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Some current problems of modern cyanobacterial taxonomy

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Cyanobacteria are remarkable organisms evolutionarily and they play an important ecological role in the world's ecosystems. Knowledge of their diversity, diversification and ecological significance are urgent questions for both terrestrial and aquatic ecology. They did not lose their vitality over their long existence from the early Precambrium and their ecological role increased with the increasing eutrophication of the whole biosphere of our planet.

Taxonomic classification and knowledge of cyanobacterial diversity belong therefore to the important and basic problems of cyanobacterial research. Modern taxonomic classification is a method for recognizing and registering organismal diversity (both in nature and cultures), dependent on evolutionary (genetic) and ecological relations and phenotypic variation. It must be based on a molecular, genotypic characterization of the natural phylogenetic clades, combined with evaluation of biochemical, morphological, cytological and ecological markers, consistent with phylogenetic diversification. The method of modern classification of cyanobacterial diversity respecting all of these characters is commonly called as the "polyphasic approach", which should be the guide–line for the modern re–classification of cyanobacterial diversity.

IAC–symposia, which are organized every 3 years already for over 50 years, are important meetings of cyanobacterial specialists, who discuss the problems, new methods and progress in cyanobacterial taxonomy. They were initiated in 1959 in the frame of the 14th International Limnological Congress (SIL) in Austria by Edith Kann (Vienna) and Otto Jaag (Zürich). All of the symposia reports and proceedings were published, first in Schweizerische Zeitschrift für Hydrologie and later, since the 9th symposium, in Algological Studies. The history of the first 9 symposia was presented by Kann & Golubić (1985). Prominent specialists in cyanobacterial taxonomy and ecology participated in IAC symposia during its history; it is necessary to remember, at least, the deceased K. Anagnostidis (Athens), P. Bourrelly (Paris), T.V. Desikachary (Madras), E.I. Friedmann (Tallahassee), O. Jaag (Zürich), E. Kann (Vienna), R.A.Lewin (San Diego), R.Y.Stanier (Paris), K. Starmach (Kraków).

One of the most important was the 8th symposium in 1979, the main theme of which was "Cyanophyta vs. Cyanobacteria, principles and problems in taxonomic treatment of natural populations vs. axenic cultures". In this meeting, Prof. Stanier stressed the bacterial character of cyanoprokaryotes and enhanced the molecular and experimental methods to solve taxonomic problems. This modernization was essential and supported distinctly the knowledge and understanding of cyanobacterial diversity. However, his proposal to transfer the nomenclature of cyanobacteria under the rules of the Code of Bacteriological Nomenclature (ICNB, later ICNP) was rather problematic (Stanier et al. 1978). This simple transfer was not possible, because all present knowledge of cyanobacterial diversity (results of about 150 years of investigation) was based on Botanical nomenclatoric principles. Moreover, the structure of cells and thallus, morphological and physiological characters, type of diversification and ecological role of cyanobacteria in nature are specific and different from other bacteria to such a degree that simple nomenclatoric changes (which must take these features in consideration) were not possible without many complications. Some of the main problems included the process of typification and the fact that the study of bacteria is based almost exclusively on cultures. On the contrary, phototrophic cyanobacterial populations are commonly important components of plant (algal) biocenoses and their characterization as phototrophic organisms in various aquatic and terrestrial communities, and special morphological diversification, means that they need to be studied also in natural environments according to morphological and ecological criteria.

A necessary modernization of cyanobacterial classification is therefore indisputable, but still there are many problems. Examples of present urgent questions are as follows:

1. **The introduction of bacterial methods into the study of cyanobacterial diversity neglected in some cases the old traditional cyanophycean/cyanobacterial system**, especially all of the species based only on morphological diversity and the ecology of natural populations. During 150 years of research several hundreds of cyanobacterial taxa were described, of which many are important for ecological or experimental studies. There was not proposed any procedure how to transfer the old knowledge, based on the botanical system, under the governance of bacteriological rules. The old binomial nomenclature is used in both modern ecological and bacteriological research and the elimination of it is impossible; unfortunately, it is used usually very arbitrarily, especially in experimental studies. This practice results in numerous misinterpretations. Examples include, e.g., many experimental strains designated as *Anacystis, Synechocystis, Cyanothece, Fremyella diplosiphon, Spirulina platensis*, and others.
2. The principal complications arose out of the **different typification method in bacteriological and phycological classification practice**. The rule of "type species" and typification are especially not uniform and often fully neglected. Bacteriological typification is based on cultured strains. However, there do not exist any type strains from almost all up to now described cyanobacterial species and corresponding strains do not exist even in many modern cyanobacterial taxa defined in the last few years. In recent literature, at least the status of reference strains is used. Reference strains are surely very important, but they should be selected only by specialists in corresponding groups; it is impossible to determine them only according to formal criteria. An example is the case of the genus *Synechocystis*. In Bergey's Manual (Castenholz 2001), this genus was divided into 4 clusters (subclusters respectively, the species were omitted). In cluster 1 of this traditional genus, the reference strain PCC 6308 (= ATCC 27150) was selected, whose phylogenetic position, according to modern molecular methods (combined with cytomorphology), was very far from other clusters of the genus *Synechocystis* and phylogenetically was quite different from this generic entity (Korelusová et al. 2009). It is also difficult to isolate and keep the typical strains of numerous populations, studied recently from various extreme ecological situations in nature.

