

Recent changes (2008) in cyanobacteria taxonomy based on a combination of molecular background with phenotype and ecological consequences (genus and species concept)

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Abstract Taxonomic classification is a method for recognizing and registering the world's organism diversity, in the context of continual changing knowledge about evolutionary (genetic) and ecological relations and phenotype variation. The present system of cyanobacteria must be modified according to combined markers, in which molecular data (as an indisputable genetic basis) should be correlated with biochemical, ultrastructural, phenotypic and ecological data. New data are necessary in order to correct or up date the system; thus, the classification must continually be revised and supplemented. The greatest problem is to transfer all modern data derived from molecular investigations to experimental research and establish the necessary and correct nomenclatural rules for scientific practice. The molecular approach

must be the baseline for the reorganisation of our knowledge; however, it should explain and be in agreement with morphological and ecological variation of cyanobacterial genotypes. The present article summarizes the main conclusions, derived from modern cyanobacterial diversity studies.

Keywords Cyanobacteria · Taxonomy · Molecular evaluation · Ecology · Taxonomic classification · Genera · Species concept · Nomenclature

Introduction

Application of molecular methods into cyanobacterial taxonomy enhanced several important principles for cyanobacterial systematics:

- (i) Morphological characters of various taxonomic units should concur with their phylogenetic position. The first molecular analyses were potential but not very conclusive, regarding this principle. The reason was that many sequenced strains were designated by incorrect names; however, the clusters obtained characterized well the natural taxonomic units after the nomenclatural revision and reconstruction of phylogenetic trees (e.g., cf. Wilmotte & Golubić, 1991; Turner, 1997; Komárek & Kaštovský, 2003a).

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- (ii) Wide genetic diversity was found particularly in coccoid and simple filamentous and pseudofilamentous types. As a result of combined molecular and phenotypic analyses, phylogenetic relationships among simple cyanobacteria were found to be non-linear and few parallel clades were recognized. Several distinct features are in agreement with these clades, e.g. ultrastructural patterns (basic position of thylakoids in cells), type of cell division, structure of cell wall, size of cells or differentiation of the thallus, etc. (Komárek & Kaštovský, 2003a; Turicchia et al., 2009).
- (iii) The taxonomic value of morphological features has to be re-evaluated. Several distinct traditional characters, used for classification of generic and suprageneric units, did not appear to be quite compatible with the molecular results, e.g. presence/absence of sheaths, size of cells (in distinct limits), false and true branching, etc. These features probably have only ecotypic value within each genotype and their mode of variation may have a genetic basis which is not presently sequenced. The morphological markers which are compatible with natural molecular clusters have to be defined.
- (iv) Numerous morphologically derived taxa, particularly on the generic level, were based only on one or a few widely conceived morphological characters. The hierarchy of characters according to genetic importance has to be revised and applied to the system.
- (v) The cluster of heterocytous types was found to be monophyletic, but for classification inside this group (families, genera) the system has been revised in light of new phylogenetic investigations (Castenholz, 2001; Lyra et al., 2001; Gugger et al., 2002; Iteman et al., 2002; Gugger & Hoffmann, 2004; Hrouzek et al., 2005; Rajaniemi et al., 2005; Willame et al., 2006).

The necessity for re-evaluating criteria used for the concept of taxonomic units (genera, species) and their characterization is therefore indispensable, following the application of molecular methods for taxonomic re-evaluation in cyanobacteria. The more or less standardized molecular method used is 16S rRNA gene sequencing, particularly for the genus level.

Generic concept

The clusters resulting from 16S rRNA gene sequencing correspond more or less to the traditional cyanobacterial genera, defined by distinct phenotypic characters. A similarity limit of 95% was established as being intergeneric between cyanobacterial genera (Wayne et al., 1987; Stackebrand & Goebel, 1994). This sharp limit cannot be used as a standard key criterion for separating biological taxa quite obligatorily, but it can be an important and the first marker for generic differentiation. From the last few years of use it follows that the characterization of genera should be based on molecular separation (about 95% or less genetic similarity) combined with at least one diacritical autapomorphic cytomorphological character. Genera, defined in this way, belong usually also to one ecophysiological type (Garcia-Pichel et al., 1998).

Almost all the traditional (Geitlerian) cyanobacterial genera have been confirmed by molecular methods, including the newly established ones on the basis of revised morphological characters after modern morphological and ecological revisions, over the past decades of the 20th century (Rippka & Cohen-Bazire, 1983; Anagnostidis & Komárek, 1985, 1988; Komárek & Anagnostidis, 1989, 2005; *Cyanotheca*, *Limnothrix*, *Planktothrix*, *Cyanobacterium* and others). Of course, the traditional genera were (and must be) only revised on the bases of the type species. From this practice it follows that the modern approach to the cyanobacteria systematics leads to the division of some existing genera into more generic units, characterized both genetically and morphologically. It is remarkable that several of these ‘newly discovered’ genera correspond to taxa originally described by old, ‘pre-starting-point’ authors (but later connected to other genera on the basis of one prominent character by classical authorities; Bornet & Flahault, 1886–1888; Gomont, 1892; Geitler, 1932; Elenkin, 1936–1949; Bourrelly, 1970; and others). Such old and recently justified genetic and generic units include *Arthrospira*, *Trichormus*, *Hassallia* and others. New generic taxa, which were separated from the traditional genera, include, e.g. *Brasilonema*, *Cylindrospermopsis*, *Cyanotheca*, *Phormidesmis*, *Halotheca/Euhalotheca* complex, *Thermosynechococcus* and *Geminocystis*. In-depth studies of some of Earths sparsely investigated

Table 1 List of nostocalean genera (November 2008). Genera, which were confirmed (at least their type species) by 16S rRNA gene sequencing are printed bold (partly from Hoffmann et al., 2005)

