytes, akinetes and necridic cells). Therefore, the morphology and revision of the value and variability of cytomorphological features play an important role in their characterization. As other cyanobacteria, they contain the complete photosynthetic system and ecologically they belong among microscopic plants. Of the morphological characters, the type of branching appears especially important. Gugger & Hoffmann (2004) confirmed that false and true branching cannot be a distinguishing character between two phylogenetic clades, but the branching type can be characteristic for different subclusters inside Nostocales (usually classified as families; Hoffmann et al., 2005; Fig. 2).

The family Nostocaceae represents a special phylogenetic line and group, which is characterized morphologically by (i) isopolar filaments, (ii) the absence of any branching (with the exception of certain anomalies), (iii) the presence of heterocytes (with the exception of secondary derived genotypes) and (iv) the facultative presence of typical paraheterocytic or apoheterocytic akinetes (which do not develop in other heterocytous clades; the resting or dormant cells are of another type). Taxonomic changes on the generic level in nostocacean cyanobacteria are summarized in the present review. These changes were proposed to the end of 2008 on the

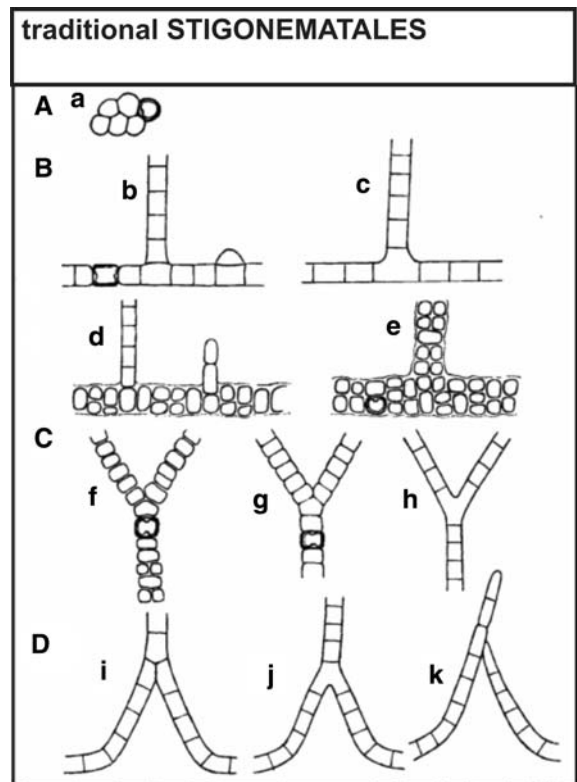


Fig. 2 Various types of true branching (Anagnostidis & Komárek, 1990), considered in traditional taxonomy as the characteristic feature of the order Stigonematales. All the genera with true branching are not monophyletic, and different types of true branching are characteristic for separate clades and distinct families (Gugger & Hoffmann, 2004). **A** irregular, **B** T-like branching (uniserial and multiserial trichomes—different examples), **C** Y-like branching, **D** reverse Y-like branching. Small letters (a–k) indicate various subtypes

basis of combined molecular, cytological and morphological studies of the diversity of this cyanobacterial group.

Methods

The results presented in this article are a compilation of taxonomic results, published in numerous papers and based mainly on molecular 16S rRNA gene sequencing, which is considered a more or less standard method for characterization of cyanobacterial genetic and generic units. However, according to the combined polyphasic approach, all results from sequences of other genomes and corresponding cytomorphological, ecophysiological and biochemical markers are important and should also be taken in consideration.

Morphological characteristics are important for practical use and identification of natural populations. The main phenotype character conforming with phylogenetic clusters (genera) inside of Nostocaceae is a metameric, symmetric or subsymmetric structure of trichomes resulting from the heterocyte and akinete position (para- and apoheterocytic development of akinetes) (Fig. 3; comp. Komárek & Anagnostidis, 1989). Both botanical and bacteriological nomenclature rules were respected throughout the whole review.

Revised nostocacean genera (state 2009)

The list of revised generic entities after the commonly used Geitler's (1932) monograph is given in Table 1. In the present review of generic units occurring in planktic environments, those genera not confirmed by 16S rRNA gene sequencing are marked with an asterisk (*). The reference strains are cited according to Castenholz (2001) or the authors of the corresponding genera.

1. *Raphidiopsis* Fritsch et Rich 1929

[type species = *R. curvata*; reference strain not selected]

Unclear and polymorphic genus, containing probably several morpho- and genotypes. The main diacritical character is the absence of heterocytes. Up to now, it has not been confirmed whether the genus is only a non-heterocytous stage of other genera (*Cuspidothrix*, *Cylindrospermopsis*). Two strains were sequenced by Li et al. (2008) and their narrow, phylogenetic affiliation to *Cylindrospermopsis* was demonstrated. However, the identity of both genera is not yet doubtless, and study of more strains is necessary. Other characters: solitary floating

