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[Review]

Cyanobacterial Taxonomy: Current Problems and Prospects for the Integration of Traditional and Molecular Approaches

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The application of modern ecological, ultrastructural and molecular methods, aided by the cultivation of numerous cyanobacterial morphotypes, has substantially changed our knowledge of these organisms. It has led to major advances in cyanobacterial taxonomy and criteria for their phylogenetic classification. Molecular data provide basic criteria for cyanobacterial taxonomy; however, a correct phylogenetic system cannot be constructed without combining genetic data with knowledge from the previous 150 years research of cyanobacterial diversity. Thus, studies of morphological variation in nature, and modern morphological, ultrastructural, ecophysiological and biochemical characters need to be combined in a "polyphasic" approach. Taxonomic concepts for generic and infrageneric ranks are re-evaluated in light of combined phenotypic and molecular criteria. Despite their usefulness in experimental studies, the limitations of using strains from culture collections for systematic and nomenclatural purposes is highlighted. The need for a continual revision of strain identification and proper nomenclatural practice associated with either the bacteriological or botanical codes is emphasized. Recent advances in taxonomy are highlighted in the context of prospects for understanding cyanobacterial diversity from natural habitats, and the evolutionary and adaptational processes that cyanobacteria undergo.

Key Words: Cyanobacteria, molecular evaluation, modern classification, nomenclature, phenotypic characters, polyphasic approach, strains, taxonomy

Cyanobacteria (Cyanophytes, Cyanoprokaryotes) are among the most fascinating organisms in the Earth's biosphere. Their origin in the Early Precambrian was one of the most important steps in evolution (Schopf 1974a, 1974b, 1993, 1996). They are prokaryotic bacteria, however, their cells developed the plant-type photosynthetic apparatus that included chlorophyl *a* and both photosystems. The subsequent evolution of the plant kingdom is based on numerous intracellular symbioses of prokaryotic cyanobacteria with eukaryotic heterotrophs. The relative ease with which cyanobacteria enter into symbioses is a characteristic of this lineage (cf., e.g., reviews of Janson 2002; Carpenter and Foster 2002, and others). Other remarkable adaptations developed in cyanobacteria enabled them to colonize variable and extreme habitats in Earth ecosystems (Carr and Whitton 1973; Fogg *et al*. 1973; Whitton and Potts 2000; Rai and Gaur 2001). Cyanobacteria are the only oxyphototrophic organisms to contain Nif-genes, and mechanisms and adaptations for fixation of gaseous nitrogen. They participate in the formation of travertine and stromatolites, and a substantial part of limestone deposits over the Earth results from their metabolic activity. Several types are adapted to colonise hypersaline locations, hot springs up to over 70°C, or to enormous oscillations of temperatures and periodical drying in both cold and hot deserts. They are able to produce toxins, which can function in competitive interactions in various ecosystems. Most noteworthy is the extraordinary vitality of this special bacterial group which has not declined during its existence that has spanned billions of years.

The massive developments of cyanobacterial populations have also become important because of increasing eutrophication of the biosphere. Thus there is major concern regarding "water blooms" in freshwaters of all continents, unexpected developments of cyanobacterial types in plankton and littoral zones of seas and oceans (e.g., picoplanktic *Prochlorococcus*, or periphytic *Lyngbya majuscula*), and cyanobacterial crusts in semideserts (*Leptolyngbya*, *Microcoleus*, *Nostoc*). From a scientific perspective the most challenging questions revolve around evolutionary strategies, the survival and diversification of cyanobacteria over the long period of their existence, and evaluation of their present diversity in nature (cf.

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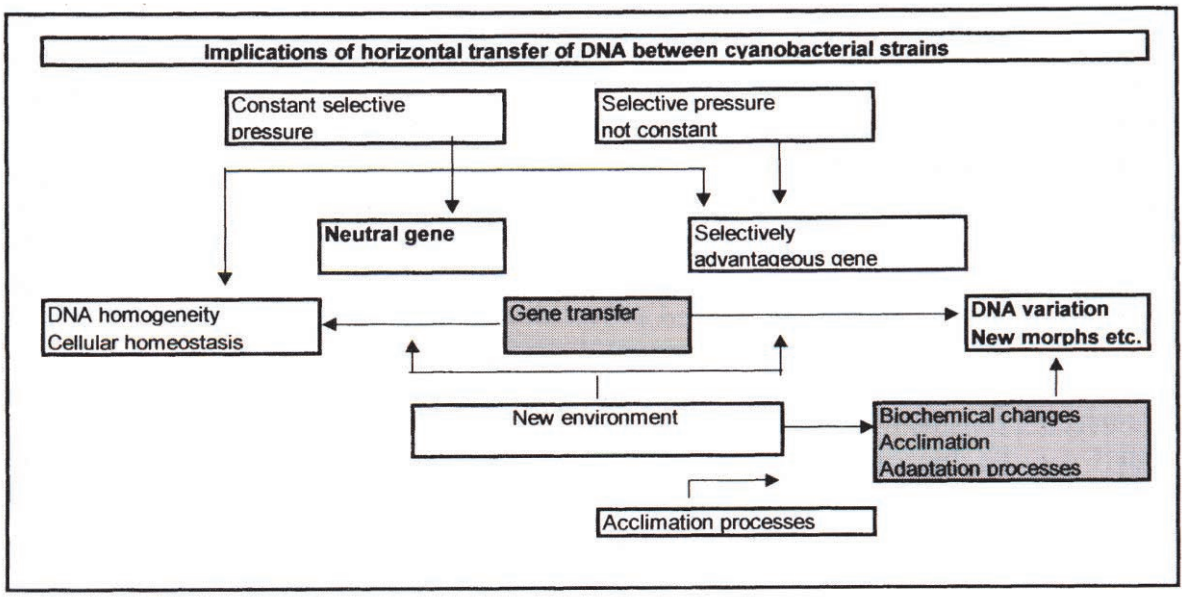

Fig. 1. Scheme of horizontal transfer of nucleic acids (DNA) between cyanobacterial strains, and acclimation strategy as a background of the continual development and origin of new cyanobacterial types (species) during long-term cyanobacterial evolution (from Komárek and Anagnostidis 2005; derived from Rudi *et al.* 1998, 2002, scheme based on Jakobsen 2002; acclimation and biochemical processes based on Hagemann 2002).

Schopf 1974, 1993).

The evolution of cyanobacteria (without any sexual reproduction) is a continual process. This is based on the horizontal transfer of nucleic acids (DNA) between cyanobacterial strains and within populations (Rudi *et al.* 1998, 2000; Barker *et al.* 1999; Hayes *et al.* 2006), combined with rapid acclimation and adaptation (Erdmann and Hagemann 2001; Hagemann *et al.* 2001, Hagemann 2002; Komárek and Kaštovský 2003) (Fig. 1). This process was called "static evolution" (Knoll and Golubič 1992; Schopf 1993, 1996; Castenholz 2001), or designated as "variation on a given theme" within a range of cyanobacterial genetic, metabolic and structural patterns. It is combined with flexibility of cyanobacterial genomes to acclimate to a wide range of environmental conditions. Sudden stress may result in a breakdown of numerous cellular functions; however, during subsequent acclimation cellular processes become readjusted, or new proteins are induced to cope with the conditions (Hagemann 2002). This process explains the long-term diversification and vitality of cyanobacteria, and the continual rapid development of new morpho- and ecotypes. A consequence of this process is the complexity of cyanoprokaryotic diversity, in which numerous ecologically specialised genotypes and morphotypes occur. Such types are stable for a period under constant conditions; however, rapid change can occur after major environmental perturbation. From this point of view, the evolution of cyanobacteria and their phylogenetic relationships are regulated by specific metabolic and genetic processes.

Using a variety of molecular, ecophysiological and morphological approaches, modern taxonomy provides combined methods for cataloguing and understanding the Earth's biodiversity. Early taxonomic classifications of cyanobacteria were elaborated based on distinct morphological characters. The introduction of modern methods in last decades of 20th century substantially changed our understanding of these organisms. The electron microscope, modern ecological investigations, introduction of numerous cyanobacterial types in cultures, explanations of toxicity, and especially molecular methods, stimulated the development of cyanobacterial research and influenced their taxonomy. Numerous "enigmatic" characters were explained (i.e., origin of baeocytes, ultrastructure of gas vesicles, cell wall structure, explanation of chromatoplasmic region in cells, keritomy etc.), and new data provided insight into the taxonomic relationships among different cyanobacterial types. Consequently, criteria for their classification had to be re-evaluated.

Molecular (phylogenetic) data provide a basic criterion for taxonomic classification. However, it is overly simplistic to assume that a correct phylogenetic system will emerge without the careful combination of genetic data with morphological diversity and variation, ecological and ecophysiological characters and ultrastructural

information. The application of convenient formal prescriptions for designation of taxa is another problem; their application is essential, however, the arbitrary use of botanical or bacteriological nomenclatoric rules produces many misinterpretations and confusions. Many experimental scientists do not use formal nomenclatoric prescriptions, and designate experimental strains with taxonomic binomials based on incorrect identifications. Alternatively, new names are have been coined without regard to the necessary nomenclatural rules (e.g., *Crocosphaera*, *Thermosynechococcus*, *Halothece* and others). The sense of name (symbol of a taxonomic unit) is to express a particular taxonomic status; it refers to a certain genetic position and certain set of biochemical, morphological and all other characters, connected with this genetic entity. Because strain designation is often based on arbitrary names selected from old, unrevised literature, there are numerous publications where the names used refer to quite different organisms than these names represent in a formal taxonomic sense (e.g., *Anacystis nidulans*, *Anabaena variabilis*, numerous *Cyanothece*-strains, etc.). This practice is unfortunately common because the formal taxonomic classification and nomenclature is often regarded as "old fashioned". The correct taxonomic identification belongs among the most serious problems in modern cyanobacterial science. Regardless of these issues, modern criteria must be applied to cyanobacterial taxonomy, and the resulting names need to be consistent with formal nomenclature. Hence cyanobacterial classification must be revised and based on studies that include molecular data. The necessary synthesis ("polyphasic" evaluation of diversity) is sometimes difficult, but only this combined methodological approach will provide a revised and logical classification system. This is an important component of a fundamental understanding of cyanobacterial diversity, and the functioning of these organisms in the biosphere.

Combined molecular and traditional approach

Already early molecular and biochemical evaluations of cyanobacterial strains indicated a general congruence of genotypic and phenotypic variation (Rippka *et al.* 1979; Wilmotte and Golubić 1991), and later studies confirmed this logical agreement. Nucleic acid sequencing of strains and populations is without doubt the basis for modern classification of cyanobacteria, but the criteria from traditional taxonomy (from the "classical" system) can not be omitted. However, because molecular approaches are considered as more predictive, and because the parallel careful evaluation of phenotypes is labour intensive, and not typically part of the training of young scientists, it is often neglected in modern experimental or ecological studies. This is despite the fact that the evaluation of morphological variability of cyanobacteria is necessary for understanding their diversity. Precise phenotype identification requires considerable time and experience, but it is also necessary for the correct evaluation of their ecological function and for the construction of a modern system. Work based solely on molecular characters can provide insight into existing genotypes and their approximate distribution in various ecosystems. However, without the complementary morphological approaches, molecular data alone have limited capacity to recognize the ecological importance of different genotypes, the morphological variability *in situ*, the ongoing adaptational processes and the continual origin of new cyanobacterial eco- and morphotypes.

The combination of both molecular and morphological approaches for modern cyanobacterial taxonomy is therefore essential. For such evaluation of cyanobacterial diversity the following approaches should be used:

(i) molecular analyses, mainly those concerning phylogenetic relationships, diversity of genotypes, diversification processes and speciation;

(ii) morphological diversity including variation in nature and in culture;

(iii) ecological, ecophysiological and biogeographical limits;

(iv) ultrastructural studies;

(v) biochemical characters and information about special metabolic processes (production of secondary metabolites, adaptation processes, etc.);

(vi) correct formal designation of taxa that respects Bacteriological and/or Botanical rules of nomenclature.

The first three and the sixth approach should be obligatory. On the one hand, such a combined approach to taxonomic classification does not mean that purely molecular or purely floristic studies (with precise documentation) are without merit. On the other hand, comprehensive taxonomic syntheses and revisions to classifications should include the combined taxonomic approach outlined above.