Nostocineae	Nostocales heterocytous, akinetes present	Scytonemataceae isopolar, false branching	Kyrtuthrix, Scytonematopsis, Scytonema , Brasilonema , Scytonema subg. Myochrotes, Petalonema
		Symphyonemataceae true branching (Y)	Brachytrichia, Handeliella, Herpyzonema, Iyengariella, Mastigocladopsis, Symphyonemopsis , Symphyonema , Spelaepogon, Umezakia
		Rivulariaceae heteropolar, hairs	Calothrix , Dichothrix, Gardnerula, Gloeotrichia, Isactis, Rivularia, Sacconema (sine typo)
		Microchaetaceae heteropolar	Borzinema, Camptylonemopsis, Coleodesmium , Fortiea, Hassallia , Microchaete , Rexia , Spirirestis , Sacconema, Seguenzaea, Tolypothrix
		Nostocaceae isopolar, without branching	Anabaena —planktic (Dolichospermum), Anabaena —benthic, Anabaenopsis , Aphanizomenon , Aulosira, Capsosira, Cuspidothrix , Cyanospira , Cylindrospermopsis , Cylindrospermum , Hydrocoryne, Isocystis, Macrospermum, Mojavia , Nodularia , Nostoc , Raphidiopsis, Richelia, Sphaerospermum , Stratonostoc, Trichormus , Wollea
		Chlorogloeopsidaceae	Chlorogloeopsis
		Hapalosiphonaceae true branching (T)	Albrightia, Brachytrichiopsis, Chondrogloea, Colteronema, Fischerella , Geitleria, Hapalosiphon , Leptopogon, Loefgrenia, Loriella, Mastigocladus , Matteia, Mastigocoleopsis, Mastigocoleus , Nostochopsis , Parthasarathiella, Thalpopbila, Westiella , Westiellopsis
		Stigonemataceae true branching, multiseriate	Cyanobotrys, Desmosiphon, Doliocatella , Homoeoptycha, Nematoplaca, Pulvinularia, Stauromatonema, Stigonema

habitats also lead to the discovery of new genetically and morphologically well defined genera. *Spirirestis* or *Rexia* from the nostocalean cyanobacteria are such genera, while a few others are prepared for validation. A review of the recently revised nostocalean genera is included in Table 1.

Examples of recently revised generic entities

Synechococcus

Simple and unicellular cyanobacteria with more or less rod-like cells are usually classified into this genus. They are commonly distributed, easily grown in cultures and many of strains have been isolated. Several of them were used as important experimental strains, but sometimes under incorrect names ('*Anacystis nidulans*' = *Synechococcus nidulans*). Many strains have already been sequenced and at least 12 clusters were separated, but their differences did not always reach 95% of similarity. A few of

them were described as separate genera, e.g. *Cyanobium* (Rippka & Cohen-Bazire, 1983), which probably now should include also the picoplanktic 'oceanic *Synechococcus*-types'. However, the name '*Cyanobium*' is not commonly used in recent literature. On the other hand, there appears to be a thermophilic genus *Thermosynechococcus* used in the experimental literature, but this is used without any valid description. The type species is designated '*Thermosynechococcus (Synechococcus) elongatus*' (Katoh et al., 2001) but *Synechococcus elongatus* is the type species of the original genus '*Synechococcus*', which is not thermophilic. Several thermophilic species were described (*S. lividus*, *S. vulcanus*, *S. bigranulatus* and others) and '*Thermosynechococcus*' is based probably on the strain of the species *Synechococcus bigranulatus* (= 'thermophilic *S. elongatus*'). *Synechococcus* should therefore be divided into several generic units, but the whole taxonomy must be evaluated and characterized using correctly selected type species and strains (Fig. 1).

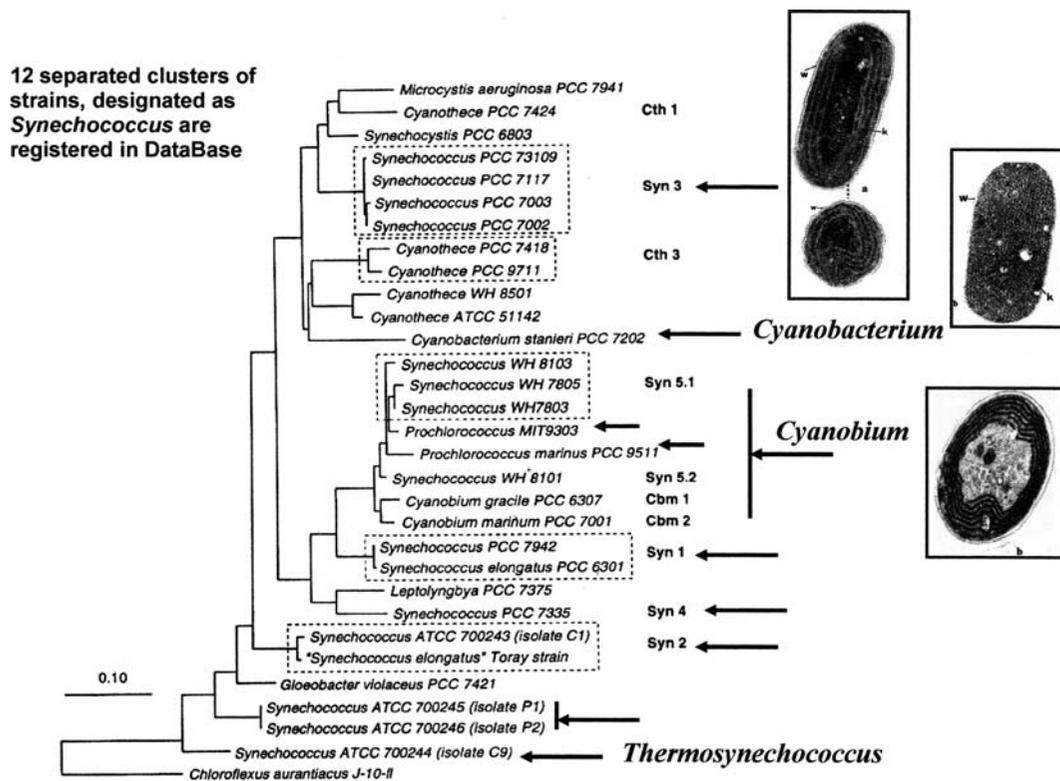


Fig. 1 Part of a phylogenetic tree of the traditional genus *Synechococcus* (derived from Castenholz, 2001). Few different clusters were classified in several genera. The EM photos illustrate particularly the position of thylakoids, characteristic for various genera