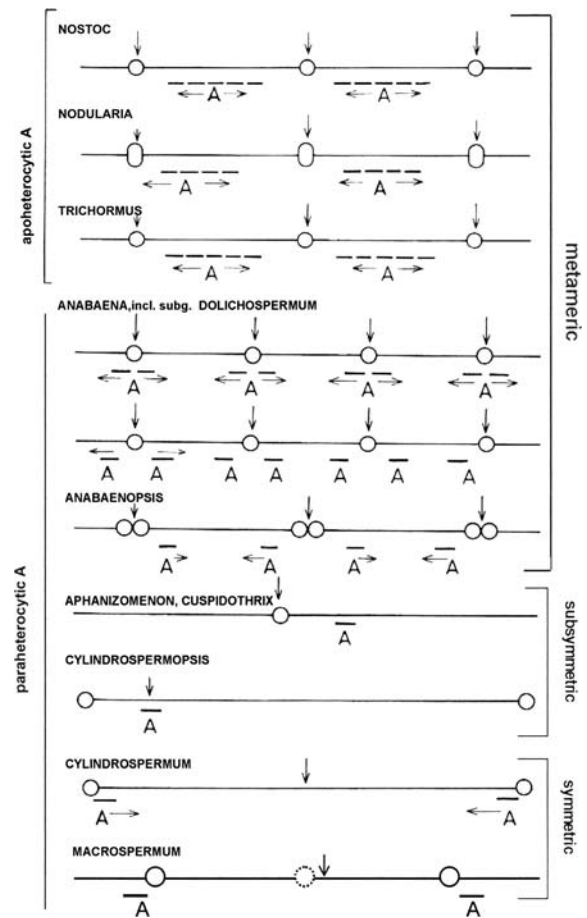


Fig. 3 Scheme of trichome structure [in relation to position of heterocytes (circles) and akinetes (A)] in main nostocacean genera. The trichome structure is in coincidence with the genetically limited genera [from Komárek & Anagnostidis (1989) and Komárek (2008)]

trichomes, narrowed ends of subsymmetric trichomes, presence of paraheterocytic (solitary or in pairs) akinetes. Five recognizable species and a few unclear morphotypes were described. The most recognized are *Raphidiopsis mediterranea* Skuja 1937 and the tropical species *R. curvata* Fritsch et Rich 1929; less known are *R. indica* Singh 1942, *R. sinensis* Jao 1951 and *R. turcomanica* Kogan 1967, named after the country of their occurrence. Other taxa, e.g. *R. longisetae* Eberly 1966 and *R. brookii* Hill 1972, are considered as problematic (Fig. 4A).

2. *Cuspidothrix* Rajaniemi et al. (2005a)

[type species = *C. issatschenkoi*, reference strain OTU37s7—Rajaniemi et al., 2005b]

Table 1 List of generic entities of the family Nostocaceae (Nov. 2008)

	1	2	3	4
<i>Raphidiopsis</i> Fritsch et Rich 1929	x	x		
<i>Cuspidothrix</i> Rajaniemi et al. 2005	x		x	
<i>Cylindrospermopsis</i> Seenaya et Subba-Raju 1972	x		x	
<i>Aphanizomenon</i> Morren ex Bornet et Flahault 1888	x	x	x	
<i>Anabaena</i> subg. <i>Dolichospermum</i> Thwaites ex Wittrock et Nordstedt 1889	x		x	x!
<i>Anabaena</i> -like cluster A (<i>Sphaerospermum</i> Zapomělová et al. 2010)	x		x	x!
<i>Anabaena</i> -like cluster B	x			x
<i>Anabaena</i> -like cluster C	x			x
<i>Anabaenopsis</i> (Wołoszyńska) Miller 1923	x	x	x	
<i>Cyanospira</i> Florenzano et al. 1985	x		x	
<i>Anabaena</i> Bory ex Bornet et Flahault 1888		x	x	
<i>Hydrocoryne</i> Schwabe ex Bornet et Flahault 1888		x		
<i>Aulosira</i> Kirchner ex Bornet et Flahault 1888		x!		
<i>Macrospermum</i> Komárek 2008		x		
<i>Cylindrospermum</i> Kützing ex Bornet et Flahault 1888		x	x	
<i>Cylindrospermum</i> -like cluster A	(x)			x!
<i>Wolleea</i> Bornet et Flahault 1888		x		
<i>Nodularia</i> (Mertens in Jürgens) ex Bornet et Flahault 1888	(x)	x	x	
<i>Richelia</i> J. Schmidt 1901	Endoph.	x		
<i>Isocystis</i> (Borzi) ex Bornet et Flahault 1888		x!		
<i>Trichormus</i> (Ralfs ex Bornet et Flahault) Komárek et Anagnostidis 1989			x	
<i>Trichormus</i> -like cluster A				x
<i>Nostoc</i> Geoffrey ex Linnaeus ex Bornet et Flahault 1888		x	x	
<i>Mojavia</i> Řeháková et Johansen 2007			x	

1 = genera with planktic species, 2 = traditional genera (Geitler, 1932) or described only by morphological characters, 3 = genera described or confirmed by polyphasic approach (molecular and morphological delimitation), 4 = phylogenetic clusters, not validly described, ! = not yet published, but will be validised (also by 16S rRNA gene sequencing) during 2009