Congruence among molecular characters of various phylogenetic clusters and morphological and ultrastructural features have been found particularly in coccoid and simple trichal cyanobacteria (Komárek and Čáslavská 1991; Komárek and Kaštovský 2003; Hoffman *et al.* 2005a). The principal arrangement of thylakoids

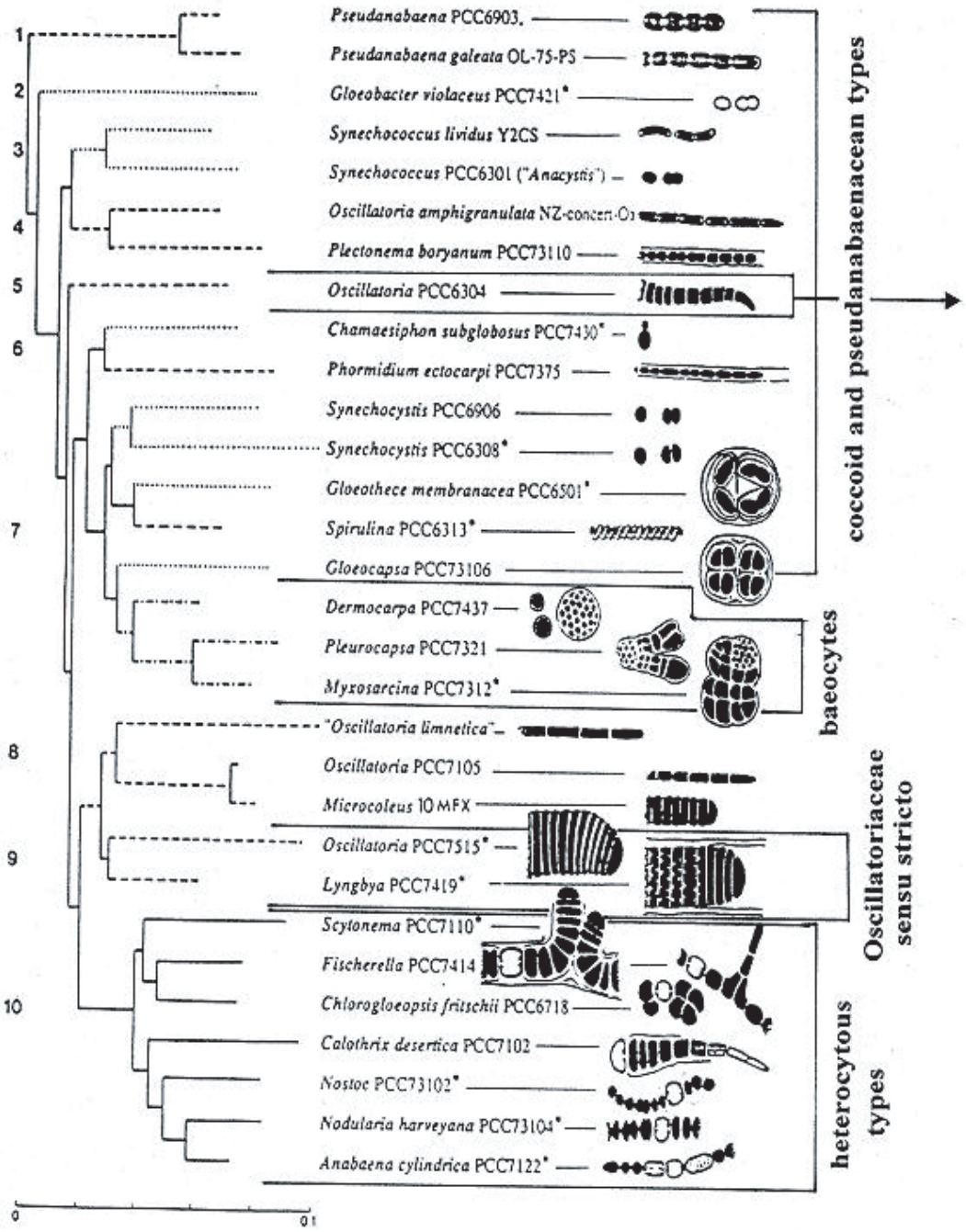

Fig. 2. Phylogenetic relationships among selected cyanobacteria based on RNA-sequencing data of Giovannoni *et al.* (1988), compared to morphological features (according to Wilmotte and Golubić 1991).

(parietal vs. radial or irregular) is very stable for different genetic clusters, characterised by 16S rRNA sequencing (Figs 4, 6, 14). The characteristic thylakoidal patterns can be modified to some extent by environmental factors (number and density of thylakoids, agglomeration of thylakoids near the outer cell walls in heterocytous types, widened thylakoids), but the principal arrangement remains stable for different genotypes. At least two evolutionary lines in simple cyanobacteria can be recognized. These are characterized solely by thylakoidal arrangement, with each line comprising both coccoid and filamentous, non-heterocytous genera (Komárek and Kaštovský 2003; Hoffmann *et al.* 2005a) (Fig. 6). The more complex filamentous types without heterocytes (Oscillatoriaceae *sensu stricto*) and heterocytous genera have a more or less uniform and irregular thylakoid arrangement.

The congruence between 16S rRNA molecular

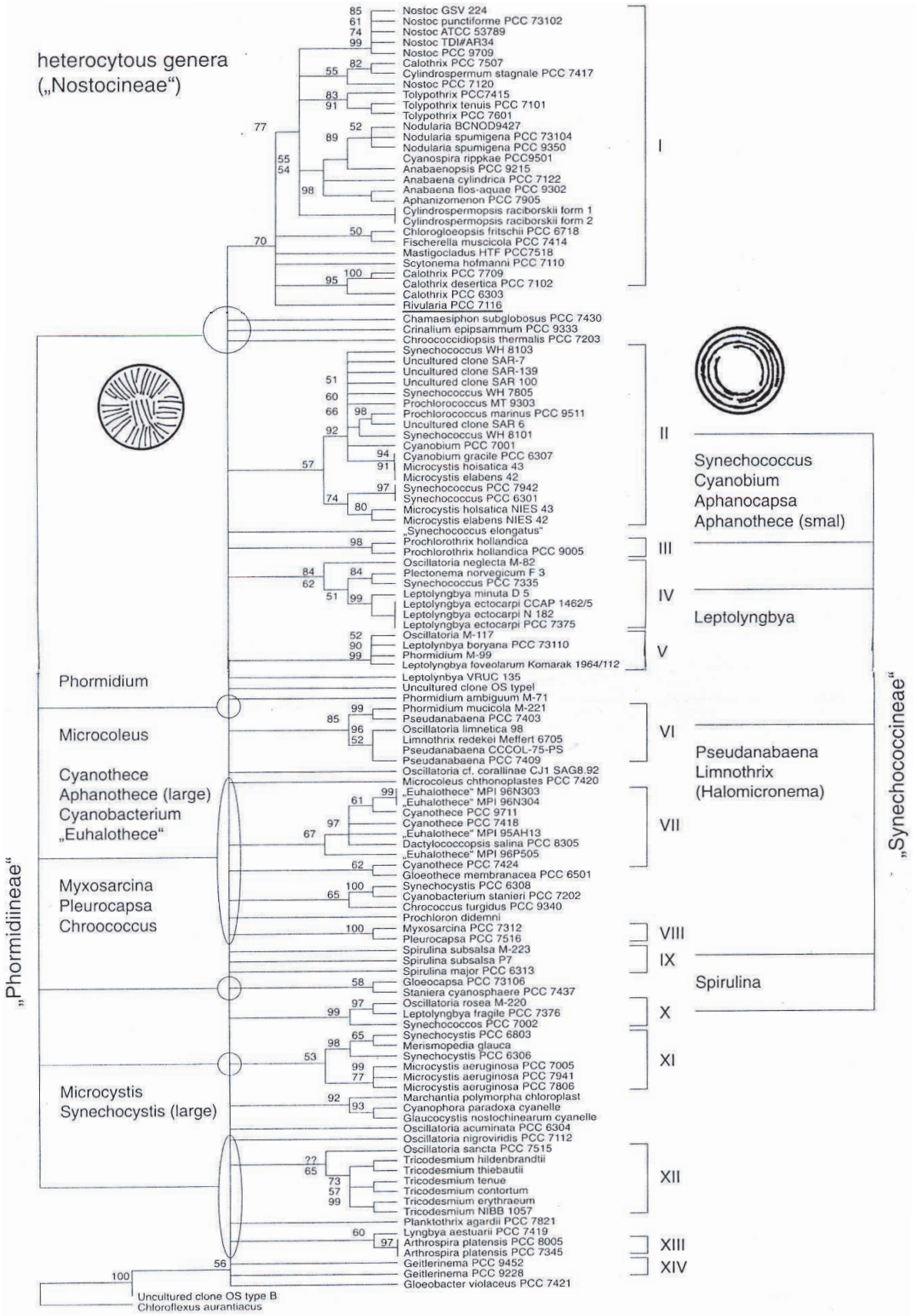

Fig. 3. Phylogenetic tree reflecting modern genetic relationships within cyanobacterial strains (genera) (from Castenholz 2001). Clusters are compared with the revised system and coincides with cell ultrastructure. Numerous strains were revised, but the taxonomic names remained unchanged (from Hoffmann *et al*. 2005a).

Abbreviations: **pl.** = planktic, **per.** = periphytic, **mot.** = motile. New defined genera: **1** = joined to *Pseudanabaena*, **2** = *Geitlerinema* (motile) or *Jaaginema* (immotile), **3** = *Limnothrix*, **4** = *Leptolyngbya*, **5** = *Planktolyngbya*, **6** = *Leibleinia*, **7** = *Heteroleibleinia*, **8–9** = *Planktothrix*, **10–12** = *Phormidium*, **13–14** = *Oscillatoria*, **15** = *Lyngbya*.

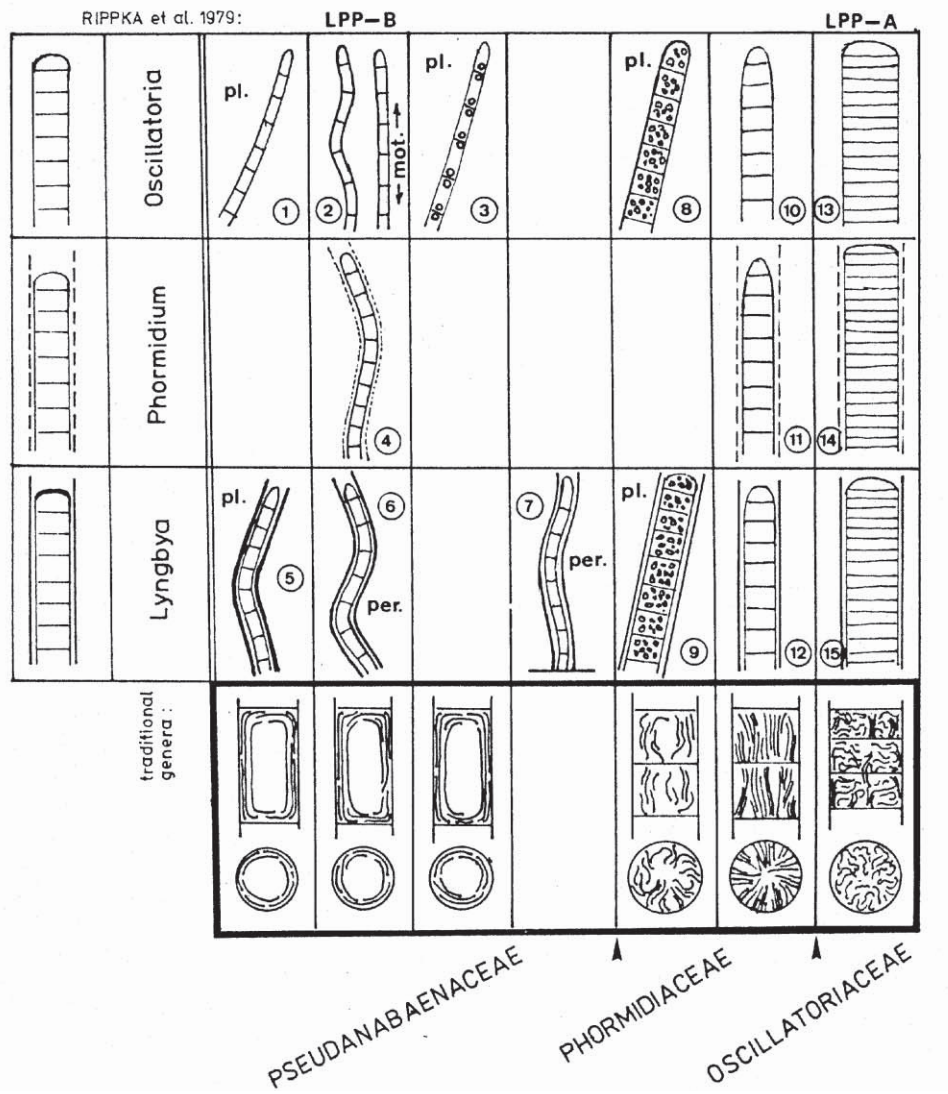

Fig. 4. Comparison of three traditional genera (*Oscillatoria*, *Phormidium*, *Lyngbya*) based on the absence or presence (facultative or obligatory) of a sheath (Geitler 1932), with new classification of oscillatorialean genera and corresponding families; characteristic thylakoid patterns given for different genera (from Komárek and Čáslavská 1991).

sequencing commonly used for evaluation of cyanobacterial diversity and traditional phenotype taxonomy was demonstrated primarily at the generic level. This conclusion, which was inherent in the first genetic evaluations (Wilmotte and Golubić 1991) (Fig. 2), was confirmed by later investigations. The first phylogenetic trees separated already clearly heterocytous types from coccoid and simple trichal genera (Wilmotte and Golubić 1991; Turner 2001, Castenholz 2001), and identified several groups characterized by prominent morphological characters (*Oscillatoria*/*Lyngbya* complex with thick trichomes and short cells, group of genera producing baeocytes, etc.) (Figs 3, 4). Numerous discrepancies (mixture of simple coccoid and trichal types) occurred, especially among coccoid and simple filamentous genera with thin trichomes (cf. Castenholz 2001). This pointed to a need for a re-evaluation of various morphological characters, or of incorrect identification of strains. For example, the traditional ("Geitlerian") genus *Oscillatoria* comprises all trichal types without sheaths and without heterocytes and akinetes. This concept of *Oscillatoria* did not take in account other characters, which appeared to be impor-