Synechocystis

PCC 6803 of ‘*Synechocystis* sp.’ is one of the main experimental strains at present. It was also the first strain which has had its entire genome described. Strain PCC 6803 really corresponds very closely to the type species of the genus *Synechocystis* (*S. aquatilis*) using all markers. The genus *Synechocystis* therefore represents a clearly separate genetic cluster with characteristic morphology and cytology. The problem is, that in Bergey’s Manual (Castenholz, 2001), not the strain PCC 6803 but PCC 6308 was designated as a type for *Synechocystis*. But this strain is very far from typical strain PCC 6803 of *Synechocystis* both genetically and morphologically–cytologically, occurs in other collection and experimental papers also under designations ATCC 27150, CCAP 143011, UTEX 1598, CALU 743 and others and was recently separated into a new genus *Geminocystis* (*G. herdmanii*, Korelusová et al., 2009;

Fig. 2). The reference strain of *Synechocystis* must be therefore determined correctly as PCC 6803. For differences of both types see Fig. 2.

Aphanothece

The genus *Aphanothece* is evidently heterogeneous, even morphologically, and must be revised together with the genus *Gloeothece*. It contains 4–5 different clusters. At least two distinct and separate clusters have been defined recently genetically, morphologically and ecologically (Fig. 3): (i) a typical benthic, subaerophytic and metaphytic genus *Aphanothece* (with cells 2.5–8 μm wide) and (ii) typical planktic morphotypes (cells 0.3–2 μm wide; Jezberová, 2006). Both of these clusters have distant positions in the phylogenetic tree, different sizes of cells, structure of mucilage and very different ultrastructure (the second cluster of planktic morphotypes has more characters resembling the genus *Cyanobium*).

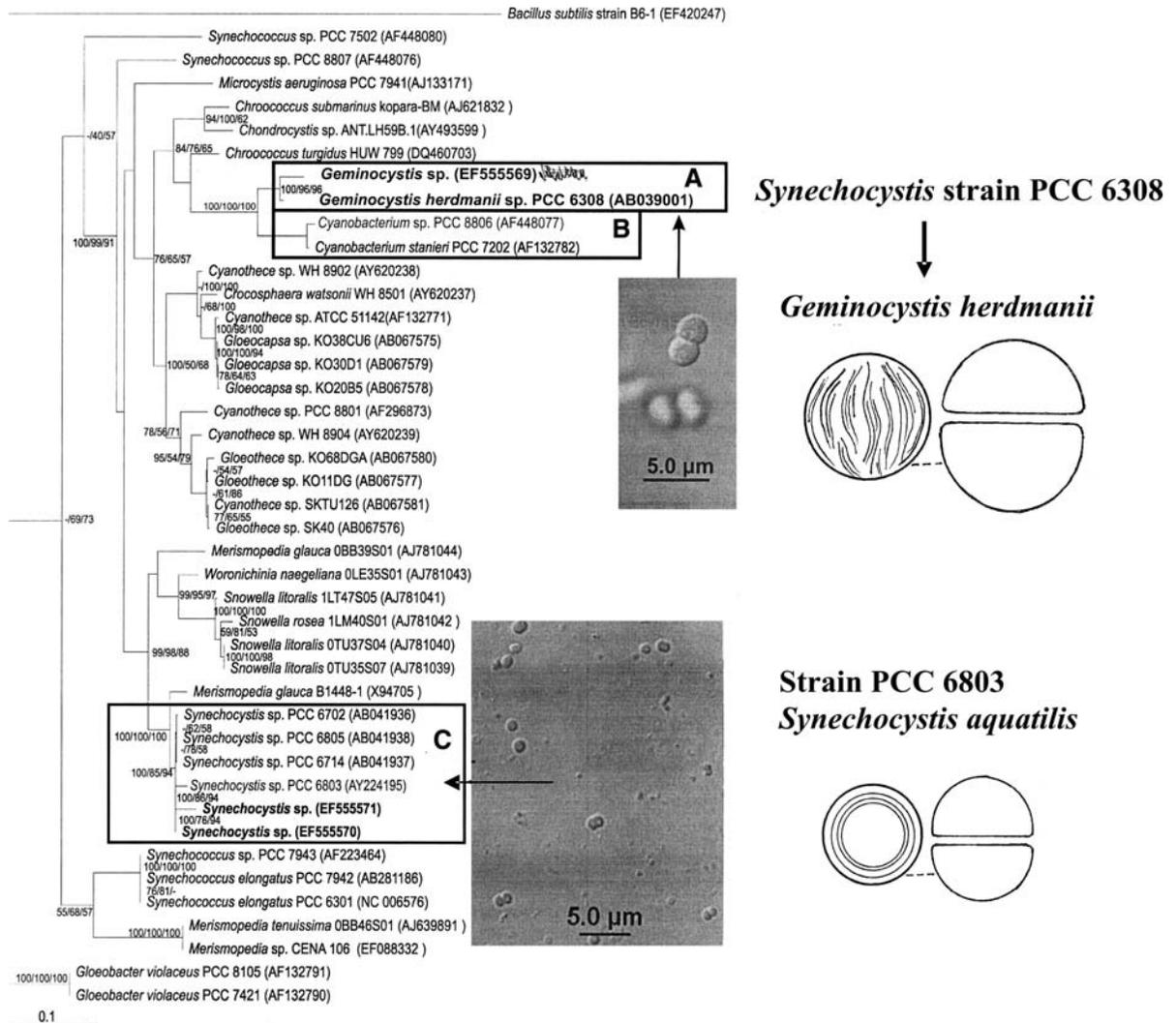


Fig. 2 Heterogeneity of the genus *Synechocystis*. The strain PCC 6308 is clearly different both genetically and cytologically from typical cluster of *Synechocystis*. The tree after Korelusová et al. (2009); A cluster corresponding to new genus