Originally classified to *Aphanizomenon*, from which it can be separated both genetically and morphologically (Rajaniemi et al., 2005a, b; Komárek and Komárková, 2006; Fig. 5). Morphological diagnostic features are solitary, narrow trichomes with subsymmetric structure, paraheterocytic akinetes situated on both sides or slightly distant from heterocytes, facultative aerotopes (groups of gas vesicles), and narrowed, elongated and \pm pointed terminal cells (Fig. 4B). Five species have been described (up to now only the type species *Cuspidothrix issatschenkoi* (Usachev) Rajaniemi et al., 2005, has been sequenced). Another rare species from East Europe is *C. elenkinii* (Kiselev) Rajaniemi et al. (2005), and from tropical regions *C. tropicalis* (Horecká et Komárek) Rajaniemi et al. (2005) and *C. capricorni* (Cronberg et Komárek) Rajaniemi et al. (2005) (both with akinetes

joined to heterocytes). *C. ussatschevii* (Proškina-Lavrenko et Makarova) Rajaniemi et al. (2005) has been recorded only from the Caspian Sea.

3. *Cylindrospermopsis* Seenayya et Subba-Raju 1972 [type species = *C. raciborskii*, reference strain AWT205]

Originally classified in the genera *Anabaena* (habitual similarity) or *Anabaenopsis* (similar type of heterocyte development), but this genus was placed into a separate generic unit according to the subsymmetric, solitary floating trichomes and development of heterocytes only from terminal cells (after asymmetrical division) (Fig. 4C). This separation was confirmed by 16S rRNA gene sequencing, but up to now only strains of *Cylindrospermopsis raciborskii* have been analysed (Fig. 5). Akinetes develop subterminally,

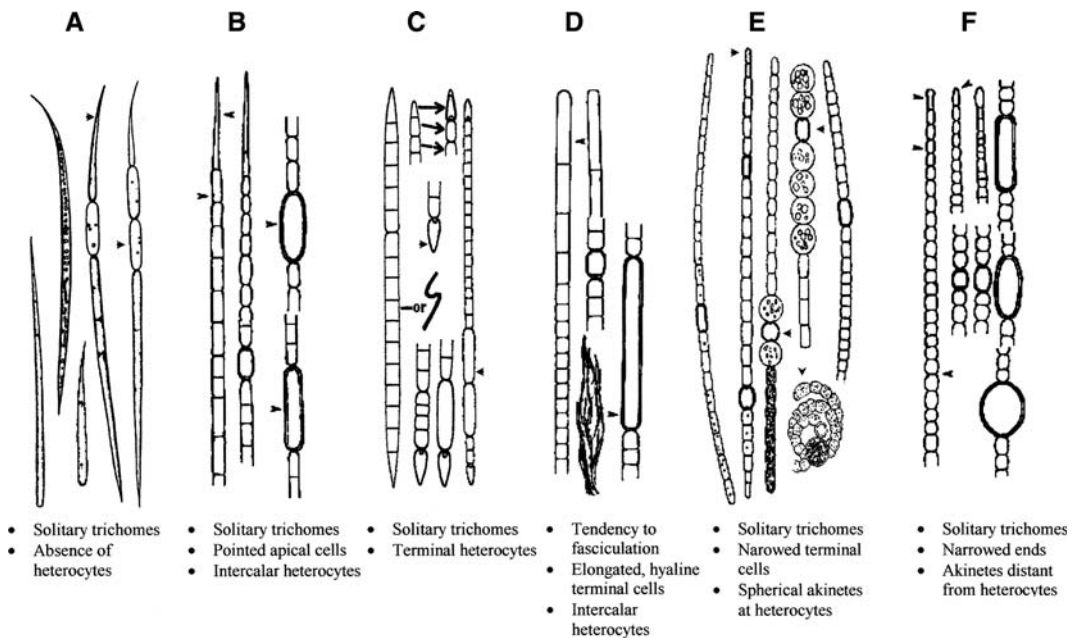


Fig. 4 Comparison of generic characters of planktic nostocacean types with filaments with more or less narrowed ends (only the main diacritical markers are added in the table): **A** *Raphidiopsis*, **B** *Cuspidothrix*, **C** *Cylandrospermopsis*,

D *Aphanzizomenon*, **E** *Anabaena* like cluster A (*Sphaerospermum*), **F** *Anabaena/Aphanzizomenon* like cluster B (drawings selected from various authors)