   Typification according to strains is problematic even in cases when the isolation of newly discovered taxa is successful. Cyanobacterial populations isolated from different habitats are ecologically distinct and if we transfer them in new, mostly standardized conditions of culture collections, they soon change their biochemical and morphological characters in different degree (cf. Hagemann 2002; Komárek & Kaštovský 2003a). The situation is complicated also by the fact that unified methods for strain designation do not exist. Each collection or laboratory uses another system, and many synonyms and misinterpretations occur (different designations of the same strains in different collections); this concerns also type and reference strains. The type strain of *Cyanobacterium stanieri* designated as PCC 7202 occurs in the literature also under the symbols CCAP 1472/2a and ATCC 29140. The combination of arbitrarily used traditional binomial nomenclature (which is impossible to eliminate) and randomly designated strains result in lot of confusion. For 13 Antarctic strains, Nadeau et al. (2001) used designations of strains like "Ant–Skua", "Ant–Lunch", "Ant–Pancreas", etc., and only in the table are given corresponding names ("classical identification"). Another good example is the Genome Atlas Database (GAD), where cyanobacterial strains are registered, for which the entire genome was analysed. Such strains should be a starting point of the modern system. However, the use of curious names ("*Anabaena nostoc*", "*Cyanobacterium bacterium*"; in GAD in October 2006), or the designation "sp." without further identification (GAD in July 2010) can be hardly a start of any classification. Also the 14 strains concerning the species "*Prochlorococcus marinus*" (with 2 "varieties"?) are not usable as a basis for any system.

Of course, isolated strains are a not substitutable precondition to modern cyanobacterial research. The wide application of molecular sequencing and study of other cyanobacterial (morphological, biochemical, ultrastructural, ecological, etc.) markers is not possible without cultivation techniques. Also the identification of reference strains connected with a distinct phylogenetic, morphological and ecological entity is necessary. However, all of these methods must be applied mutually and the type must represent a distinct phylogenetic + phenotypic taxonomic unit. The combination with traditional "botanical" typification seems to be more prospective and the idea of typification of cyanobacteria by perfectly defined protologue (instead of strains or exsiccates) is most prospective.

3. Disagreements between classical and experimental (bacteriological) methods in taxonomic results concerning cyanobacteria led to proclamation of **the idea of constructings two parallel, phycological** (based on traditional taxa and morphological and ecological approach) **and bacteriological** (based on strains and molecular methods) **systems**. The existence of two systems for cyanobacteria is *eo ipso* a nonsense. In experimental taxonomy using strains, it is impossible to ignore the natural populations and *vice versa*. The world of cyanobacteria is quite unique and experimental and ecological studies on them are connected one to another to such a degree that separation of the two classifications is impossible. Our task must be to elaborate such a system, which describes and illustrates exactly the entire cyanobacterial diversity and which can be accepted by both experimentally and ecologically oriented scientists.
4. **Problem of the concept of taxonomic categories "genus" and "species"** is another problem of modern cyanobacterial taxonomy. The usual morphological criteria, as applied in phycological practice, are not usable in cyanobacteria without corrections, because the morphology is relatively very simple and variability is dependent on environmental factors. It was found that the value of various characters must be sometimes drastically re–evaluated. Distinct characters (presence of sheaths, false or true branching) are in agreement with molecular results to a certain degree, but their importance is lower than it was applied for the traditional taxonomic classification. On the other hand, some neglected markers (motility, morphology of apical and vegetative cells, morphology of calyptra, presence and type of necridic cells, position of akinetes, and others) can be congruent with results obtained by molecular analyses. It is interesting that the basic pattern of the internal structure of cells (the thylakoidal system) is in good agreement with phylogenetic clades (Komárek & Kaštovský 2003b). Heterocytous cyanobacteria represent a monophyletic cluster (Giovannoni et al. 1988; Turner 1997, 2001; Castenholz 2001; Litvaitis 2002; Gugger & Hoffmann 2004), but coccoid or simple filamentous types (in which the morphological criteria are particularly unclear) are heterogeneous, etc.