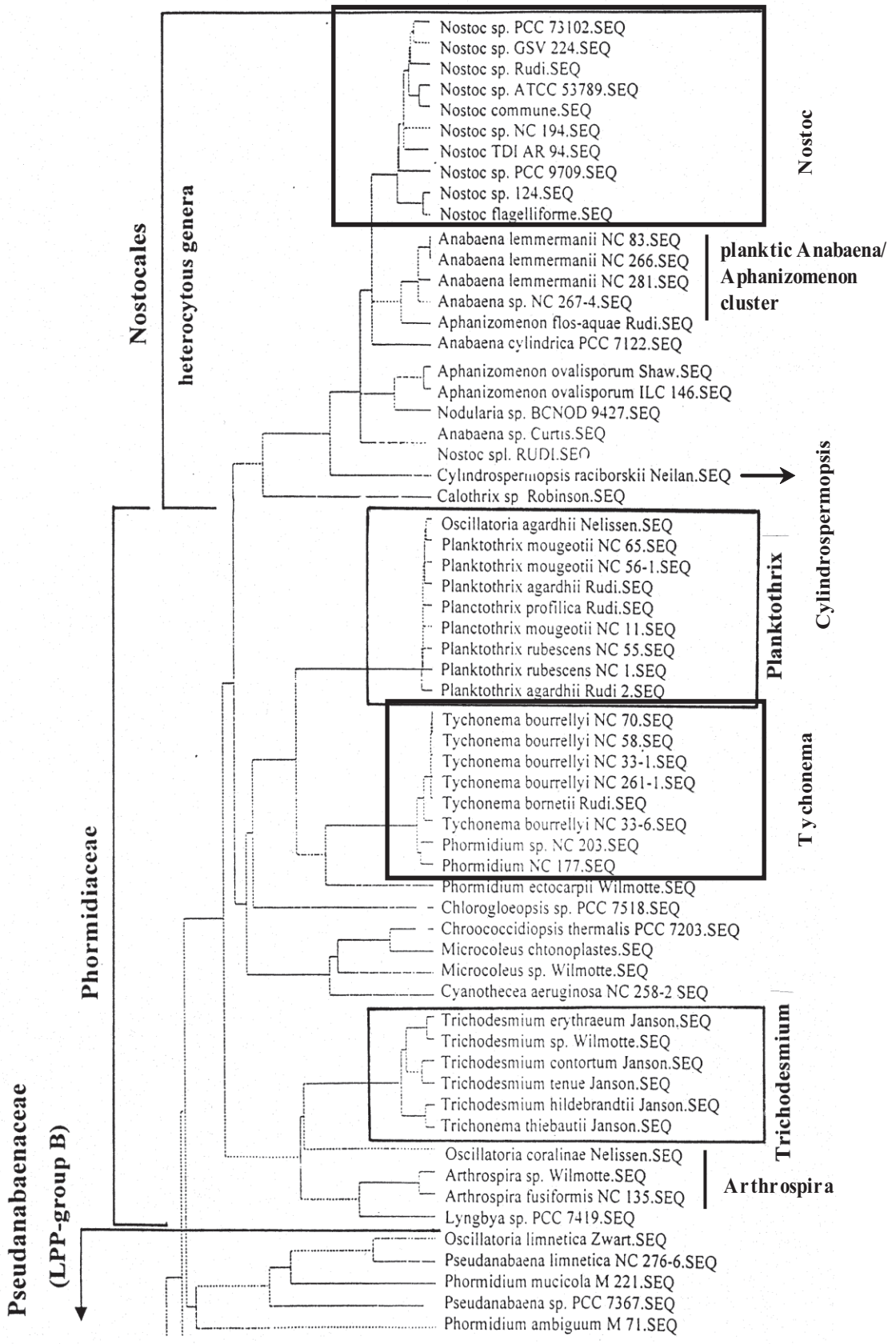

Fig. 5. Portion of cyanobacterial phylogenetic tree based on molecular sequencing, showing the integrity of traditional genera and molecular clusters (partly from Komárek and Anagnostidis 2005, derived from International GeneBank, NCBI, February 2002).

tant in the light of genetic analyses (i.e., presence of gas vesicles, thylakoid patterns, pores in cell walls, motility, length/width ratios of cells, constrictions at cross-walls, morphology of terminal cells, etc.). If we accept the revised system with re-evaluated morphological features (Anagnostidis and Komárek 1985, 1988, 1990; Komárek and Anagnostidis 1986, 1989), and if we accept revised morphological characters (as a feedback) in agreement with molecular sequencing, we obtain the generic (phylogenetic and phenotypic) system corresponding almost exactly to molecular background (Fig. 5). The discrepancies (e.g., in Fig. 5 the *Oscillatoria*-strain "Nelissen.SEQ" in the cluster of *Planktothrix*) are usually associated with old names, that were valid for the respective taxa before revision. More serious is that incorrect names of strains remain in culture collections, and continue to appear in phylogenetic trees without change. This situation misrepresents taxonomic advances by obscuring previous identifications. This problem is associated with all the strains designated as "thin *Oscillatoria*", "thin *Phormidium*", "thin *Lyngbya*" (= LPP group B sensu Rippka *et al.* 1979), etc. The starting point for these developments was a scheme of Komárek and Čáslavská (1991) (Fig. 4). The ongoing use of misidentified strains in culture collections gives the impression that taxonomic problems in cyanobacteria are more pervasive than they actually are. Incorrect names are still being used, and must be corrected based on subsequent studies. Unfortunately, there are no procedures for the updating and correction of misidentified strains in databases and strain collections.

In light of the above discussion it is useful to point out studies that combine the morphological and molecular approaches discussed above. Some key studies have been published, e.g., by Flechtner *et al.* (2002) on *Spirirestis*, Iteman *et al.* (2002), Gugger *et al.* (2002a, 2002b), Rajaniemi *et al.* (2005a, 2005b) and Willame *et al.* (in press) on the planktic bloom-forming *Anabaena* /*Aphanizomenon* complex (Fig. 10), Suda *et al.* (2002) on planktic oscillarioid species, Hrouzek *et al.* (2005) on *Nostoc*, Komárek *et al.* (2004) on *Cyanothece* and *Cyanobacterium*, Gugger and Hoffmann (2004) on the stigonematalean types, and Abed *et al.* (2002) on the new genus *Halomicronema*.

Importance of strains

The use of pure cultures of cyanobacteria has become an essential component of taxonomic studies. The modern molecular criteria are derived mostly and necessarily from the study of cultured strains. This does, however, also contribute a major source of confusion and emphasizes the need for correct and careful selection of experimental strains in all experimental studies.

The transfer of numerous natural populations in culture and their long-term maintenance is fraught with difficulty. Thus, their use for taxonomic purposes must be carefully considered. Different species have different ecological demands, and they have differential adaptations to the conditions at their source locality. Therefore they may have differential responses to the transfer into standardized conditions of cultivation. Consequently, the transfer of cyanoprokaryotic genotypes into culture is usually stressful, and leads to physiological adaptations not observed in nature (cf. Hagemann 2002). It has also been noted that no two strains are identical, even if they are isolated from the same locality (Komárek 1972; Kohl and Nicklisch 1981) (Fig. 7). Isolated strains are particularly stressed when transferred to standardized culture conditions from ecologically distinct (extreme) habitats. Thus the act of culturing wild strains can lead to selection of ecophysiological and morphological modifications, which are not necessarily representative of the original population. Standardized culture conditions can change both morphology and ecophysiological characters. The extent to which these changes are based on genetic mutations or merely the selection of particular genotypes remains to be established. Recently, methods enabling preservation of genotypes in cultures were tested. Cryopreservation is considered as the most prospective from these methods (Park 2006).

Another issue is the problematic designation of strains. This is variable in different strain collections and experimental laboratories, and the application of taxonomic names for isolated strains is often perfunctory. To prevent confusion, binomial nomenclature and names for taxon should be used and these names should agree with modern taxonomic usage. Below are two examples where antiquated names of strains has resulted in considerable confusion.

(i) The model strain of "*Anacystis nidulans*", isolated by Kratz and Allen (Kratz and Myers 1955; Starr 1964) has been used in several hundred studies as an experimental model. The taxonomic identification was incorrect, because the strain does not correspond or to the species *Aphanothece nidulans*, from which the epithet "*nidulans*" was derived, nor to the generic diagnosis of the genus *Anacystis* (Padmaja and Desikachary 1967; Pringsheim 1968; Komárek 1970; Bourrelly 1970). According to all

taxonomic criteria it belongs to the genus *Synechococcus*. Regardless, this strain has appeared with the incorrect scientific name in different culture collections under numerous numbers and designations: ATCC 27144, PCC 6301, SAUG 1402/1, CCALA 188, UTEX 625 (from which is derived PCC 7942 [*A. nidulans* R2]; other designations appear in experimental papers from various laboratories. When several of these strains from different collections are compared, they show different characters (Fig.11).

(ii) The model strain PCC 8801, designated as "*Cyanothece* sp." is cultured in other collections under the designations RF 1 and AF 296873 (and its relation to strains PCC 5501 and AF 296872 are not clear). This strain does not correspond phenotypically with the genus *Cyanothece* (with the type species *C. aeruginosa*), the reference strain of which (NC 258) has very distant position in the phylogenetic tree from the strain PCC 8801 (cf. Komárek *et al.* 2004), and also differs morphologically and ultrastructurally.

The discrepancies with strain designations and the disagreement between genotypic status of strains and their taxonomic names is therefore a substantial problem. Taxonomic names are based on the type method, and their misapplication is misleading and results in major confusions. The traditional system is based mostly on the morphology and ecology of natural populations collected from natural habitats, but many morphological characters have been demonstrated to be of no or limited use in modern investigations. Regardless of the problematic taxonomic value of some traditional morphological features, numerous experimental and molecular studies use names (at least, generic ones) derived from the traditional system (cf. Castenholz 2001). Strains often have provisional identifications according to "old" characters from nature; the designation of different geno- and phenotypes by the same name is unfortuantely quite common. In addition. strains selected for molecular studies are often based on cultured isolates that have not been carefully identified.

Concept of genera

Sequencing of 16S rRNA has confirmed the existence of several morphologically uniform and well-defined traditional genera including *Microcystis* (Fig. 12), *Planktothrix*, *Tychonema*, *Microcoleus*, *Arthrospira*, *Cylindrospermum* and others (Fig. 5). However, recent results have shown that the majority of large traditional genera is heterogeneous, even when their recognition is supported by molecular sequencing. Thus morphologically similar forms classified into one generic complex according to traditional criteria appear in distant positions in phylogenetic trees after molecular sequencing. This necessitates the classification of these clades as new genera. This situation is reflected in the majority of traditional genera including *Aphanothece, Synechocystis, Synechococcus, Chroococcus, Limnothrix, Phormidium, Anabaena, Nostoc, Stigonema* and others. The re-evaluation of their diagnostic phenotypic characters is now essential.

Good examples of this re-evaluation are planktic freshwater heterocytous cyanobacteria from the traditional genera *Anabaena* and *Aphanizomenon* (Fig. 9). The separation of a typical *Anabaena*-cluster with benthic species forming mats and without gas vesicles from the planktic species with gas vesicles is necessary. On the other hand, the close position of the traditional genus *Aphanizomenon* to the planktic *Anabaena*-types (subg. *Dolichospermum*) was demonstrated (Iteman *et al.* 2002; Gugger *et al.* 2002a, 2002b; Rajaniemi *et al.*2005; Willame *et al.* in press). Moreover, the both genera, planktic *Anabaena* and *Aphanizomenon*, were found heterogeneous, and were divided in several subclusters, spread among diverse groups of the planktic *Anabaena/Aphanizomenon* complex. The questions become: Are the prominent morphological characters (e.g., prevailing spirality of *Anabaena* trichomes) characterizing known morphospecies congruent with molecular position or not? Or, are they characterized only by additional biochemical and ecophysiological markers? From previous results it follows that new morphological markers must be found for new taxonomic entities following from molecular analyses (Rajaniemi *et al.* 2005b; *Cuspidothrix*) (Fig. 10). This is further complicated by the fact that 16S rRNA represents only a part of the whole genome, whereas the stable morphological markers, which were traditionally used for distinguishing taxa at the generic level, have not yet been thoroughly explored.