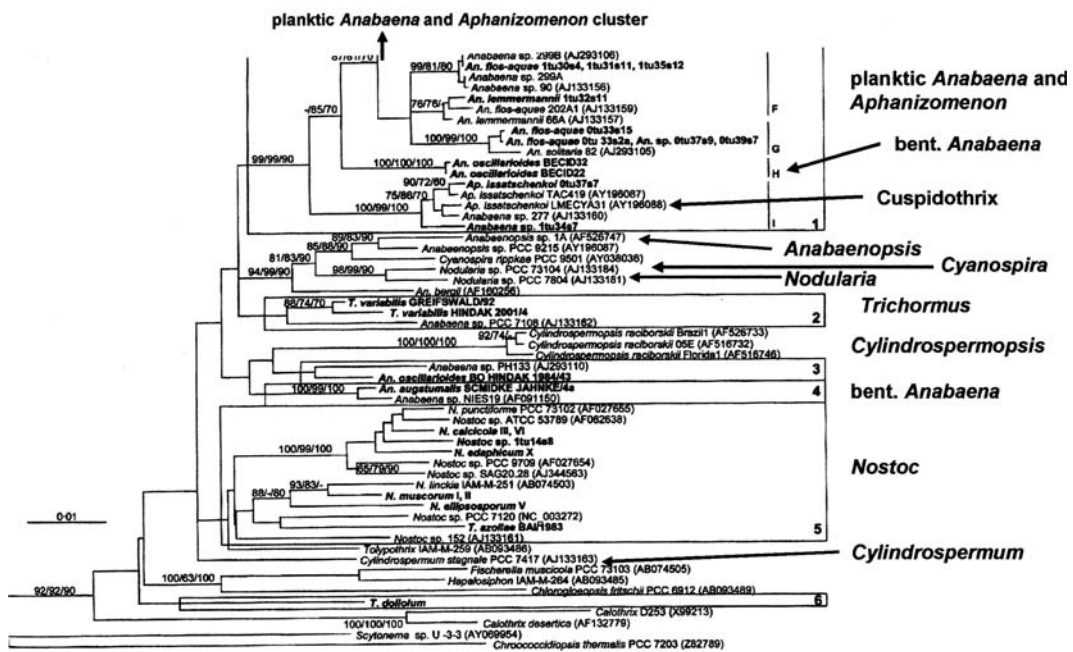


Fig. 5 Part of a phylogenetic tree from Rajaniemi et al. (2005). Distinctly separated genera with planktic species are in the tree

aerotopes occur facultatively in cells. The type species produces toxins and seems to be expanding geographically in recent years. Since the middle of the twentieth

century, it has expanded from its original tropical regions into subtropical and temperate areas. Gugger et al. (2005) discovered a genetic divergence of the

expanding *C. raciborskii*. The fact that the majority of 11 morphospecies described were published after 1991 confirms the expulsive development of this genus in recent decades. From the 11 morphospecies described, 9 are known only from tropical habitats. The lists and characteristics of described species are reviewed in papers of Komárek & Komárková (2003) and Couté & Bouvy (2004).

4. *Aphanizomenon* Morren ex Bornet et Flahault 1888 [type species = *Aph. flos-aquae*; reference strain PCC7905]

Planktic heterocytous cyanobacteria with more or less straight trichomes and slightly narrowed or elongated terminal cells were classified traditionally into this genus. Modern genetic and morphological studies restricted the genus in a well-defined cluster of morphospecies, which all have subsymmetric structure of trichomes, a tendency to aggregate straight trichomes in parallel fascicles and which do not have distinctly narrowed ends. The terminal cells are cylindrical, elongated and hyaline in well-developed mature filaments, but not or only very slightly narrowed. All other types with narrowed ends and non-cylindrical, elongated end cells must be classified in other genera (Fig. 4D). The revised genus contains eight morphospecies, which also differ slightly in their ecological demands. The most common and important are *A. flos-aquae* Ralfs ex Bornet et Flahault 1888, *A. klebahnii* Elenkin ex Pechar 2008 and *A. yezoense* Watanabe 1991, which all are distributed only in temperate zones. Other species occur only in isolated areas, but no *Aphanizomenon* species occurs in tropical regions (Komárek & Komárková, 2006). There are ecologically and toxicologically interesting types forming water blooms in eutrophic stagnant waters.

5. *Anabaena* subg. *Dolichospermum* Thwaites ex Wittrock et Nordstedt 1889

[type species = *An. flos-aquae* Brébisson ex Bornet et Flahault, reference strain PCC9332]

This genus contains a group of planktic members of the traditional *Anabaena*, characterized by solitary free-floating trichomes (or living in clusters), and by cells with gas vesicles (forming aerotopes). Genetically, this genotype is clearly differentiated from the group of benthic, metaphytic or periphytic species, based on the type species *A. oscillarioides*. The

phylogenetic separation was confirmed by Iteman et al. (2002), Gugger et al. (2002a, b), Rajaniemi et al. (2005a), Willame et al. (2006) and others (Fig. 5). The morphospecies are more or less recognizable in natural populations, but they have transient features in cultures. Of the traditional characters, particularly coiled or straight trichomes and type of coiling (used mainly for the separation of species) are not stable under culture conditions (Zapomělová et al., 2008). On the contrary, position and form of akinetes, morphology of terminal cells and (in certain limits) size and form of cells seem to be stable for different morphospecies (Fig. 6A). The genus contains about 45 planktic species after revision. For the lists and morphological descriptions see Komárek (1999) and Komárek & Zapomělová (2007, 2008). The validation of the genus *Dolichospermum* was published recently (Wacklin et al., 2009).

6. *Anabaena*-like cluster A (*Sphaerospermum* Zapomělová et al., 2010)

[type species = *S. reniforme*, reference strain: 06(FM161348)—Zapomělová et al., 2010]

This cluster contains one part of the planktic *Anabaena*/*Dolichospermum* cluster, which was phylogenetically distinctly separated from other *Dolichospermum* types (Zapomělová et al., 2010; Fig. 7). The newly defined genus is morphologically characterized by solitary (coiled or straight), free-floating trichomes, the obligatory presence of gas vesicles, slightly modified terminal cells and the position of spherical akinetes on both sides of heterocytes (Fig. 4E). It contains three species with uncommon and dispersed distributions, *Sphaerospermum aphanizomenoides* (Forti) Zapomělová et al. (2010), *S. kisselevianum* (Elenkin) Zapomělová et al. 2010 and *S. reniforme* (Lemmermann) Zapomělová et al. (2010).