However, the present concept of the category "genus" has been already commonly more or less accepted by many researchers. Distinct differences in position in the phylogenetic tree based on 16S rRNA gene sequences (less than about 95% of genetic similarity), plus the presence of autapomorphic feature(s), are considered as the main criteria. Both of these markers should be obligatory, but other criteria (biochemical and ecophysiological characters, other sequences) can also be accepted to the final evaluation. There remains the problem of "cryptogenera", which are morphologically almost not recognizable, but their phylogenetic position is distinctly different. This concerns especially morphologically simple types derived, e.g. from the present genera *Synechococcus, Cyanobium, Pseudanabaena, Leptolyngbya, Spirulina* and others.

More confused is the concept of species. The situation is complicated by the fact that within every generic unit different principles of infrageneric diversification can be recognized. This diversity is complicated by a wide and various variability under environmental and ecological conditions and by different strategies of life cycles. Therefore, different species concepts were applied in the taxonomic literature; the traditional "hiatuses" at least in one character, units with distinct morphological or ecological stability, and also various types of ecospecies, morphospecies or cryptospecies are discussed. The idea of the existence of only (mere) populations (strains) inside genera without possibility to separate various "species" also appeared. It seems that with species identification a rather conventional criteria with a certain emphasis to ecology must be applied. The papers by Golubić (1961), Komárek (2003, 2006, 2010), Gold–Morgan & Gonzalez–Gonzalez

(2005) and Johansen & Casamatta (2005) present arguments supporting this question. Usually the formal definition of a specific category is used ["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"], but still the problem of cyanobacterial species needs further precision and specification.

5. With respect to the importance of cyanobacteria in ecological research**, the application of modern (molecular) methods was recently used in a study of the diversity of cyanobacteria in natural habitats**. DGGE or TGGE analyses for such modern "floristic" or ecological procedures (see, e.g., Ventura in Komárek et al. 2005) are often employed. The complete number of genotypes in the studied biotopes can be recognized more or less with the help of these methods, but it by itself is not satisfactory because of there being usually too short a portion of the gene sequences. However, numerous genotypes are designated often as "uncultured clone" or "uncultured cyanobacterium" in such studies. This method does not yield any information about life cycles, periodicity or ecological functions of different genotypes. Molecular method was used, e.g., in several studies from Antarctica. In the article of Jungblut et al. (2005), 11 of 32 phyllotypes (recognized units) were designated as "uncultured clone". Jungblut et al. (2010) present the "global distribution of cyanobacterial ecotypes in the cold biosphere" with the help of a phylogenetic tree, in which over 50% of the more than 110 evaluated taxonomic units were designated as "uncultured cyanobacteria" and less than half were designated by any name, but often only on the generic level ("sp."). The information value of such data (distribution of cyanobacterial ecotypes) is very low.

   Another method is the phenotypic analysis of a community, and the isolation and transfer of recognized types in cultures with the consequent study of such strains by biochemical and molecular procedures. However, this method has also many complications. It is impossible to recognize all genotypes by microscopic observation. Also the transfer of all recognized taxa into monospecific strains, cultured usually under standardized conditions, never can be realized. As examples can be presented two of our studies from extreme habitats: (i) In alkaline swamps in Belize, 29 oscillatorialean morphospecies were recognized, but only 19 taxa were isolated and studied by molecular methods (Turicchia et al. 2009). (ii) There were 42 recognized morphospecies from Antarctic habitats on James Ross Island, but only 13 species were successfully transferred into culture (Komárek et al. 2008). Certain morphological and ecological markers must be respected in all observed natural cyanobacterial populations, which are sometimes impossible to transfer to cultures.