In a few cases, where the new generic entities were revised primarily by cytomorphological characters, they were later confirmed as genetically unique clusters (*Planktothrix*, *Limnothrix*, *Tychonema*). Genetically supported and validly described new generic units with complete molecular and phenotypic characters have been described only rarely. Some key exceptions are *Spirirestis* Flechtner *et al.*, *Halomicronema* Abed *et al.* and *Brasilonema* Fiore *et al.* They are good examples for the future investigation of cyanobacterial genera. Unfortunately, new generic names have appeared in lit-

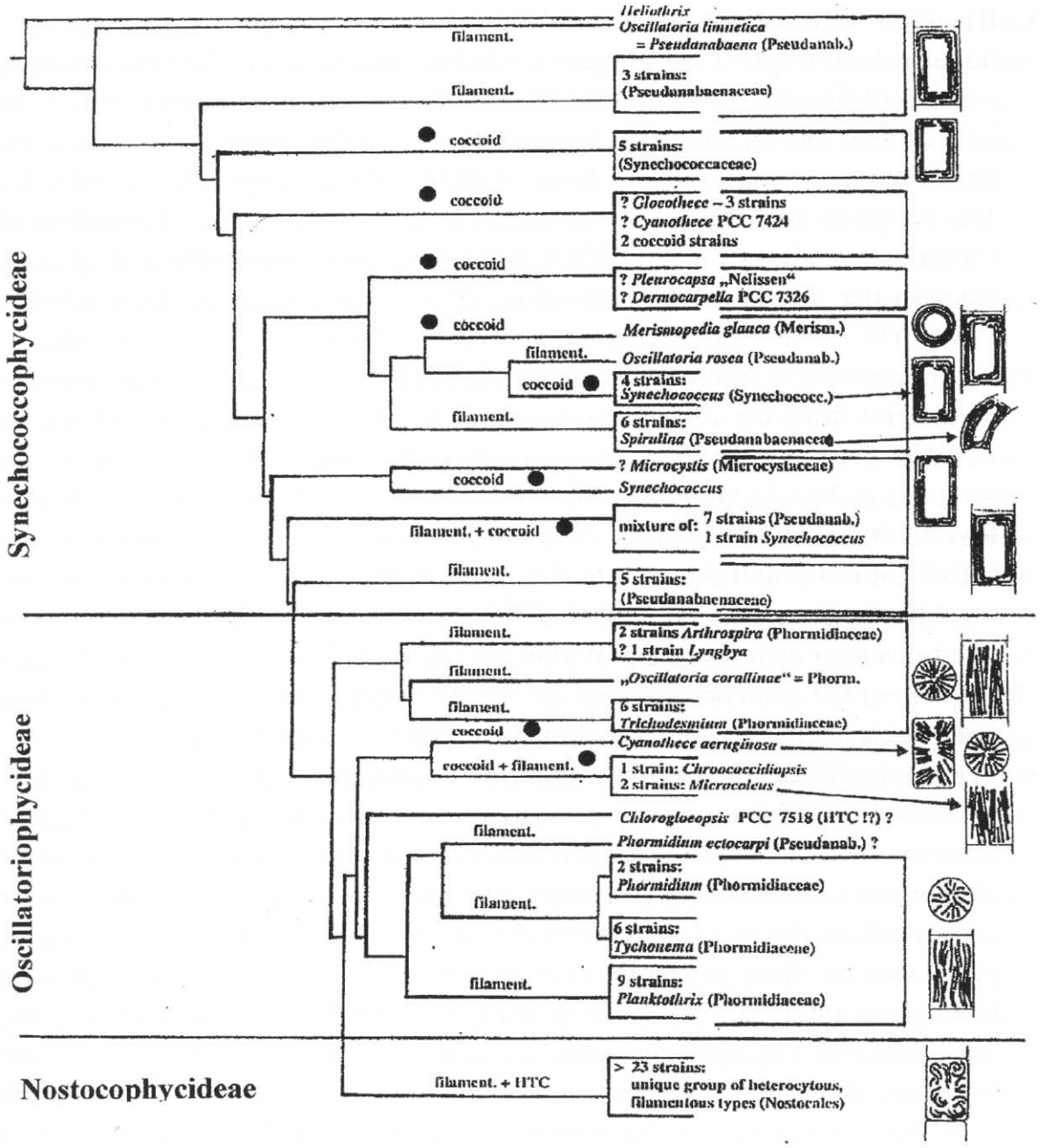

Fig. 6. Part of a phylogenetic tree derived by Megalign (DNAStar) from GeneBank of NCBI with thylakoid arrangements and coccoid types (black points) indicated (from Hoffmann *et al.* 2005b).

erature connected with important experimental model strains, but without taxonomic descriptions and without characters that would enable comparison of such units with other taxonomic entities. Notwithstanding the lack of adherence to bacteriological and/or botanical nomenclature, the impossibility of comparing such constructs with other cyanobacterial genera is *eo ipso* nonsense. The genera *Thermosynechococcus*, *Crocosphaera*, *Halospirulina*, *Euhalothece*, *Halothece* are examples of this practice. On the one hand, modern cyanobacterial taxonomists should apply modern (molecular) data in their studies. On the other hand, experimental scientists also need to respect the principles of taxonomic classification.

Another problem in cyanobacterial generic taxonomy is not respecting the rules of typification. If we use the molecular analysis as decisive for separation of genera, many heterogeneous genera must be divided into new generic entities, as mentioned above. However, the generic names (which are used automatically by all experimentally oriented scientists) must be connected

only with these clusters, which contain the type of the appropriate genus, and the other clusters must be renamed and newly typified. This practice is usually ignored, and results in many misunderstandings and errors. For instance, in the division of *Anabaena* in two distinct generic entities, the name "*Anabaena*" must be accepted only for the cluster containing the benthic species *Anabaena oscillarioides*, because it is the type-species of the genus *Anabaena*, and the cluster of planktic species must be re-named (perhaps as *Dolichospermum* with the type species *Dolichospermum flos-aquae*).

The generic name "*Cyanothece*" is used for numerous strains, of which several are important as experimental model organisms. However, the type species of this genus is *Cyanothece aeruginosa*, which belongs to a quite different generic cluster according to molecular sequencing (but also according to detailed morphological, cytological and ecological analyses) (cf. Komárek *et al.* 2004, Fig. 8). Regardless, strains designated as "*Cyanothece*" appear in many important experimental studies. Unfortunately, there is no simple way to correct this mistake. The later "*Cyanothece*"-strains should be resolved together with validation of other invalidly and poorly characterized generic units as *Halothece* and *Euhalothece*, and with taxonomic revision of the heterogeneous *Aphanothece*. Even when comprehensive revisions are published, one can not mandate that they be accepted.

The genus *Synechocystis* contains several important strains, including the famous "*Synechocystis* strain PCC 6803". This was the first cyanoprokaryotic strain for which the entire genome was sequenced. This choice of strain (and the name) was fortunate, because this strain was correctly identified and is included in the cluster, that contains the type species of the genus *Synechocystis*, i.e. *S. aquatilis*. However, the genetic position of some experimental strains is very different. For example the strain "*Synechocystis* strain 6308" belongs to another cluster, and evidently belongs also to another genus than *Synechocystis* PCC 6803. It does not mean, that the genus *Synechocystis* does not exist, but that the strain PCC 6308 must be re-classified into another genetic entity (probably in the genus *Cyanobacterium*, with which it also shares similar ultrastructure), and must be re-named (Korelusová 2005) (Fig. 11).

Without question, a modern taxonomy of cyanobacterial genera should be based on 16S rRNA sequencing. The resulting clusters correspond to traditional, morphologically characterised genera, the names of which can be used as a nomenclatoric basis for further classification. If this is to be successful, the following objectives and principles must be accepted:

- The clear generic entities (e.g., *Microcystis*, *Halothece*, *Planktothrix*, *Cylindrospermopsis*, *Cyanobacterium*, *Halomicronema*, *Arthronema*) according to both molecular and phenotype criteria should be universally accepted, and the taxonomic status of corresponding and revised "species" and strains of these genera should be corrected to agreement with their diagnostic features.
- The limit of 95% of genetic similarity derived from molecular sequencing was proposed as the criterion for separating generic cluster (Wayne *et al.* 1987, Stackebrand and Goebel 1994). This is a reasonable value, however, if similarity is close to 95%, the presence of a clear phenotypic difference, or other criteria (biochemical, ecophysiological), should be decisive. In the case of molecular groups where there are morphologically different subclusters, the classification into two (or more) subgenera is a reasonable solution. A precedence for this approach is the description of the subcluster (genus) *Cuspidothrix* from the complex of the traditional genus *Aphanizomenon*; its similarity with related subclusters was around 95% using different molecular criteria, but the phenotype markers are quite unique and without transitions to other *Aphanizomenon*-subclusters (Rajaniemi *et al.* 2005a, 2005b; Willame *et al.* in press) (Figs 9, 10). The term "form-genera" (Castenholz 2001) is adequate for such taxonomic entities.
- Several clusters exist which should be separated as distinct genera based on molecular criteria, but for which diagnostic morphological features ere not determined. The re-evaluation of morphological and cytological characters is necessary in such taxa. We must accept the reality that some generic entities will be morphologically distinguishable only after careful study. Up to now, some morphological (phenotypic) markers could be found to characterise genera, but it needs to be recognized that this will be particularly difficult in clusters of simple coccoid and filamentous types (*Synechococcus*, *Pseudanabaena*, *Leptolyngbya*, *Spirulina* and others).
- In heterogeneous genera which are distinguished based on sequencing, phenotypic characters must be revised and re-evaluated in with the context of the newly defined generic entities.

Species concepts

Cyanobacteria have greater morphological differentiation compared with other bacterial groups, but their "species" delimitation is also problematic. Numerous species have been described using only morphological characters. However, their wide variability was recognised, which resulted in the tendency of some authors to classify different similar types into large taxonomic units at specific and generic levels (Drouet and Daily 1956; Drouet 1968, 1973, 1977). Nevertheless, this "Drouet's concept" is not consistent with the variation and ecology of cyanobacteria in natural biotopes, and has been definitely discredited by modern molecular investigations. Cyanobacterial biodiversity is higher than was previously suspected.

Induced morphological variability, diversification processes and molecular (genetic) diversity influence the complex of cyanobacterial diversity in all ecosystems, and the resulting classification of species is particularly difficult. However, the genetic, ecophysiological and morphological diversity within generic clusters identified by molecular approaches is extensive and includes stable types that occur in various habitats over many generations and in distant regions. Thus, if the different roles of cyanobacterial populations in various habitats are to be understood, then infrageneric classification is necessary. The determination of criteria for such recognized morphospecies are not simple (Komárek 2003; Castenholz 1992; Gold-Morgan and González-González 2005), and the genetic criteria (limits in % of genetic similarity; Stackebrand and Goebel 1994; Wayne *et al*. 1987) can not be applied without exceptions. The use of all sharp numerical limits in taxonomy will inevitably be problematic since "intermediate" types always occur and complicate the "clear" classification. The criterion of genetic similarity must therefore be taken in account, but morphological and cytological markers must be respected and synthesized with molecular data.

A modern species concept for cyanobacteria incorporates several key ideas. First, groups of populations (+ strains) which belong to one and the same genotype (genus), should be characterized by stabilized phenotypic features that are definable, have distinct limits to their variation, AND have the same ecological demands. They should occur repeatedly (in time) in different localities with similar ecological conditions. The most sophisticated evaluation of species concepts was presented by Johansen and Casamatta (2005), and their premises should be accepted as the basis for further evaluation of infrageneric cyanobacterial diversity. They discuss phylogenetic species concepts and express the idea that "only with described species will be able to test taxonomic hypothesis".

The genera in nature comprise numerous stable morpho- and ecotypes which differ in their ecophysiological, biochemical and phenotype markers, and occur repeatedly for long periods in habitats with similar ecological conditions. Such types could be considered as a special "species". In majority of cases such species are not supported by molecular evidence, or only imperfectly or unconvincingly so. However, they are important for ecological evaluations. Since they represent existing stable types in various ecosystems, and they should be classified by some way. The terms "morphospecies" and "ecospecies" are probably the most appropriate for such entities, and their taxonomic and nomenclatoric treatment at the species level can be applied in their investigation.

This species concept is, of course, different from the species concept generally applied to eukaryotic groups. However, cyanobacterial diversity is also different from eukaryotic groups, and it is difficult to apply a single species concept to all organisms. It may be therefore, that the species concept in cyanobacteria needs a more conventional approach, at least in the present state of their classification.

To distinct morphospecies also belong such morphologically (and sometimes also ecologically) distinguishable entities. These can be genetically quite uniform (according to 16S rRNA sequences), but they occur sometimes in nature as ecologically and ecophysiologically different, stable morphotypes. For example, *Microcystis* and *Planktothrix* are such genera, in which morphological, ecophysiological and biochemically different types have been repeatedly demonstrated, but without supporting evidence from molecular sequence methods (Via-Ordorika *et al.* 2004) (Figs 5, 12). The re-evaluation of morphological and other characters is especially important in these cases. Sometimes traditionally used impressive morphological characters are quite worthless (spirality of filaments in planktic populations of *Nodularia spumigena* from the Baltic Sea), but, on the other hand, the indistinct characters (e.g., width of trichomes, constrictions at cross walls, morphology of apical cells) can be congruent with ecophysiologically different, stable types.