7. **Anabaena*-like cluster B

[type species and reference strain not selected]

This group contains planktic filamentous and heterocytous cyanobacteria, characterized by floating, solitary, more or less straight or slightly flexuous, metameric trichomes, usually slightly narrowed towards the ends and with elongated akinetes in a paraheterocytic position (Fig. 4F). They were described partly as *Aphanizomenon* (terminally narrowed cells) or *Anabaena* (similarity with planktic straight “*Anabaena*” species). The cells contain

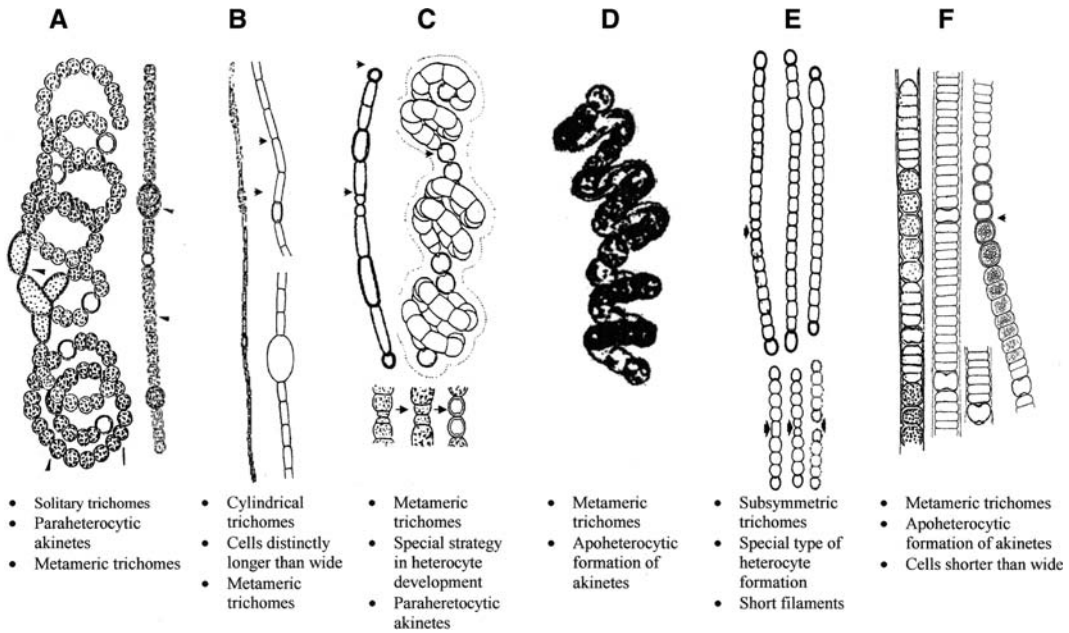
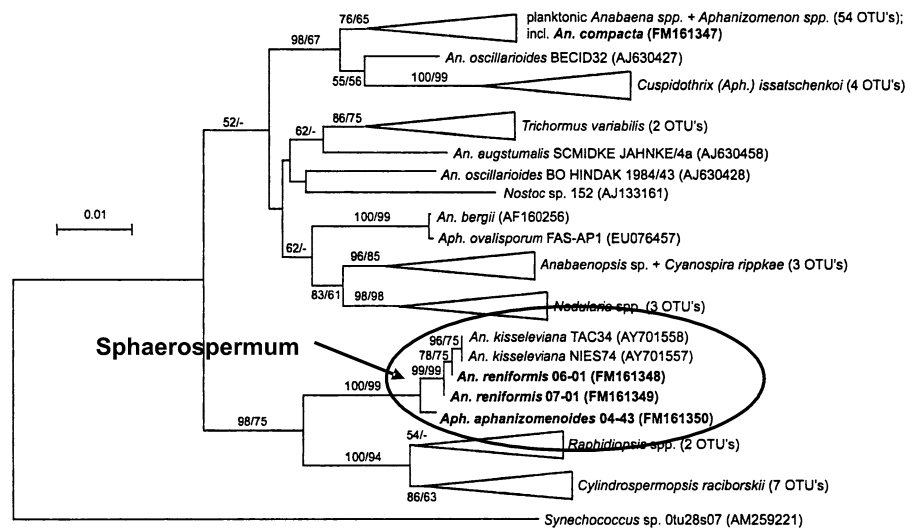


Fig. 6 Comparison of generic characters of planktic nostocacean types with filaments with not narrowed or elongated end cells (only the main diacritical markers are added in the table): **A** *Anabaena* subg. *Dolichospermum*, **B** *Anabaena*-like cluster

C, **C** *Anabaenopsis*, **D** *Cyanospira*, **E** *Cyalindrospermum*-like cluster **A**, **F** *Nodularia* (drawings selected from various authors)

Fig. 7 Phylogenetic tree separating the cluster of *Sphaerospermum* from other *Anabaena*-like species (Zapomělová et al., 2010)



facultative or obligatory gas vesicles, with the exception of the end cells. More than 20 known morphospecies belong to this group. They surely do not belong to *Dolichospermum* or *Aphanizomenon* according to genetic investigations, and the determination of several genetic clusters within this group is possible: *Aphanizomenon gracile* (Lemmermann) Lemmermann 1907, *Aphanizomenon skujae* Komárková-Legnerová et

Cronberg 1992, *Aphanizomenon ovalisporum* Forti 1911, *Aphanizomenon manguinii* Bourrelly 1953, *Anabaena minderi* Huber-Pestalozzi 1938, *Anabaena bergii* Ostenfeld 1908, and others (cf. Komárek & Kováčik, 1989; Komárek & Komárková, 2006).