Geminocystis, B cluster corresponding to the genus *Cyanobacterium*, C *Synechocystis* cluster with the reference strain PCC 6803

Cyanothece

This genus was originally separated from the genus *Synechococcus* on the basis of morphological and cytological markers (Komárek, 1976). Later, this separation was supported by molecular analyses (Rudi et al., 1997). However, smaller unicellular types with oval cells were later falsely designated as *Cyanothece* by Rippka & Cohen-Bazire (1983). Several of these were later used as important

models in biochemical and molecular laboratories. Their genetic position and morphological features are far from the type species *C. aeruginosa*. However, the name *Cyanothece* is commonly used in this incorrect sense. The first steps to correct this error can be found in the studies of Garcia-Pichel et al. (1998), Margheri et al. (1999) and Komárek et al. (2004). The names *Euhalothece*, *Halothece* and *Cyanobacterium* (the last one, a generic name introduced by Rippka & Cohen-Bazire, 1983)

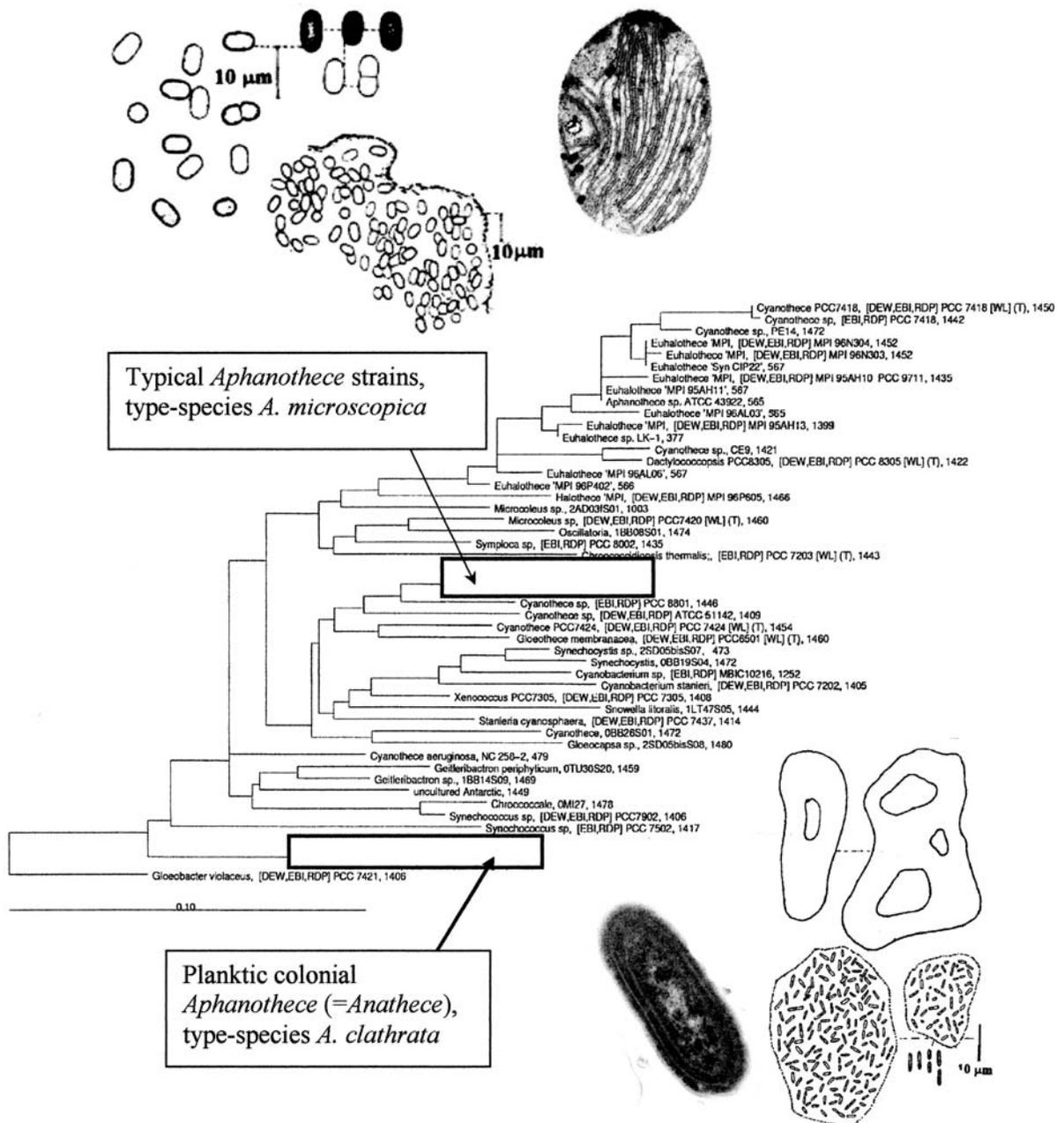


Fig. 3 Heterogeneity of the traditional genus *Aphanothece*. The planktic types (*Anathece*) are clearly separated from typical cluster of *Aphanothece*, based on *A. microscopica*. Phylogenetic tree according to Jezberová (2006)

should be used to correct this taxonomic confusion; (Fig. 4).

Phormidium

Another very heterogeneous genus is *Phormidium*, which contains several morphologically recognized

genetic clusters. Revision of this genus is just beginning and recently a special genus *Phormidesmis* was already distinctly separated. It appears to be more related both genetically and ultrastructurally by markers closer to pseudanabaenacean than to phormidiacean genera (Komárek et al., 2009; Turicchia et al., 2009).