Separated clusters in phylogenetic trees form another type of (intra)generic diversity in cyanobacteria. In these

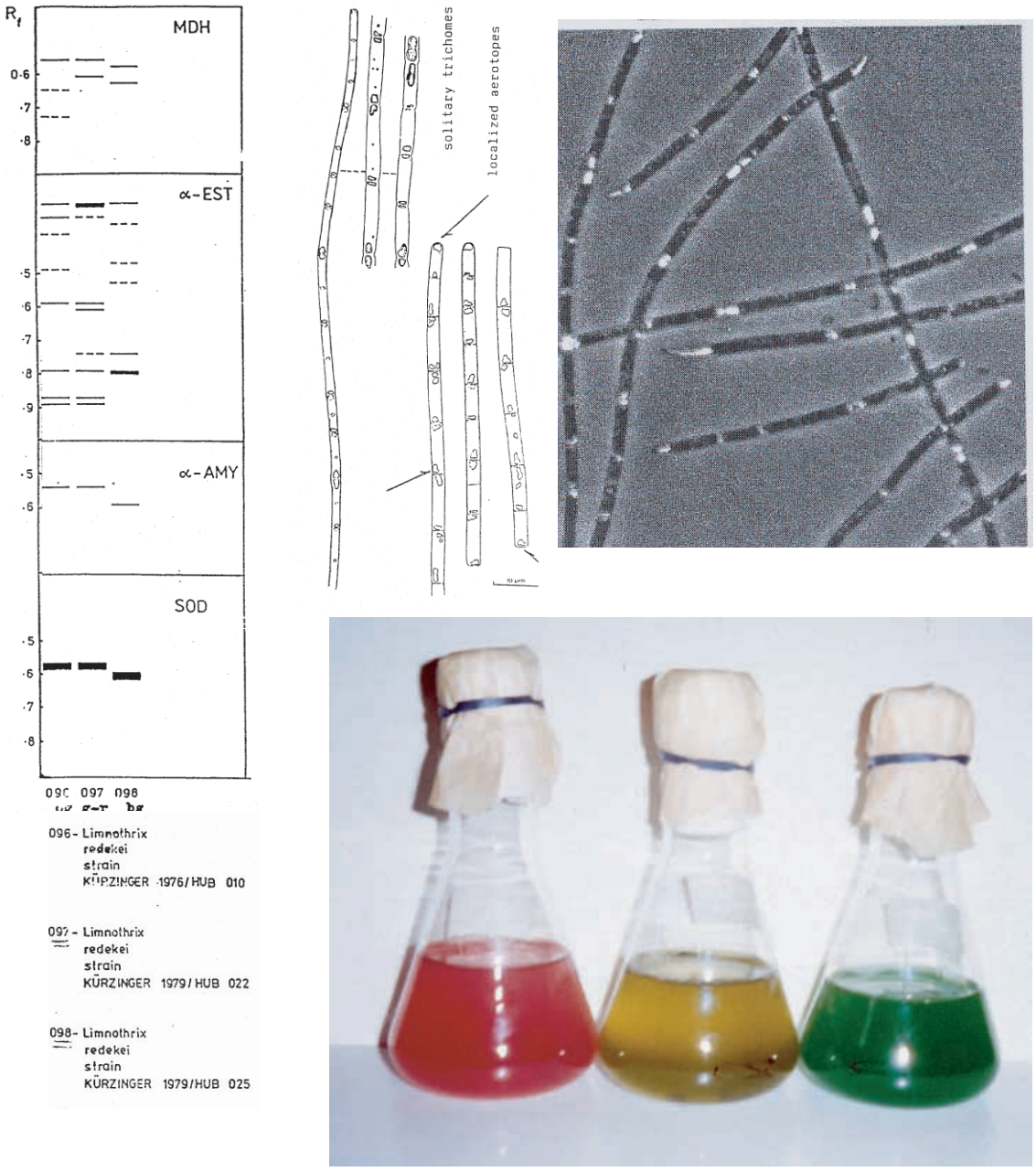

Fig. 7. Three strains from one population of planktic *Limnothrix redekei* (Lake Müggelsee near Berlin, Germany) differing in phycobilin pigment ratios and 29 isozyme characteristics stable in cultures. The morphology of trichomes is uniform and unchanged (strains isolated by Kürzinger, cf. Kohl and Nicklisch 1981; drawing after Van Goor 1920 and Hindák 1975, photo after Canter-Lund and Lund 1995).

clusters morphology is almost identical and the different entities can be classified (according to traditional taxonomy) to one and the same taxon (sometimes at the species level). Genetic differences are evident, sometimes larger than 95% (limit for different genera), but morphological differences are not apparent. Such was the case in *Spirulina*, where the genus *Halospirulina* was described as a special generic entity in spite of its close morphological similarity with other *Spirulina* types (Nübel *et al.* 2000; Castenholz 2001), in *Leptolyngbya* (Casamatta *et al.* 2005), and in *Pseudanabaena* (Turicchia *et al.* in press). The separation of special genera seems to be superfluous in these cases, because such types are not identifiable in nature without molecular analyses and also their distances in the phylogenetic trees are not substantial. However, they are represented by special strains, important for understanding of cyanobacterial diversity and should be registered in the system. The terms "cryptic species" or "cryp-

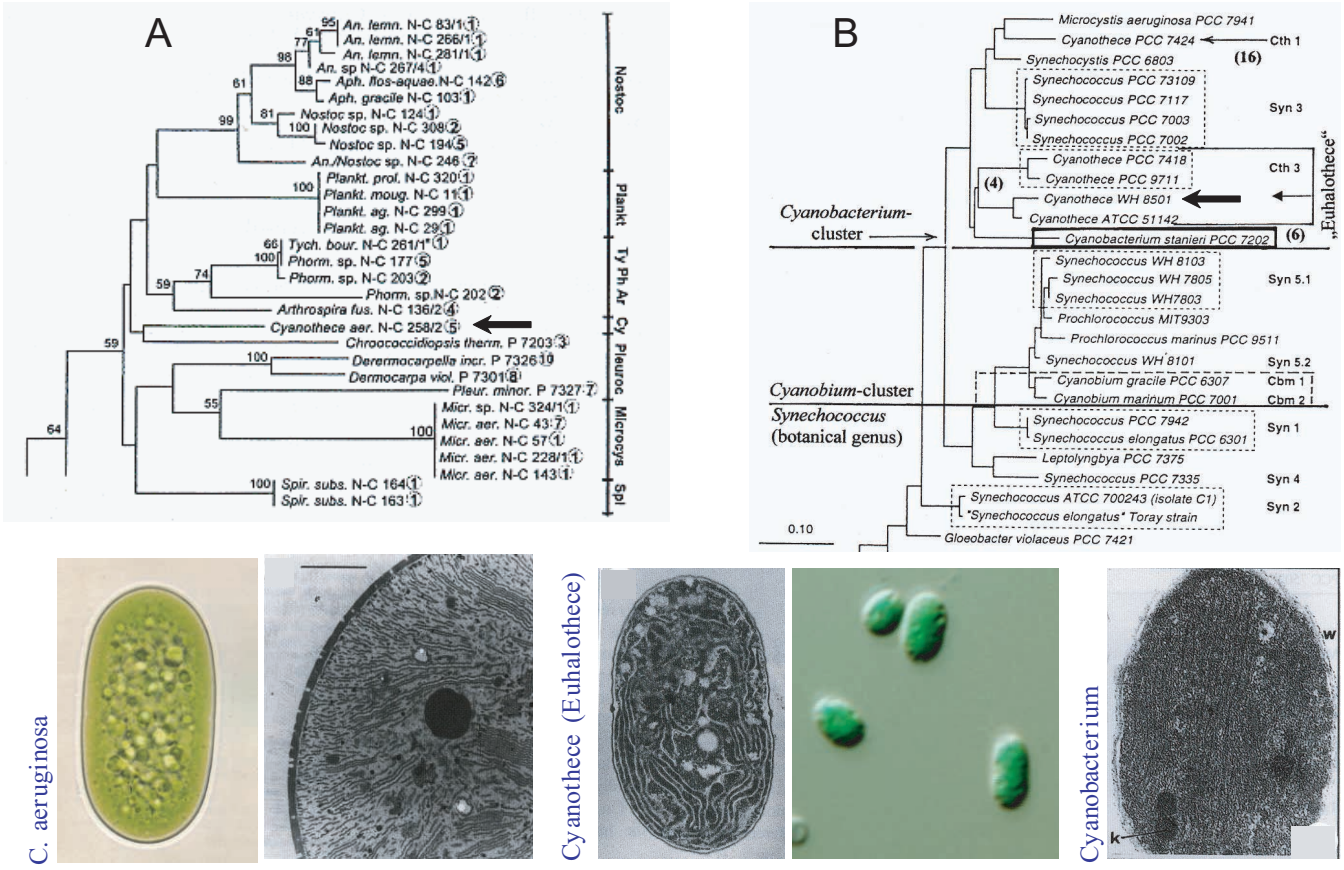

Fig. 8. Parts of phylogenetic trees (**A** - from Rudi *et al.* 1997; **B** - from Castenholz 2001), showing different genetic positions of strains N-C 258/2 (representing morphologically the type-species of *Cyanothece*, *C. aeruginosa*) and *Cyanothece* in later concepts (PCC, WH, ATCC strains). Their separated position indicates different generic classification and necessity of transferring later strains into a different genus; cells ultrastructure agrees with the genetic position of various strains (according to Komárek *et al.* 2004).

tospecies" (Saez and Lozana 2005, Johansen and Casamatta 2005) are appropriate for such taxa (*Pseudanabaena* in Fig. 13). These entities can be treated nomenclaturally as in other "species" or "morphospecies".

Nomenclature

The nomenclature of cyanobacteria was traditionally treated based on the International Code of Botanical Nomenclature (cf. Compère 2005). Up to now, the majority of cyanobacterial taxonomic units are designated by names created according to botanical rules. The name must be considered as a symbol of all (genetic, morphological, biochemical, ecophysiological) characters of the respective taxonomic unit (genus, species), in accordance with the taxonomic hierarchy. This is the best method for representing biodiversity, and no better method has been proposed. Therefore, traditional names are used commonly, though sometimes arbitrarily, in modern phylogenetic trees. Unfortunately, newly discovered clusters at the generic level have sometimes been designated with scientific names (e.g., *Crocosphaera*, *Thermosynechococcus*, *Halothece*, *Euhalothece*) without proper diagnoses. A major problem is that modern scientists often ignore any (botanical or bacteriological) nomenclatural rules, and such names appear in literature without sufficient phenotypic characterization and typification. This precludes the comparison of such geno- and morphotypes with other cyanobacterial entities. Such names are officially invalid (Oren 2004; Oren and Tindall 2005), but the corresponding taxa really exist and can not be ignored.

After introducing the scientific name "Cyanobacteria" to replace "Cyanophyta" (Stanier and Cohen-Bazire 1977; Stanier *et al.* 1978), it was proposed that cyanobacterial nomenclature should be considered under the rules of nomenclature code for bacteria. However, this proposal could not be applied completely. First, all diversity of cyanobacteria had been treated by botanical prescriptions, and it was impossible to apply for them the bacteriological rules. In addition, the application of bacteriological rules in subsequent research (definition of new

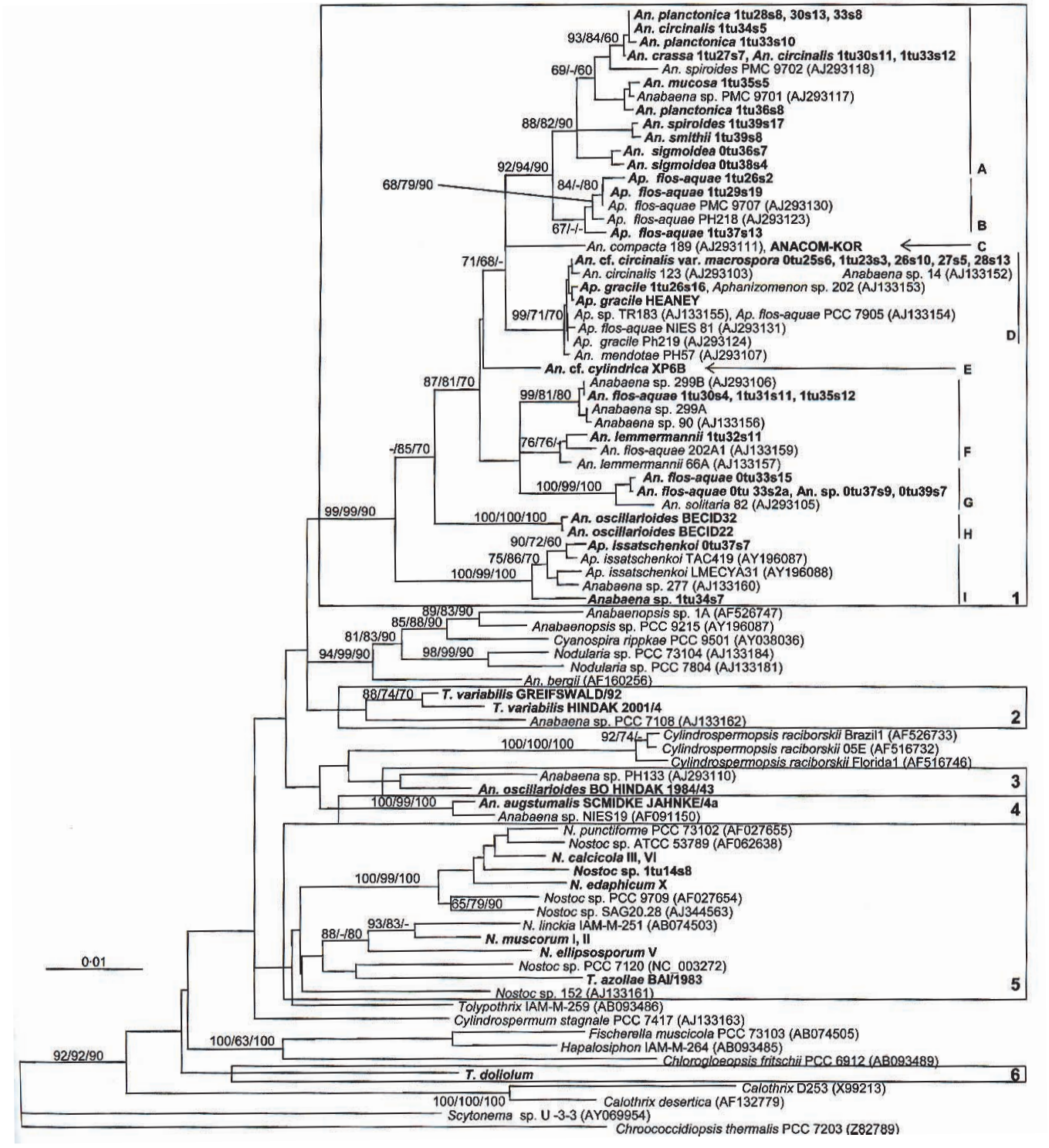

Fig. 9. Cladogram showing close relationship of planktic *Anabaena* and *Aphanizomenon strains* (cluster 1); benthic *Anabaena* strains mostly separated in other clusters (3, 4) (from Rajaniemi *et al*. 2005a).

described cyanobacterial taxa) was problematic. There were numerous problems with typification, with rules regarding priority, and particularly with mutual incompability of cultured strains, taxonomic classification, and identification of natural populations. A compromise solution was the arbitrary use of both Codes and the mutual acceptance of correctly named entities. Regardless, in many cases rules from both Codes were ignored when new scientific names were proposed (e.g., *Crocosphaera*). Alternatively, some authors described new taxa in accordance with both Codes (*Spirirestis*, *Brasilonema*).