8. **Anabaena*-like cluster C
[type species and reference strain not selected]

Another group of planktic, nostocacean types with metameric, solitary, straight or flexuous, rather narrow (1.5–4(7) μm wide) trichomes and elongated cells, obligatory with gas vesicles, and elongated, paraheterocytic akinetes distant from heterocytes (Fig. 6B). These types do not belong to any revised genera, but they were not yet evaluated by molecular methods and sequencing. Four morphospecies from northern, oligotrophic or mesotrophic lakes, described as various species of “*Anabaena*” (*A. elliptica* Lemmermann 1898, *A. levanderi* Lemmermann 1906, *A. miniata* Skuja 1956, *A. tenericaulis* Nygaard 1949) and possibly also two little known species from central Asia (*A. abnormis* Proškina-Lavrenko 1968, *A. attenuata* Kiselev 1940) belong to this morphological cluster.

9. *Anabaenopsis* (Woloszyńska) Miller 1923

[type species *A. elenkinii*; reference strain PCC9420]

The type species was described originally in 1912 as planktic *Anabaena* by Woloszyńska, but was later classified as a special subgenus and genus by Miller 1923 based on one unique character: The trichomes are metameric, but the heterocytes develop in a specific way (two intercalar neighbouring cells divide synchronously and asymmetrically with smaller daughter parts oriented one to another; from these two smaller cells develop mirror-like unipored heterocytes oriented by pores to trichomes). Trichomes between heterocytes disintegrate later and short trichomes with apical heterocytes arise from this process (Komárek & Anagnostidis, 1989; Figs. 6C, 8). The trichomes are *Anabaena*-like, solitary, free-floating cells with obligatory or facultative aerotopes. The genus is clearly defined phenotypically and has been confirmed by sequencing (Fig. 9). About 20 morphospecies are described, which differ slightly ecologically. The majority of the species prefer alkaline or slightly saline inland waters. The differential morphological features between species are mainly the width and shape of cells, but numerous transitional types exist (Komárek, 2005). The genus is mainly distributed in tropical and subtropical regions; only a few types occur in temperate zones. The various species develop massive populations (in the form of water blooms). The various morphospecies appear rarely only in cultures, but the separate genetic cluster was confirmed (Iteman et al., 2002; Rajaniemi et al., 2005a; Figs. 5, 9).

10. *Cyanospira* Florenzano et al., 1985

[type species: *C. ripppkae*; reference strain MAG II 702]

Described according to molecular sequencing (Florenzano et al., 1985; Iteman et al., 2002; Figs. 6D, 9). It is genetically related to *Anabaenopsis* and *Nodularia*, however, habitually is similar to coiled planktic *Anabaena* types (= *Dolichospermum*). Diacritical markers are (besides phylogenetic position) solitary, free-floating, coiled and metameric trichomes with a facultative occurrence of gas vesicles and apoheterocytic formation of akinetes. Two species were described from Africa (*Cyanospira ripppkae* Florenzano et al. 1985 and *C. capsulata* Florenzano et al., 1985). “*Anabaena*” *globosa* Hirano, described from Nepal, also morphologically corresponds to this genus.

11. *Cylindrospermum*-like cluster A

[type species and reference strain not selected]

This cluster contains a few morphospecies with a special intercalar development of the heterocytes. One vegetative, barrel-shaped and intercalar cell changes its form into a narrower, cylindrical and more elongated proheterocyte, which divides into two parts, from which two heterocytes develop. The trichome later disintegrates between them (Hindák, 2000). From this process, short trichomes with heterocytes in an apical position develop; this stage habitually resembles *Cylindrospermum*, *Anabaenopsis* or *Cylindrospermopsis*, but the different origin of the heterocytes (connected with the subapical origin of akinetes) indicates a special generic entity (Fig. 6E). Three well-recognizable species with these characteristics were described up to now under different generic names: *Anabaena siamensis* Antarikanonda 1985 from a rice field in Thailand, *Richelia* sp. in Hindák, 2000 from the metaphyton of pools in Slovakia and *Cylindrospermum planctonicum* Cronberg, 2003 from plankton of the Baltic Sea. The taxonomic position of this type can be solved only by molecular studies (cf. Hindák, 2000; Cronberg, 2003).