6. The microflora (incl. Cyanobacteria) from various tropical and extreme habitats is intensely studied over the last years. It was already recognized, that not all cyanobacteria can occur everywhere and that the ecology of various genotypes is usually clearly restricted (Golubić 1961; Garcia–Pichel et al. 1998; etc.). Almost 2/3 of species from the famous world monograph and identification key by Geitler (1932) are described originally from temperate European and American zones. However, the **diversity of cyanobacteria in various tropical habitats is wider than in temperate ecosystems**, and the rich diversity in tropical forests, desert soils, mineral lakes, volcanic and halophytic areas, various types of marshes, isolated dripping rocks with various substrates and microclimate etc. has been discovered even in quite recent studies. Many new types were already recognized; these had not yet been described and their isolation is difficult. There are many examples especially from Pacific Islands, and all tropical and polar ecosystems. Komárek et al. (2005) identified 87 morphospecies in alkaline marshes in northern Belize, from which only 6% can be designated as "cosmopolitan", 20% pantropical, 40% known only from similar alkaline habitats in the Caribbean district, and 34% were not identifiable according to the literature available. Richert et al. (2006) recorded more than 28 taxa from microbial mats in ecologically special ponds in Rangiroa, Tuamotu Archipelago, French Polynesia, and only 6 species were clearly identified (all other types are designated by "cf." or "sp."). Flechtner et al. (2008) recognized 32 cyanobacterial species from 19 genera (isolated strains) from soils of San Nicolas Island, but only 16 (50%) were identified; 7 were evidently not yet known species, and

9 taxa were designated by "cf." (the identification was uncertain). With these problems appears a question how to characterize the "new" taxa, especially these ones, in which cultivation is complicated (up to now there do not exist strains of cyanobacteria from the benthos of mountain streams, many types from dripping rocks, endolithic marine habitats, etc.) and the application of molecular methods for such populations is almost impossible.

In principle, two final solutions are available: (i) Designation of various populations by names of known species, which have a similar morphology. This method is most easy and is commonly used (the authors do not like to describe "new species", it is not popular), but it is an evident falsification, and ecology is usually quite neglected; in serious science such a method is not acceptable. Or, (ii) description of numerous new species according to "old" botanical criteria (prescriptions), sometimes without molecular support. The detection of many new cyanobacterial entities should be now expected, especially after molecular analyses of strains or precise investigations of cyanobacterial populations from numerous habitats (especially in tropical regions). But it is necessary to mention that such studies are not welcome in modern phycological journals; the fashion of "modern" reviewers is often to reject automatically all descriptions without molecular methods (however, this practice is unfortunately far from scientific objectivity).

7. Many of the problems of modern cyanobacterial taxonomy follow from the fact that **both botanical and bacteriological nomenclatoric rules are applied to cyanobacteria**. This situation has already lasted about 50 years and there exist more complications in this field than positive proposals. Both Codes (Greuter et al. 2000; McNeill 2006; Lapage et al. 1992) are not applicable without corrections for cyanobacteria, due to their special morphological, ecological and phylogenetic characters. Several proposals were published in this field (cf. Oren 2004; Hoffmann 2005; Komárek & Golubić 2005; Oren & Tindall 2005) and several committees were established, but no decision was accepted up to now. The common tendency in science is rather to unify the existing Codes as much as possible (see, e.g., the PhyloCode; www.ohio.edu/phylocode). The tendencies of existing nomenclatoric committees to minimize possible exceptions of existing Codes as much as possible is quite understandable. The elaboration of a special Code for cyanobacteria has therefore a minimal chance to be accepted. However, it is highly urgent to solve this problem.

   The first solution to solve this situation was initiated at the 8th IAC symposium in Kastanienbaum (1979), where the proposal for preparation of a special nomenclatoric Guide for cyanophytes was recommended. This Guide was elaborated, published and now is available at www.cyanodb.cz (cf. Komárek & Golubić 2005). However, up to now, this Guide is not used and its novelization is necessary. We hope that this symposium will initiate progress in this field (Oren & Komárek in press).

It is possible to summarize that modern cyanobacterial taxonomy uses the polyphasic approach as the only prospective method for the modern revision of the classification system and the following premises should be accepted:

1) A unique system is quite necessary.
2) The traditional classification and binomial designation of taxa should be used as the logical background of further studies.
3) Molecular evaluation must be included as the priority in the polyphasic approach, together with the obligatory definition of autapomorphic characters (cytomorphological evaluation), ecological characterization and biochemical markers.
4) The possibility of typification and determination by type material should be widened (preserved strains, exsiccates, protologues, etc.) and the type must be exactly defined and should be constantly revisable.
5) The study of natural material, ecological significance and natural variability must not be neglected.
6) The nomenclatoric guide–lines should be adopted to the form corresponding with the bacterial character of cyanobacteria, but respecting also their morphological diversification and ecological specificities.

I believe that we shall be able to elaborate a good picture of the world of cyanobacterial diversity in the future and that our 18th IAC symposium will result in progress in this field. Best wishes and good luck in cyanobacterial research!

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