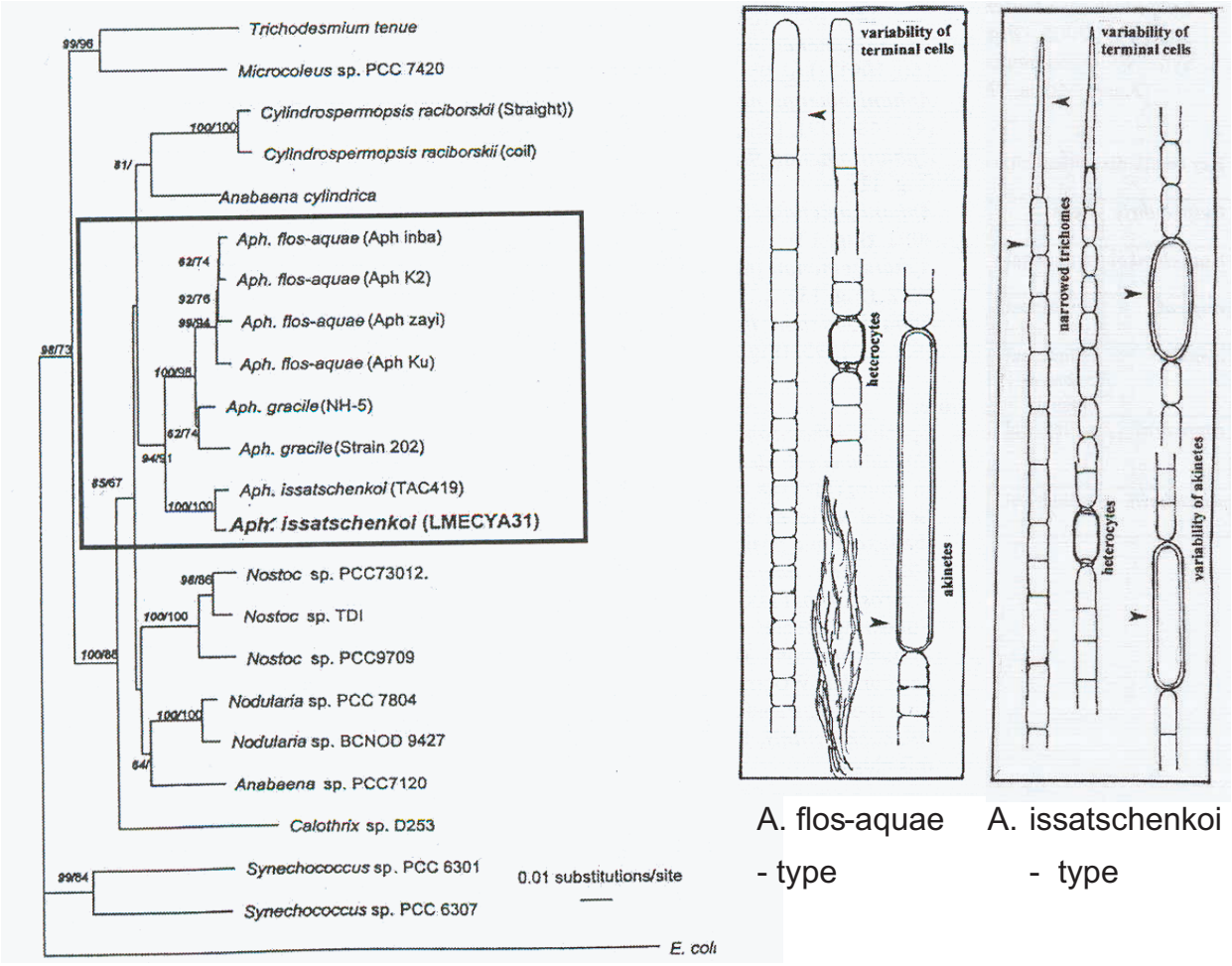

Fig. 10. Cladogram of heterocytous strains including various morphotypes of traditional genus *Aphanizomenon* (from Li *et al.* 2003). The type "*A. issatschenkoi*" is also phenotypically distinct subcluster (*Cuspidothrix*) (from Komárek and Komárková 2006; drawings from Rajaniemi *et al.* 2005b).

From the bacteriological perspective, the designation of "type strains" or "reference strains" is important. However, the stability of strains has been discussed several times (e.g., see in Friedmann and Borowitzka 1982), and such strains have limited utility for typification. The category of "reference strains" should be accepted and respected, but cannot be decisive for typification in cyanobacterial taxonomy. Consequently, the compromise "Guide to the nomenclature and formal taxonomic treatment of oxyphototroph prokaryotes" was elaborated by Komárek and Golubić (2005; see www.cyanodb.cz). This document includes a detailed method for the description of new cyanobacterial taxa and provides nomenclatoric procedures respecting all the major prescriptions and recommendations of both Codes. This proposal is open to discussion and correction and contains a regularly updated list of all approved cyanobacterial generic names and their synonyms. However, this database has not yet been seriously discussed, and problems with cyanobacterial nomenclature are an ongoing source of discussion. Unfortunately, any alternative nomenclatoric system which respects the uniqueness of cyanobacteria (bacterial origin and genetic background, photosynthetic apparatus and their resulting role in ecosystems, specific cytological and morphological diversity and diversification processes in the biosphere, ease of symbiotic interactions) has not yet been proposed. Nomenclatoric misinterpretations are therefore the serious problem of current cyanobacterial systematics, and several hundreds of incorrect names of strains in phylogenetic trees (which do not represent the genotype and phenotype of the strain) complicate terribly our work. There is currently no method for automatically including corrections to the cyanobacterial system and into the Data-Bases.

Currently (Oct. 2006), there are 17 cyanobacterial strains (7 genera, 10 species) in the Genome Atlas Database, from which the entire genome has been

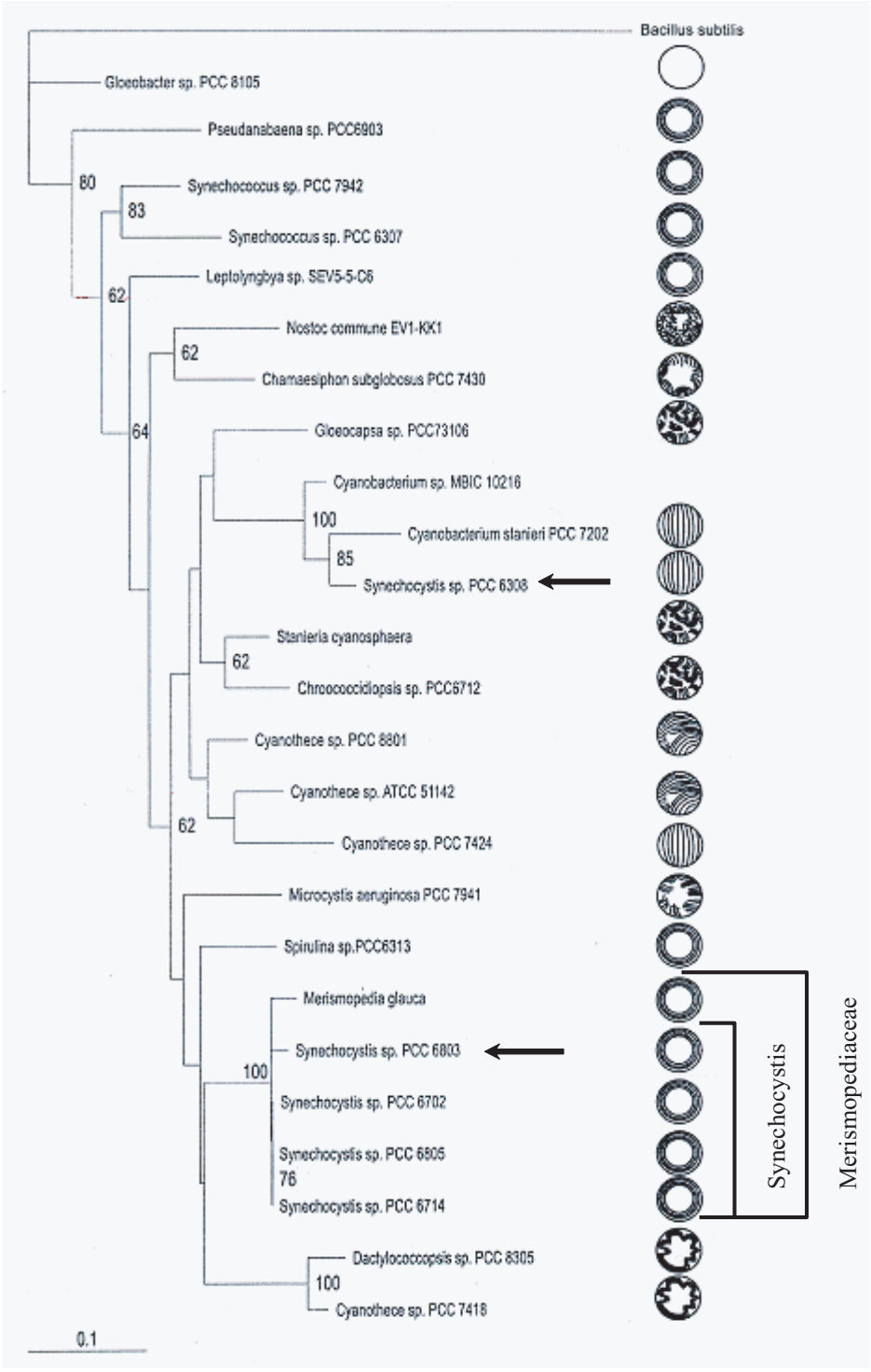

Fig. 11. Phylogenetic tree showing separate genetic position and different thylakoidal arrangements of *Synechocystis* strains PCC 6803 and PCC 6308; strain PCC 6308 is close to *Cyanobacterium* and must be re-classified and re-named (after Korelusová 2005).

sequenced. Binomial nomenclature is used to the designation of generic and specific names. Unfortunately, three names are nonsensical ("*Anabaena* nostoc", two strains of "Cyanobacteria bacterium"), in four strains the species are not identified, in two strains old, unrevised and invalid synonyms are used, and one type ("*Thermosynechococcus* elongatus") was never validly described. These analyses of cyanobacterial genomes are important; however, the neglect of formal taxonomic procedure is irresponsible and can lead to serious confusions in the future.