12. *Nodularia* (Mertens et Jürgens) ex Bornet et Flahault 1888

[type species: *N. spumigena*; reference strain: PCC9350]

This genus was described on the basis of a common habitual appearance of trichomes with short

Fig. 8 Morphological characteristics of *Anabaenopsis* in comparison with related genera *Anabaena* and *Nodularia*. The review of cell form in *Anabaenopsis* is described in the lower part of the figure [from Komárek & Anagnostidis (1989), Hindák (2001) and Komárek (2005)]

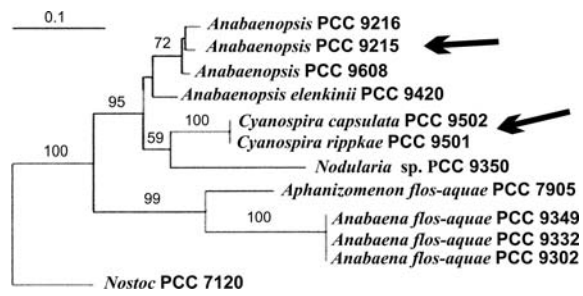
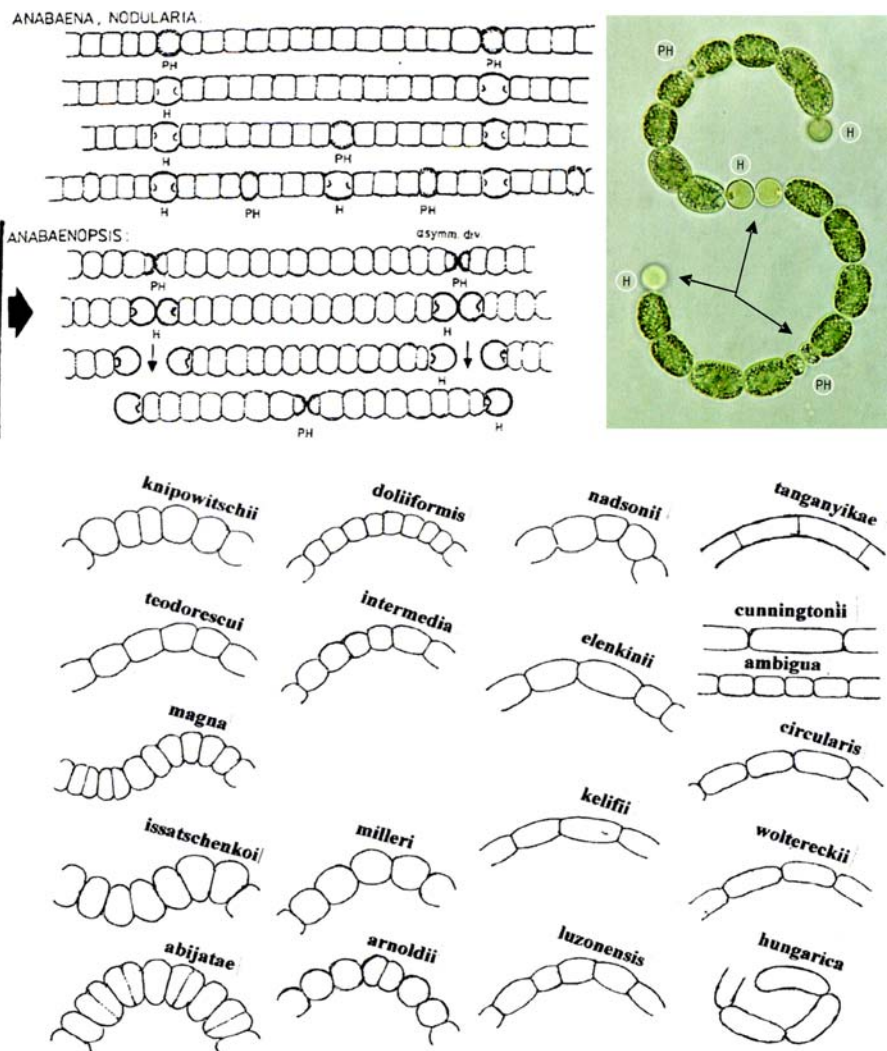


Fig. 9 Comparison of the phylogenetic position of the genera *Anabaenopsis*, *Cyanospira*, *Nodularia* and *Aphanizomenon* [according to Iteman et al. (2002)]

(discoid) cells and irregular apoheterocytic formation of akinetes (Fig. 6F). It is the only genus in which the species with gas vesicles were (according to present

knowledge) not genetically separated from morpho-species, which never form gas vesicles and never grow in plankton. Particularly, the planktic species prefer brackish and slightly saline water habitats, but they occur in very separated and distant localities. Planktic species are mostly known from the Baltic Sea (where they form heavy water blooms). Other recent localities are the Caspian Sea, several lakes near the western coast of North America, volcanic lakes in Mexico, coastal lakes in Uruguay and sea bays in SW Australia. All these populations are classified near *N. spumigena* (or like species), but preliminary genetic analyses indicate that there are specifically different. They differ slightly (but distinctly) also morphologically, e.g. the coiled filaments of *N. spumigena* occur only in populations

from the Baltic Sea. Four to five morphospecies were described on the basis of morphological criteria. The populations from the Baltic Sea were already studied several times by the molecular methods (Bolch et al., 1996; Hayes et al., 1997; Bolch & Blackburn, 1998; Lehtimäki et al., 2000), but these results did not agree one to another. The species concept of *Nodularia* and their diversity must therefore be studied further. A review of 8–10 benthic *Nodularia* species is simpler, and the morphospecies are easier characterized.