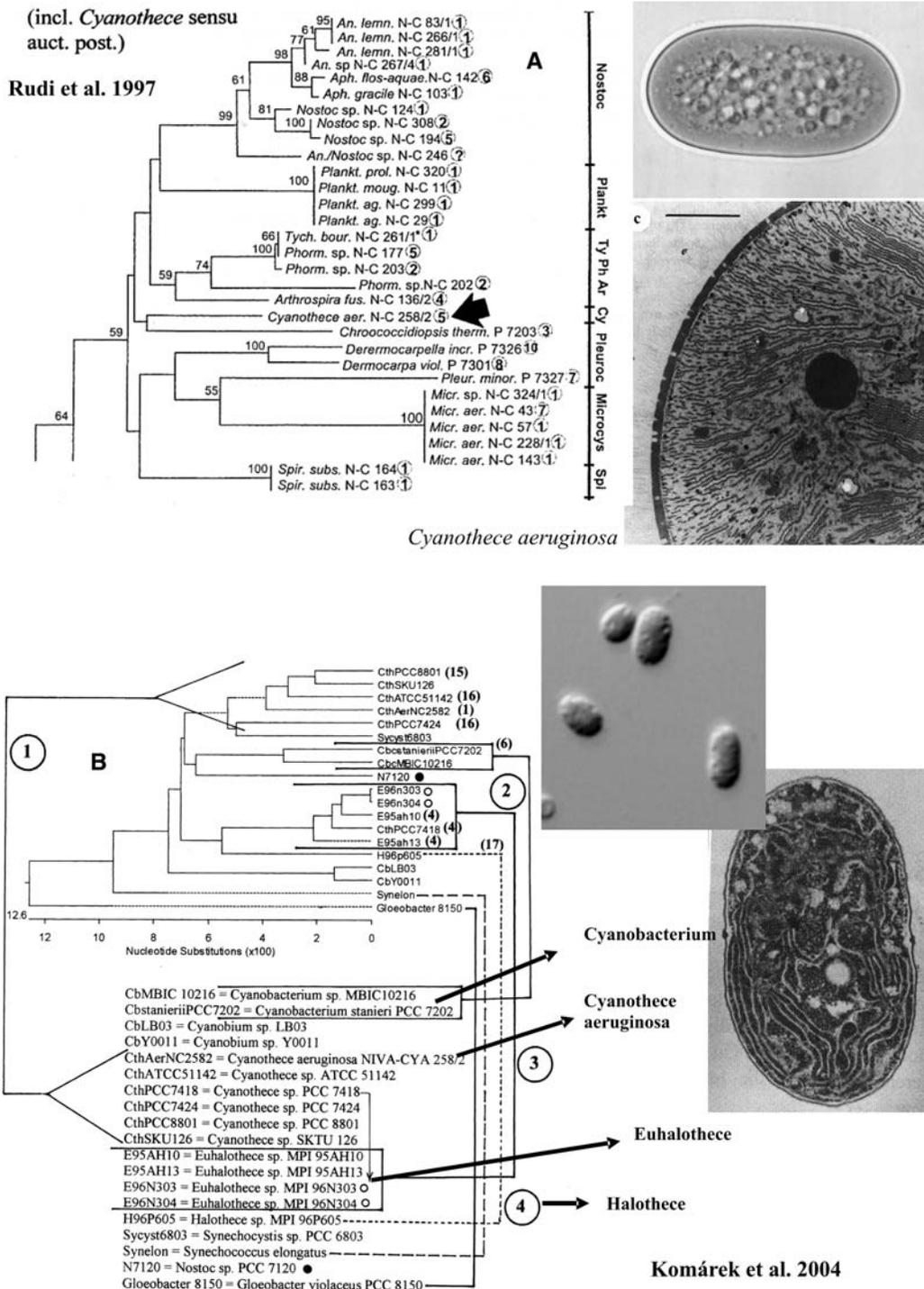


Fig. 4 Basic review of *Cyanotheca* like cyanobacteria: **A** Phylogenetic tree with isolated position of the type species (reference strain) of *Cyanotheca aeruginosa* (type species of the genus *Cyanotheca*) among filamentous cyanobacteria. The phylogenetic tree according to Rudi et al. (1997), photos from

Komárek et al. (2004). **B** Review of strains designated as the genera *Halothece*, *Euhalotheca*, *Cyanobacterium* and *Cyanotheca*, from Komárek et al. (2004); 1–4 clusters classified to different genera. The phylogenetic tree from Margheri et al. (1999)

Nostocales

Many genera in nostoclean cyanobacteria are evidently heterogeneous, especially *Anabaena*, *Aphanizomenon*, *Trichormus*, *Nostoc* and others (Gugger et al., 2002; Iteman et al., 2002; Hrouzek et al., 2005; Rajaniemi et al., 2005; Willame et al., 2006; etc.). The results are included partly in another review (Komárek, 2009).

Examples of new described genera

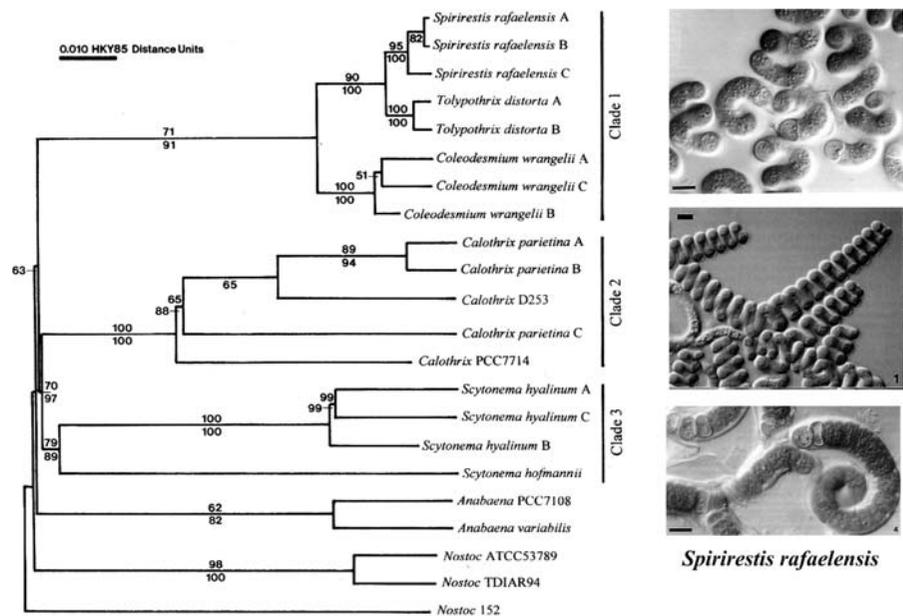
Modern investigation of various biotopes has yielded significant new data concerning cyanobacterial diversity. New genera and morphotypes were discovered using new molecular methods combined with precise morphological analyses, particularly among taxa from extreme and tropical habitats. These morphotypes cannot be included in any previously known and/or genetically revised genotypes. Three methodological procedures are used to describe new genera in recent papers:

- (1) New genera can be described according to only morphological characters (based on botanical nomenclatoric rules) if they cannot be included by their phenotype into any known and

genetically confirmed genus. In the future, they must be confirmed by molecular methods, and this support is very feasible or likely. Up to now, all generic entities, defined by revised morphological markers, have been found to be genetically separated clusters (*Cylindrospermopsis*, *Planktothrix*, *Arthrospira*, *Limnothrix*, *Tycho-nema*, *Trichormus*, etc.). Two new genera, *Catenula* Joosten (2006) from planktic habitats in the Netherlands and the tropical genus *Macrospermum* Komárek (2008), were recently described using this method.

- (2) New generic names appeared in prominent molecular or biochemical studies based on strains, which started to be used as important models and experimental organisms. However, these did not have valid descriptions or proper morphological and ecological comparison with other genera. Such genera are possibly acceptable, but they must be validly described with all pertinent characteristics, and their nomenclature must be resolved. Ignoring nomenclature leads to confusion. Such genera include, e.g. *Thermosynechococcus* Katoh et al. (2001; Fig. 1) or *Crocospaera* Zehr et al. (2001).
- (3) Acceptably, there appear to be more and more descriptions of new genera in the literature

Fig. 5 Example of the new described genus according to polyphasic method (combined molecular, morphological and ecological markers). The clade 1 contains the genera classified into the family Microchaetaceae. Phylogenetic tree and photos after Flechtner et al. (2002)



16S sequence similarity of *Spirirestis* to related *Tolypothrix* = 90.4 - 91.4%

satisfying all the modern criteria. The authors use combined molecular and phenotype markers and guidelines incorporating both botanical and bacteriological nomenclatoric rules to avoid questions and doubts about validity. Examples of such recently published genera are, e.g. *Spirirestis* Flechtner et al. (2002) (Fig. 5), *Acaryochloris* Miyashita et al. (2003), *Chlorogloeocystis* Brown et al. (2005), *Rexia* Casamatta et al. (2006) or *Brasilonema* Fiore et al. (2007).

Species and strain concept

While sequencing by 16S rRNA gene can be used as a standard genetic approach to delimitate cyanobacterial genera, a similar method is problematic for populations and species. It is evident that ecologically and morphologically stable and recurring (in various localities and over time) morpho- and ecotypes occur within various genera, but their diversification process was evidently different within generic clusters from different habitats. All populations of cyanobacteria are continually changing and evolving. The horizontal exchange of genetic material (Rudi et al., 1998; Barker et al., 1999; Hayes et al., 2006) and rapid adaptation to changing environmental factors (Kohl & Nicklisch, 1981; Erdmann & Hagemann, 2001; Hagemann, 2002; Komárek & Kaštovský, 2003b) result in various speciation within various generic clades. This variability in adaptation combined with mutation process complicate the unique criteria for species delimitation.

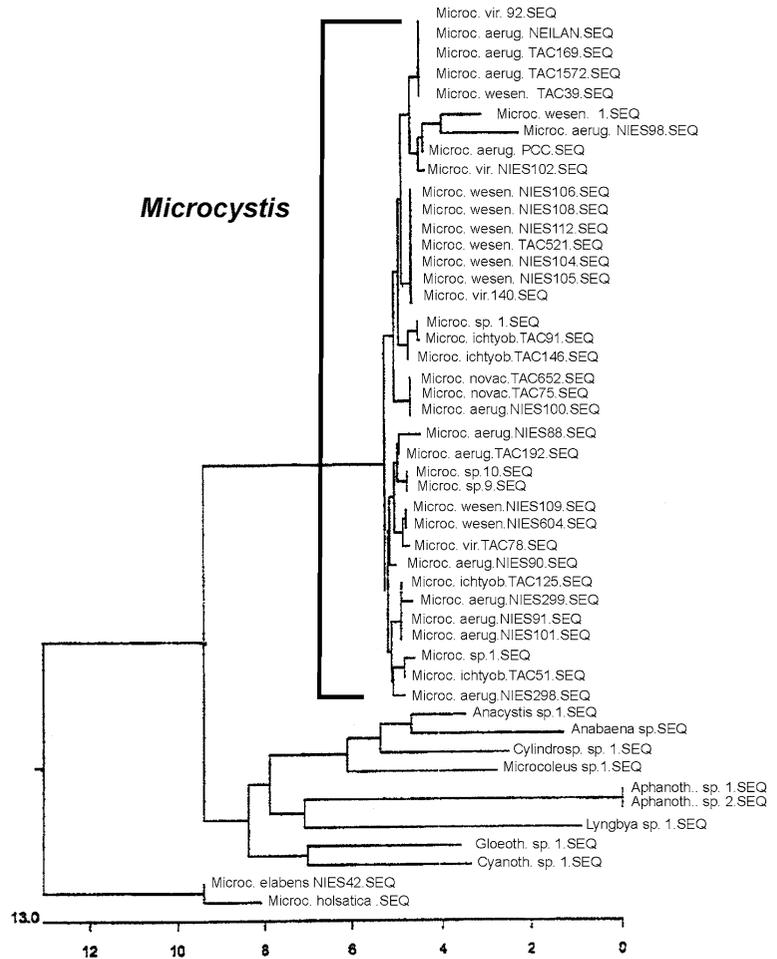
Different subgeneric clusters (traditional species) are characterized by more or less stable and recognizable ecological, morphological or biochemical modifications (over a certain time period), which are important particularly for ecological scientists (in problematics of different toxicity, primary production, activity of fixation of gaseous nitrogen, etc. in strains and species). However, there are problems in delimitation of such subgeneric clusters. Several examples of various speciation:

- Pigment types: Several genera produce different pigment mutants (green, aeruginose, olive-green, orange-yellow, red, etc.) in one population, which can stabilize in different habitats or cultures.