The mere designations of strains without scientific

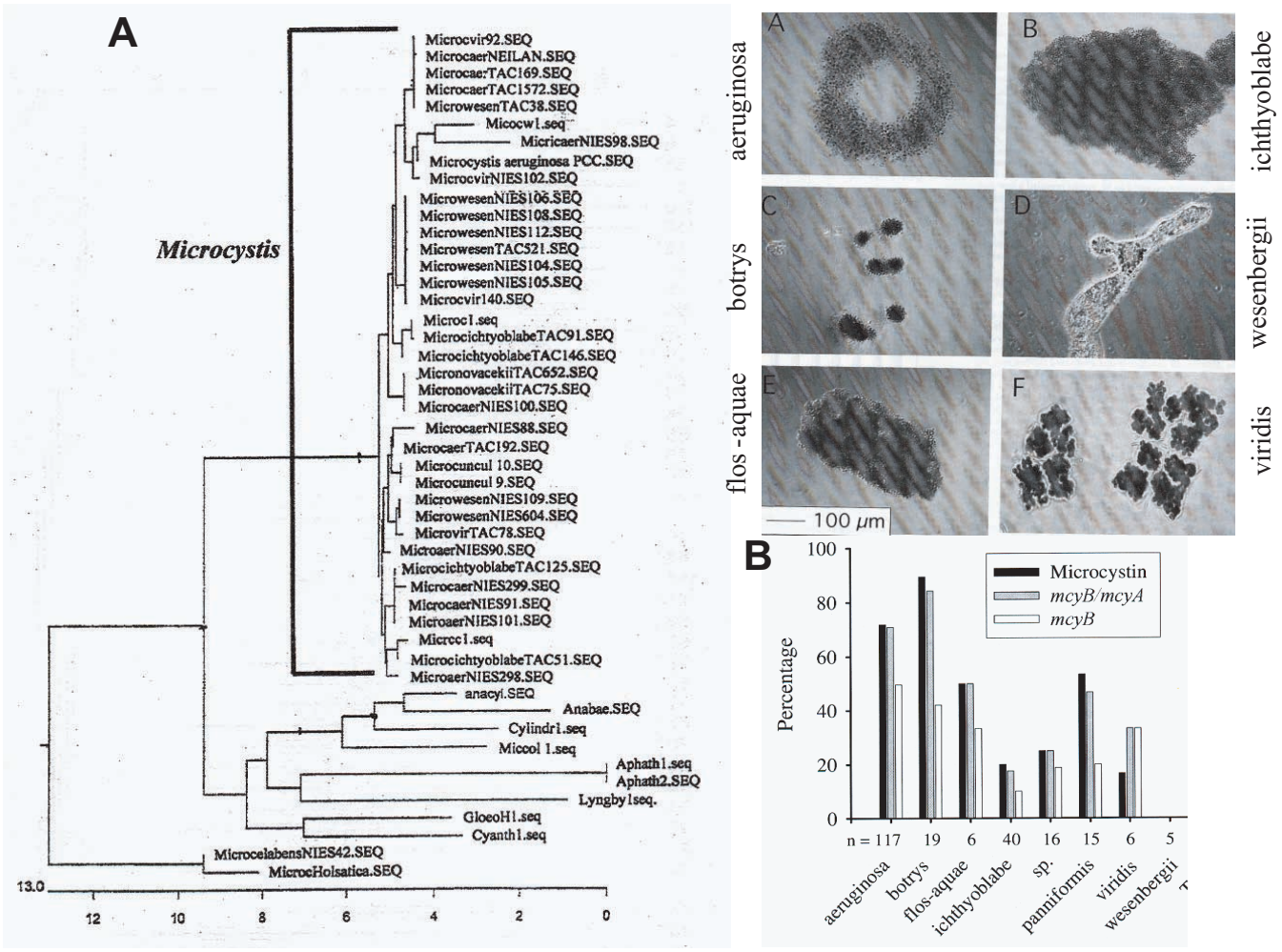

Fig. 12. Part of phylogenetic tree derived from Megalign (DNAStar Inc.) GeneBank NCBI (2002) showing generic uniformity of *Microcystis* (**A**). The different morphospecies are distinct morphologically, and differ in several biochemical markers (**B**) (e.g., production of toxins; from Via-Ordorika *et al*. 2004).

names may have been sufficient for laboratory investigations, but cyanobacteria also exist in nature. The elaboration of two different systems (i.e., molecular and "natural") is nonsense, unless there is a means of making them compatible.

Taxonomic evaluation of natural populations

Several different ecological projects are underway in which the whole diversity of natural cyanobacterial communities are being characterized. However, the evaluation of entire cyanobacterial communities from various habitats using the suite of combined modern methodological procedure (i.e., combined molecular, ecological and morphological approaches), remains extremely difficult. The different populations and species are ecologically restricted, and special types in various distinct habitats differ with respect to ecotypes and morphotypes. Evaluation of entire natural assemblages usually results in the recognition of a wider spectrum of genotypes than we are able to recognize using traditional methods. Thus, molecular sequencing usually yields wider genetic diversity than would be expected under the traditional system based purely on morphological characters.

The close dependence of cyanobacterial taxonomic entities on specialised habitats was recognised by the middle of 20th century. This was especially the case among scientists, particularly who joined the International Association of Cyanophyte Research (IAC) and who recognized ecological specializations of various cyanobacterial geno- and ecotypes (e.g., the papers of S. Golubić, O. Jaag, E. Kann, A. Zehnder, D. Mollenhauer, K. Anagnostidis). This school of "ecological taxonomy" was progressive for the cyanobacterial research in this period. Rapid adaptation has been recognised in cyanobacteria recently (Hagemann 2002), and this has demonstrated the role of environmental conditions in

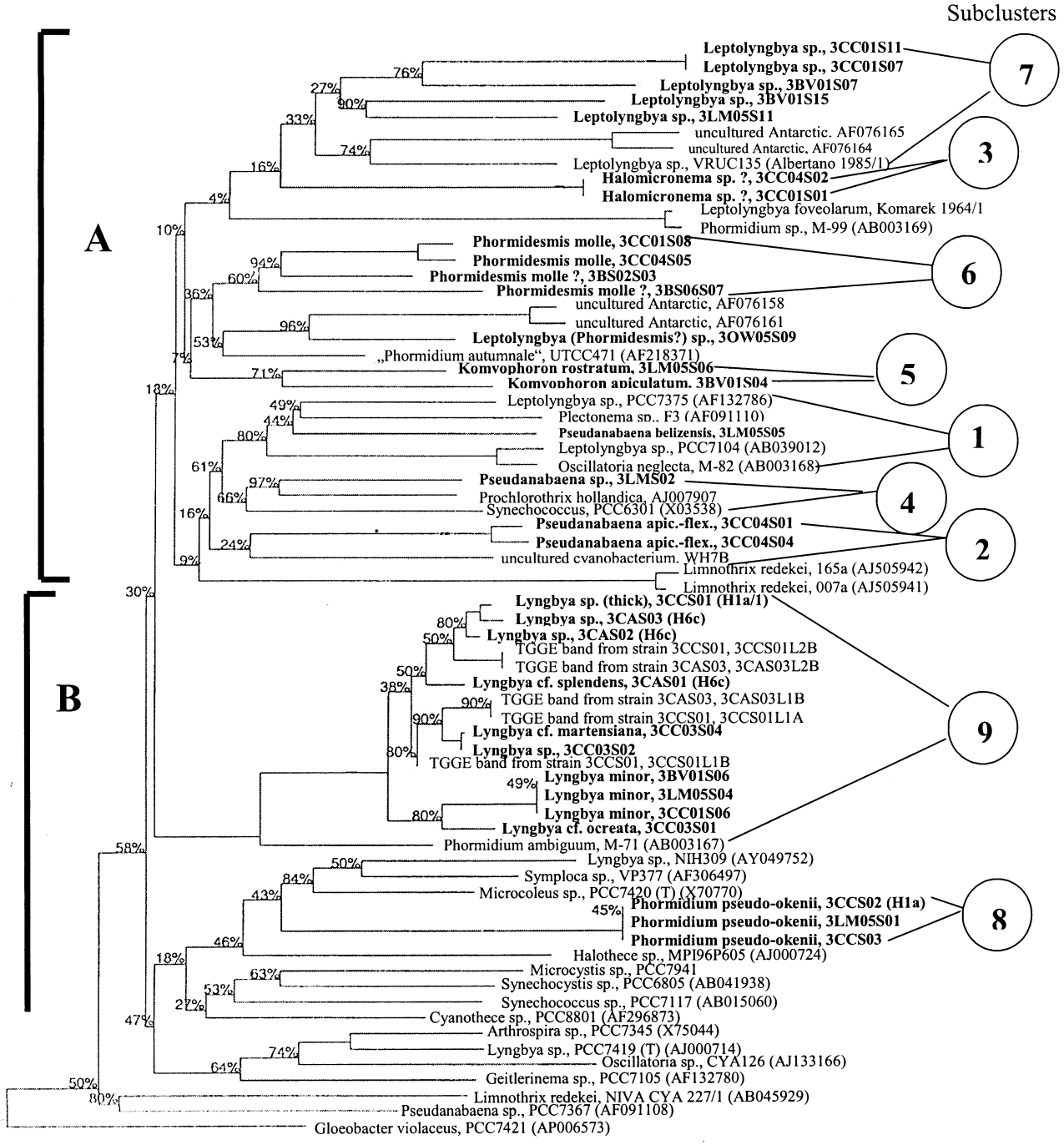

Fig. 13. Taxonomic evaluation of strains isolated from cyanobacterial assemblages of alkaline marshes in northern Belize, compared to phenotype analysis. Different clusters (1-9) correspond with morphologically defined units and show the taxonomic entities of various natural species (from Turicchia *et al.* 2007).

adaptational processes, and the diversification and speciation of cyanobacteria in various habitats. The various diversifying populations can appear in distant areas, in which the ecophysiological and biochemical characters change first and this is followed by changes in genotypes (Bolch and Blackburn 1998; Gugger *et al.* 2005). Thus, the conditions of a special habitat can invoke a convergence of similar metabolic activities and biochemical reactions in different morphotypes (Garcia-Pichel *et al.* 1998). These results are important not only for understanding diversification, but also for application of classification criteria in taxonomic practice.

These observations show that the characters of cyanobacterial populations can rapidly change, and that the study of stability and diversity of populations in distinct habitats is a continual task of cyanobacterial

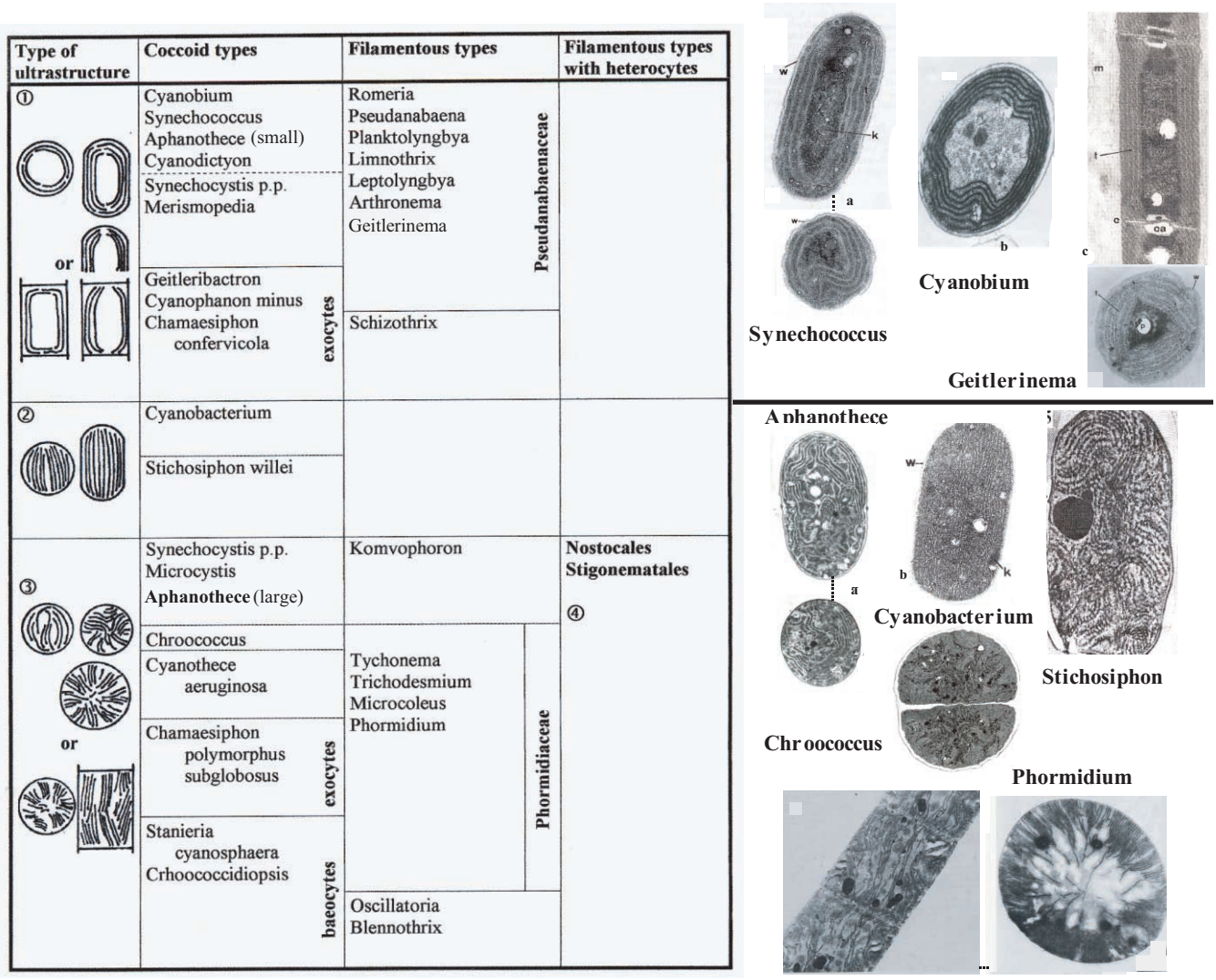

Fig. 14. Combined molecular and ultrastructural evaluation of various genera as a background for modern revision of cyanobacterial system (example) (modified from Hoffmann *et al.* 2005a).

research. In particular the assemblages in special habitats are still poorly known, and their diversity and ecological significance provide the most urgent questions of cyanobacterial taxonomy. Several authors estimate that in tropical biotopes less that 10% of all recognisable morphospecies of microorganisms are known (DiCastri and Younèz 1994; Watanabe 1999). This low percentage also likely reflects diversity in cyanobacteria. The necessity for studying cyanobacterial diversity, particularly in extreme and tropical ecosystems is the continual development of new eco- and morphospecies under changing environmental conditions.