The family Nostocaceae contains the following genera, which only exceptionally occur in planktic habitats. They probably do not have genes for gas vesicle production:

- *Anabaena* Bory de Saint-Vincent ex Bornet et Flahault 1888—Type species is *A. oscillarioides*. Confirmed by molecular sequencing (Gugger et al., 2002a, b; Rajaniemi et al., 2005a, b; Willame et al., 2006). It contains only non-planktic (benthic, periphytic, metaphytic, edaphic) morphospecies, and gas vesicles never occur in cells. About 60 described and well-defined morphospecies. They possibly will be divided into more genetic clusters and separated into various genera.
- **Hydrocoryne* Schwabe ex Bornet et Flahault 1888—Defined only by morphological criteria, not yet studied by molecular methods. However, few morphospecies are known and repeatedly recorded. Confirmation of generic status and importance of morphological markers is desirable.
- *Aulosira* Kirchner ex Bornet et Flahault 1888—About 25 morphospecies were described, mostly from tropical aquatic habitats. Main diacritical features are apoheterocytic formation of akinetes and firm sheaths around *Anabaena*-like trichomes. Confirmed by molecular methods (but not the type species; Lukešová et al., 2009); the existence of one or a few generic units inside this morphotype is probable (Geitler, 1932).
- **Macrospermum* Komárek, 2008—Four tropical species. Originally classified with *Anabaena*, but morphologically clearly separated by symmetrical trichomes and the special morphology of large akinetes. Metaphytic species, but with facultative gas vesicles. Confirmation by sequencing is necessary.
- *Cylindrospermum* Kützing ex Bornet et Flahault 1888—A morphologically unique, well-defined traditional genus, which has been confirmed by molecular analyses. Approximately 35 recognizable morphospecies (Geitler, 1932; Bourrelly, 1970; etc.).
- **Wollea* Bornet et Flahault 1888—A poorly known genus, which is not yet sequenced with certainty. Morphologically distinct (Desikachary, 1959; Bourrelly, 1970), molecular support is desirable. About six morphospecies were described, mostly from tropical regions.
- **Richelia* J. Schmidt 1901—Interesting oceanic genus with 1–2 morphospecies, living endophytically, mainly within frustules of planktic diatoms (see, for example, Desikachary, 1959). Not yet confirmed by molecular evaluation, but existence of its genetic homogeneity is highly probable. The later classification of three ecologically and morphologically different freshwater species into this genus (Hindák, 2000) is questionable.
- **Isocystis* (Borzi) ex Bornet et Flahault 1888—A poorly known genus with about four to eight species. Without heterocytes and with atypical nostocacean akinetes. Classification in the family Nostocaceae is therefore improbable, it must be studied by molecular methods (Komárek & Anagnostidis, 1989).
- *Trichormus* (Ralfs ex Bornet et Flahault 1888) Komárek & Anagnostidis, 1989—A well-defined and genetically confirmed genus with apoheterocytic formation of akinetes. The genus with about 40 (mostly tropical) morphospecies is based on the commonly distributed soil type species *T. ("Anabaena") variabilis*, which yields commonly used laboratory model strains. Important N-fixing types belong to this genus. A few other genetically diversified clusters may appear in the genus (Desikachary, 1959; Rajaniemi et al., 2005a).
- *Trichormus*-like cluster A—Represented by one thermophilic species, which is morphologically similar to the typical *Trichormus*, but belongs genetically to a separate, not taxonomically validated cluster (Kaštovský & Johansen, 2008).
- *Nostoc* Geoffrey (ex Linnaeus) ex Bornet et Flahault 1888—Very wide and heterogenic cluster, which will surely be divided into several genetic units (Hrouzek et al., 2005). Up to now, about 60 recognizable (many unclear) morphospecies and strains were described. Genetic diversity is wide and must be investigated by

the help of combined molecular and phenotype methods.

- *Mojavia* Řeháková et Johansen 2007—A monospecific genus described from American desert soils by combined molecular and morphological methods. From the vicinity of a complex cluster of *Nostoc*; up to now the only defined cluster, with one species, separated from this genus (Řeháková et al., 2007).

Conclusions

The taxonomic classification of Cyanobacteria must be substantially changed. The introduction of molecular and other modern methods corrected our knowledge of phylogenetic relations of different types of cyanobacterial taxa, which were evaluated up to now mostly on the basis of morphological characters. Populations from geographically and ecologically distant ecosystems were found different by numerous markers, and also the importance and hierarchy of morphological features must be re-evaluated. However, the morphology and morphological variability is important part of the diversity and diversification processes in cyanobacteria in all ecosystems over the world. The complex and combined studies containing both the modern molecular procedures and detailed morphological, ecological, cytomorphological and biochemical studies are also indispensably necessary to the knowledge of the cyanobacterial diversity.

The process of the reorganization of nostocacean taxonomic system was already initiated. The orientation in all changes, which must be in evaluation of cyanobacterial diversity respected, is not easy, particularly for the users of the system, ecologists and experimental researchers. This review is therefore the summarized information about the main changes in nostocacean diversity, which were already published to the end of 2008. Of course, the further corrections and modification are expected already in next few years.

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