Classification of such types is unclear. Similar situations were described, e.g. by Kohl & Nicklisch (1981) in *Limnothrix redekei*, Skulberg & Skulberg (1985) and Suda et al. (2002) in *Planktothrix*, Waterbury et al. (1979), Six et al. (2007) and Dufresne et al. (2008) in oceanic *Synechococcus* and *Prochlorococcus* etc. Sometimes such stabilized pigment mutants are classified traditionally like species (*Planktothrix agardhii/rubescens*), but the taxonomic evaluation of such differentiation has been still commonly unclear. In several cases, we can isolate a wide spectrum of differently coloured and in cultures stabilized strains (Six et al., 2007).

- Several genera are clearly separated genetically, but subgeneric units (species) cannot be recognized by 16S rRNA gene sequencing methods. However, they contain a stable number of distinct morphotypes and ecotypes, which differ also according to secondary metabolites. Their easy recognition in natural populations is important for ecological and applied hydrobiological studies. For example, planktic and toxin-producing genera include *Microcystis* (Fig. 6) and *Planktothrix*, for which identification of various morphospecies is necessary for ecological research.
- Different genetic clusters and subclusters, separated by 16S rRNA gene sequencing method may contain morphologically very similar types, which differ only ecologically or can be scarcely distinguished based on slight phenotypic variation. Such types, usually designated as cryptospecies (Sáez & Lozano, 2005; Johansen & Casamatta, 2005; Turicchia et al., 2009) are not identifiable according to morphological markers (sometimes only as ecological species), and their status also needs further discussion for taxonomic classification.
- Another case is where the genetic differences between distinct morphospecies, classified traditionally in one and the same genus, are so large that they corresponded to genetic clusters separated by more than 95% similarity from each other, but their morphology does not allow them to be separated into various genera. The characteristic example is the genus *Halospirulina* Nübel et al. (2000), which comprises one sub-cluster within the traditional genus *Spirulina* (Fig. 7). If we accept *Halospirulina*, we must divide the

Fig. 6 The phylogenetic delimitation of the genus *Microcystis*. The *Microcystis* species, well characterized by morphological and ecophysiological characters, are not distinguishable according to 16S rRNA sequencing. Phylogenetic tree derived from GeneBank NCBI 2002



whole genus *Spirulina* into more units. Almost all traditional morphospecies of *Spirulina* have the similar isolated position like *Halospirulina* and they could be therefore all classified as distinct genera. The type species of *Halospirulina* (*H. tapeticola*) does not differ phenotypically from *Spirulina subsalsa*.

- The species concept is complicated also by the fact that almost all populations and strains differ slightly one from another. Two exactly identical strains do not exist. This situation supports the idea that only strains within genera can be designated by a number or symbol, but not just the species. However, the diversity is more complicated, intrageneric clusters are very diverse, many of them must be identifiable and recognizable for ecological and experimental studies, and designation only by symbols is not acceptable.

For cyanobacterial subgeneric diversity it follows that, according to current knowledge, the category ‘species’ is useful, but its concept or definition can be probably only a conventional measure, with different criteria in different genera. The most appropriate present definition is as follows:

“Group of populations (+strains) which belong to one and the same genotype (genus), characterized by stabilized phenotypic features (definable and recognizable, with distinct limits of variation) and having the same ecological criteria. They occur repetitively (in time) in a variety of ecologically similar localities”.

Nomenclature

The Latin names of taxa are not only formal designations, but they symbolize the complex set of

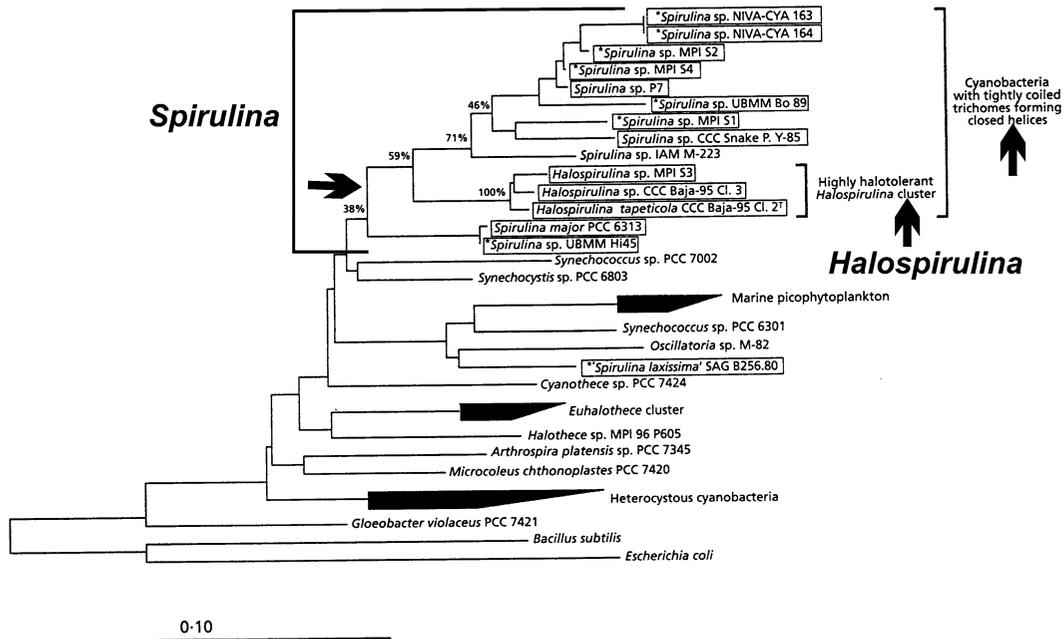


Fig. 7 The phylogenetic tree of *Spirulina* and *Halospirulina* strains. After Nübel et al. (2000) from Komárek & Anagnostidis (2005)