Floristic studies are unpopular in modern phycological research. However, the comparative studies of populations from different habitats (or from similar habitats from different regions) are important for understanding of the world cyanobacterial diversity. Nevertheless, floristic and ecological-taxonomic studies must respect correct and modern knowledge of cyanobacterial taxonomy. Floristic studies are particularly important if they combine molecular with phenotype analysis; however, combining these methodological approaches is complicated and time consuming, and requires experience with cyanobacterial morphological diversity. Floristic papers based only on phenotype review or using only genotype analysis prevail in studies describing natural cyanobacterial populations. Examples of such molecular studies are analyses of halophilic vegetation from coastal regions of California (Garcia-Pichel *et al.* 1998), extreme habitats in Antarctica (Moorhead and Priscu 1998; Nadeau *et al.* 2001) and planktic communities (Lyra *et al.* 2001). Examples of detailed studies based on the precise phenotype analyses are Richert *et al.* (2006) from French Polynesia, Llames and Vinocur (2007) from Deception

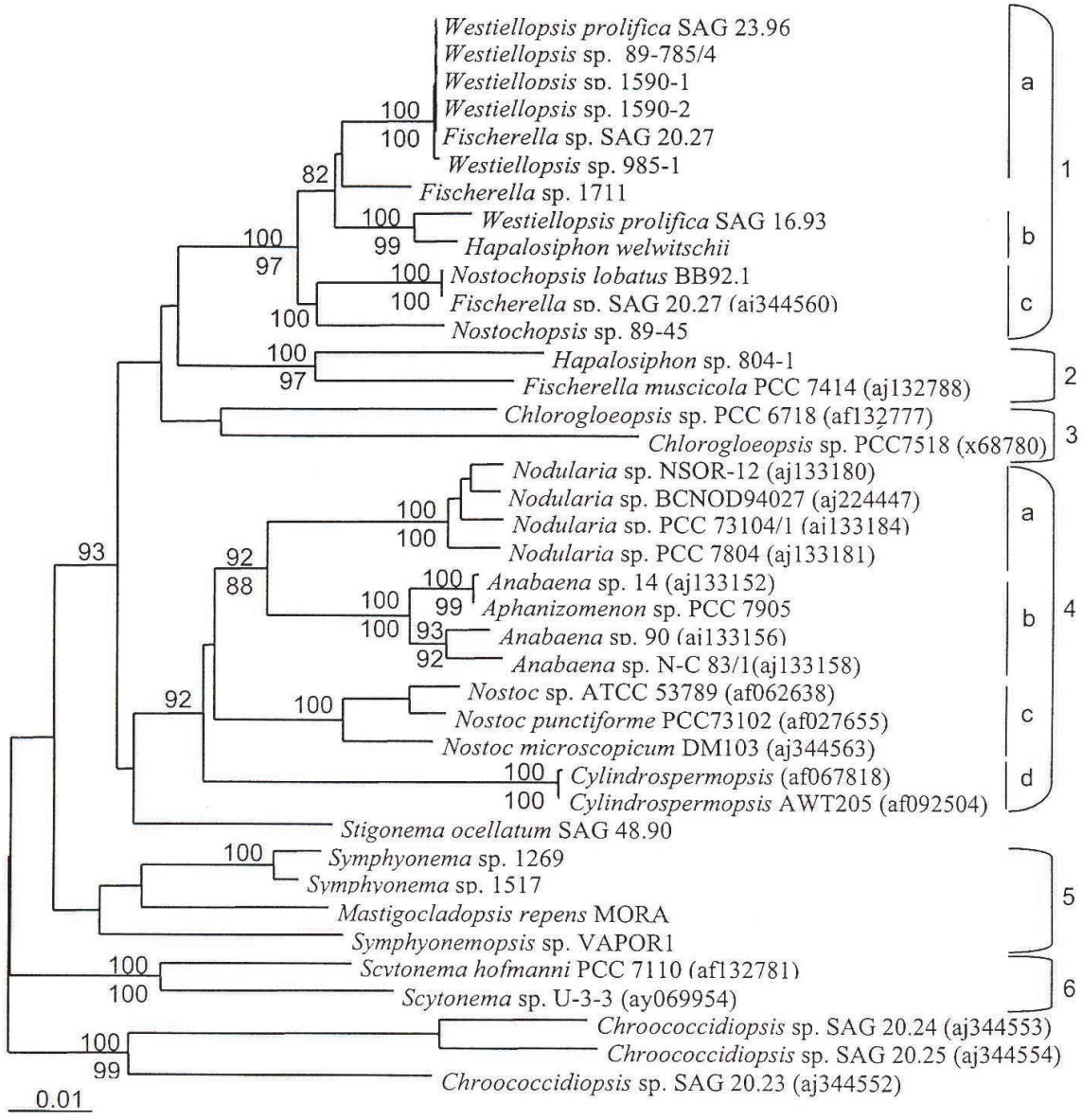

Fig. 15. Phylogenetic relationships of heterocytous filamentous strains from traditional orders Nostocales and Stigonematales based on 16S rDNA sequences. Note mixed position of nostocalean genera (cluster 4) among different stigonematalean clusters (from Gugger and Hoffmann 2004).

Island in Antarctica, and Komárek and Komárková-Legnerová (2007) from alkaline marshes in Belize, Central America (Fig. 13).

The combined approach in the case of natural populations is more difficult. From this perspective, molecular approaches (e.g., Temperature Gradient Gel Electrophoresis, TGGE; or Denaturing Gradient Gel Electrophoresis, DGGE) are more precise and allow for the recognition of all genotypes present in the cyanobacterial assemblages (Muyzer 1999). More difficult is the evaluation of the ecological role of different genotypes in the natural community. This includes the seasonality, the relative abundance of different types in the ecosystem, and the structure of the community. Comparison of the different phenotypes of each taxon is therefore necessary.

The methodology first must include genotype analysis, for which TGGE and DGGE are appropriate. The advantage of molecular evaluation is that it can reveal all genotypes in the habitat, even if the ecology of different eco- and morphotypes in the ecosystem remains unclear. The isolation of all populations into cultures from any particular habitat and their subsequent sequencing should be the next necessary step for complex evaluation. However, the isolation of all genotypes identified in the habitat is problematic (cf. Turicchia *et al.* in press). Another problem is that the morphology of different

Gl.			
	[Glocobacterales]	Glocobacteraceae	Glocobacter
Synechococcineae	**[Synechococcales]** **coccoid**	Synechococcaceae **coccoid**	Aphanothece (small-celled), Cyanobium, Cyanodictyon, Cyanonephron, Prochlorococcus, (Rhabdoderma), Synechococcus
		Merismopediaceae **coccoid**	Aphanocapsa (small-celled), Chroococcus subg. Limnococcus?, Merismopedia (small-celled), Synechocystis (small-celled)
		Chamaesiphonaceae **coccoid, heteropolar**	(Chamaesiphon subg. Euchamaesiphon), (Clastidium), Cyanophanon, Geitleribactron
	[Pseudanabaenales] **trichal**	Pseudanabaenaceae **trichal**	Arthronema, Geitlerinema, Halomicronema, (Heteroleibleinia), Leptolyngbya, Limnothrix, Planktolyngbya, Pseudanabaena, Romeria, (Tapinothrix)
		Schizotrichaceae **trichal**	Schizothrix
Oscillatoriineae	**Chroococcales** **coccoid**	[Cyanobacteriaceae]	Aphanothece (large), Cyanobacterium, Cyanothece, "Euhalothece", Microcrocis, Myxobaktron
		Microcystaceae	Aphanocapsa (large), (Gloeocapsa), Microcystis, Prochloron, Synechocystis (large)
		Gomphosphaeriaceae	(Gomphosphaeria), Snowella, Woronichinia
		Chroococcaceae	(Asterocapsa), Chroococcus, (Cyanosarcina), (Gloeocapsopsis), Merismopedia (large)
	polarized	Entophysalidaceae **bin. fission**	(Chlorogloea), Cyanoarbor, (Entophysalis)
	polarized	Stichosiphonaceae **exocytes**	Chamaecalyx, Chamaesiphon subg. Godlewskia, Stichosiphon
	polarized	Dermocarpellaceae **baeocytes**	(Cyanocystis), Dermocarpella, Stanieria
	polarized	Xenococcaceae **baeocytes x bin. fission**	Chroococcidiopsis, (Myxosarcina), (Xenococcus)
	polarized	Hydrococcaceae **bin. fission x baeocytes**	(Hydrococcus), Hyella, (Pleurocapsa)
	Oscillatoriales **trichal**	Spirulinaceae **necrids -**	Spirulina
		Borziaceae **necrids -**	(Borzia), Komvophoron
		Phormidiaceae **necrids +**	Arthrospira, Microcoleus, Phormidium, Planktothrix, Symploca, Trichodesmium, Tychonema
		Ammatoideaceae **heteropolar**	(Ammatoidea)
		Oscillatoriaceae **necrids +**	Blennothrix, Lyngbya, Oscillatoria, (Plectonema)
		Gomontiellaceae **necrids +**	(Crinalium), (Gomontiella), Starria
Nostocineae	**Nostocales** **heterocytous, akinetes**	Scytonemataceae **isopolar, false branching**	Scytonema
		Symphyonemataceae **true branching (Y)**	(Mastigocladopsis), (Symphyonemopsis), Y-Stigonematales-Symphyonema
		Rivulariaceae **heteropolar, hairs**	Calothrix, (Gloeotrichia), (Rivularia)
		Microchaetaceae **heteropolar**	(Microchaete), Spirirestis, (Tolypothrix)
		Nostocaceae **isopolar, without branching**	Anabaena (pl.), Anabaena (benth.), Anabaenopsis, Aphanizomenon, Cylindrospermopsis, Cylindrospermum, Nodularia, Nostoc, Trichormus
		Chloroglocopsidaceae	Chlorogloeopsis
		Hapalosiphonaceae **true branching (T)**	Hapalosiphon, Mastigocladus, Nostochopsis, T-Stigonematales-Fischerella, Westiellopsis
		Stigonemataceae **true branching, multiseriate**	Stigonema

Fig. 16. Outline of cyanobacterial classification (2004) based on combined (polyphasic) re-evaluation of cyanobacterial genera using molecular, phenotype, ultrastructural, biochemical and ecophysiological criteria (from Hoffmann *et al*. 2005a).

cyanobacterial populations sometimes changes after transfer under the stress of culture conditions. Regardless, the recognition of all genotypes in the ecosystem by molecular procedures, their phenotypic characterization and final taxonomic evaluation of the whole cyanobacterial community should be the ultimate objective for ecological studies of cyanobacterial assemblages. Examples of such studies of special habitats with rich cyanobacterial vegetation are the analysis of freshwater planktic cyanobacteria by Rajaniemi *et al.* (2005a, 2005b) and Willame *et al.* (in press), and the review of oscillatorialean cyanobacteria dominating cyanobacterial mats of northern Belize (Turicchia *et al.* in press) (Fig. 13).

The present cyanobacterial system

A modern cyanobacterial system should reflect current and confirmed knowledge of the genetic background, phylogeny, and the variability and ecology of all cyanobacterial organisms in nature and in culture (Hoffmann *et al.* 2005a, 2005b). It must have a genetic basis, and continually be corrected and updated. For cyanobacteria, many important revisions have occurred in recent decades as a result of the introduction of modern molecular and electron-microscopic methods. This is an ongoing process that provides for continual revision of cyanobacterial taxa. These advances should be respected after synthesis with phenotype diversity. It is an urgent and ongoing challenge for cyanobacterial taxonomists. However, it is important that scientists in experimental laboratories do not ignore the modernized system, but use it as part of a critical evaluation of their own work.

Recent studies in cyanobacterial systematics include the following primary advances, which should have general acceptance:

- Coccoid and non-heterocytous filamentous cyanobacteria must be classified in at least two phylogenetic lines that are characterized by similar ultrastructural patterns; both these lines comprise coccoid and filamentous genera (Synechococcineae and Oscillatoriineae) (Figs 3, 6, 14).
- Numerous genera are heterogeneous genetically and must be divided in various new generic entities. The phenotypic markers of such newly defined genera must be revised and respected. This involves numerous traditional genera from all categories (*Synechococcus*, *Aphanothece*, *Cyanothece*, *Chroococcus*, *Pseudanabaena*, *Phormidium*, *Oscillatoria*, *Anabaena*, *Aphanizomenon*, *Nostoc* and many others).
- Heterocytous cyanobacteria represent a uniform cluster (Nostocineae) in which branching type ("false" vs. "true"), previously considered as a diagnostic marker separating different orders, can be used only for the definition of genera and families (Gugger and Hoffmann 2004) (Figs 2, 3, 15).
- Numerous strains in world collections and laboratories are registered under incorrect and unrevised names. These need to be revised, and experimental scientists need to use strain names based on the revised system.
- The taxonomic and nomenclatural transfers of species within revised genera (of all species corresponding to the revised generic contents) are urgently needed in published taxonomic revisions of genera.

The present system was published by Hoffmann *et al.* with recent proved changes (2005a, 2005b) and numerous modifications and corrections have become necessary (Fig. 16). The modernization of cyanobacterial taxonomic classification was initiated by molecular biologists. It is ironic that now when taxonomists have accepted molecular approaches and present the results of such studies, that the acceptance of the revised taxonomy by experimental scientists has been so limited.

Although much has been accomplished in recent decades, much remains to be studied. Future systematic work must emphasize the validation and definition of genetically supported and revised generic entities, and the definition of infrageneric taxa. In addition, it is critical that this new understanding should be recognized and utilized by the wider scientific community.

ACKNOWLEDGEMENTS

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