characteristics of different taxa, including genetic, biochemical and ecophysiological markers and morphological plasticity. Cyanobacteria were traditionally identified by the Botanical Nomenclature Code, but since their bacteriological nature was stressed, the tendency to apply the Bacteriological Code was intensely promoted (Stanier et al., 1978; Oren, 2004; Oren & Tindall 2005). Because the respective nomenclatural committees did not propose any compromise or come up with a new convenient proposal, many authors use combined instructions and recommendations of both Codes for descriptions of new taxa (e.g., Fiore et al., 2007; etc.). However, new taxa appear that do not adhere or respect either Code. These often appear in experimentally oriented articles. Such studies sometimes have high scientific value, but the ignorance of formal taxonomic prescriptions substantially devalues these investigations and creates a lot of confusions. Examples of such insufficiently described taxa are *Anacystis nidulans*, *Thermosynechococcus*, *Prochlorococcus*, *Crocospaera*, etc.

The origin of cyanobacteria and their basic cytological structure is, of course, bacterial, but their ecological, biological and morphological features are very precise. Cyanobacteria play a distinct role as phototrophic primary producers in natural ecosystems,

just like other microscopic algae. They have both photosystems, thus a plant-like photosynthetic system, and many types form morphologically diversified, multicellular individuals with specialized cells, not known in other bacteria. In the last few years, efforts of nomenclatorists have tended towards attempting to establish a unified nomenclatural system for all groups of organisms, but the idea of creating special nomenclatural rules for cyanobacteria (respecting demands of both, botanical and bacteriological Codes) seems to be more logical and practical. In agreement with this conclusion, a special nomenclatural guide was initiated from International Association for Cyanophyta/Cyanobacteria Systematics and Ecology (IAC) symposium in 1989 and designed and published (Komárek & Golubić, 2005; www.cyanodb.cz). Unfortunately, it has been a priori rejected by nomenclatural specialists from both communities and thus it is not yet used by specialists in cyanobacterial taxonomy.

Proposals to completely eliminate the names of taxa from cyanobacterial research were particularly apparent in bacteriological circles. In principle, there is no good a reason to not accept another convenient system for the registration of cyanobacterial taxa, based on numbering or various other coding. But it is possible only if this system is at least as convenient as

the traditional system of names, is applicable to the entire diversity of cyanobacteria from both natural habitats and cultures, and has potential for all users of a cyanobacterial classification system, including especially ecologists. In case that such a system will be designed, it can surely be accepted, but it must be improved in all aspects, emphasizing the knowledge of cyanobacterial diversity. Various chips and molecular arrays for precise coding of cyanobacterial genotypes certainly will be increasingly used. However, replacement of the present nomenclatural system by an inconvenient system, which does not express all cyanobacterial diversity, is premature and irresponsible. A good example is the problematics of strains PCC 6803 and PCC 6308 of *Synechocystis* described above (Fig. 2). The correct taxonomy and designation of strains without the help of binomial nomenclature is still now hardly possible. Nomenclatural practice is connected also with the problem of arbitrary use of names in experimental works. Many model strains are identified quite arbitrarily, unfortunately even those which were already sequenced. The incorrect names are still often used in the Database of Sequences (GenBank), as well as in biochemical and molecular studies. Of course, taxonomic methods evolve and the taxonomist must continually update to use the most modern methods. This practice results in many necessary nomenclatural changes, which are an integral and indispensable part of modern taxonomic work, and ideally should be continually applied to all strain collections (strain designations) and experimental studies. But there does not exist any authority, which can implement such changes, and experimental workers completely undervalue such revisions (e.g., *Anacystis nidulans* = *Synechococcus nidulans*, *Anabaena variabilis* = *Trichormus variabilis*, omitting such genera as *Cyanobium*, etc.). Ignorance of corrections and use of revised and valid names is the same error as the use of incorrect application of chemical or physical symbols, or use of old-fashioned methods.

Concluding remarks

Taxonomic classification is the only way to evaluate the diversity of all natural populations and strains on a genetic (molecular) background, combined with stable cytomorphological and ecophysiological

markers. The use of computers and databases is the most progressive method for future taxonomic registration.

The modern system of cyanobacteria must be based on the molecular definition of genotypes (= basic clusters with a similarity index of $\pm 95\%$ or less using the 16S rRNA gene sequencing, considered the standard method), which correspond to the traditional taxonomic category of 'genus'. Obligatory separation of genera must be done also by at least one diacritical phenotypic character (or autapomorphic set of characters) and ecological, ecophysiological, ultrastructural and biochemical characteristics, which are included as an integral part of the generic definition.

This revised system confirms in principle the traditional cyanobacterial genera, which must be continually corrected and updated (Hoffmann et al. 2005). This revised system justifies the definition of numerous new generic entities, which have arisen through genetic (and morphological) separation of existing genera, and/or are described from newly studied habitats, extreme ecosystems or by revision of cultured material.

The species concept is not uniform and must be modernized according to the diverse nature of various genera. The characterization of species can then be appreciated rather conventionally within different genera.

Use of Linnean (binomial) nomenclature is still quite indispensable for the characterization and understanding of the entire (both natural and cultivated–experimental) diversity of cyanobacteria. No other convenient system exists. However, the demand for transferring confirmed taxonomic and nomenclatural revision into ecological and particularly experimental studies is highly desirable. Molecular cyanobacteriologists pay attention to the use of molecular methods for taxonomic articles, but unfortunately they often do not accept the results of modern investigations into cyanobacterial diversity in their studies and strain collections.

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