Review

Cyanobacterial systematics and nomenclature as featured in the *International Bulletin of Bacteriological Nomenclature and Taxonomy / International Journal of Systematic Bacteriology / International Journal of Systematic and Evolutionary Microbiology*

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Surprisingly few papers on cyanobacteria have been published in the *International Bulletin of Bacteriological Nomenclature and Taxonomy / International Journal of Systematic Bacteriology / International Journal of Systematic and Evolutionary Microbiology* (IBBNT/IJSB/IJSEM) during its 60 years of existence. The first papers featuring the group appeared in volume 28 and, in the 32 years that have passed since, 42 articles on cyanobacteria have been published in the journal. Very few of these papers deal with the description of new taxa and this is understandable in view of the current difficulty in validly publishing new names of cyanobacteria under the rules of the International Code of Nomenclature of Prokaryotes (ICNP). Other papers discuss the problems of the nomenclature of the group under the International Code of Botanical Nomenclature (ICBN)/ICNP and the ICBN. The largest group of articles on cyanobacteria consists of papers on systematics, in which isolates are compared using different approaches, without any implications for the nomenclature of the group under either Code. The fact that on average these papers have been highly cited shows that IJSEM and its predecessors have been an excellent framework for publications on cyanobacteria and should remain so in the future.

Introduction

In the sixty years that have passed since the first issue of *International Bulletin of Bacteriological Nomenclature and Taxonomy* (IBBNT) was published in 1951, IBBNT and its successors *International Journal of Systematic Bacteriology* (IJSB) and *International Journal of Systematic and Evolutionary Microbiology* (IJSEM) have published papers on the systematics of all categories of prokaryotes. The journal has been the prime framework for the publication of new genera and species of Bacteria, Archaea and also eukaryotic micro-organisms. However, there is one group of prokaryotes that, because of its special status, has featured relatively little in the journal: the cyanobacteria.

Abbreviations: IBBNT, *International Bulletin of Bacteriological Nomenclature and Taxonomy*; ICBN, International Code of Botanical Nomenclature; ICNB, International Code of Nomenclature of Bacteria; ICNP, International Code of Nomenclature of Prokaryotes; ICSB, International Committee on Systematics of Bacteria; ICSP, International Committee on Systematics of Prokaryotes; IJSB, *International Journal of Systematic Bacteriology*; IJSEM, *International Journal of Systematic and Evolutionary Microbiology*.

The cyanobacteria first featured on the pages of IJSB as late as 1978, in volume 28. The publication of two short papers by Gibbons & Murray (1978) and Stanier *et al.* (1978) was a direct result of the recognition that the cyanobacteria (cyanophyta, 'blue–green algae') belong to the prokaryotes. Stanier & van Niel (1962) wrote in their classic paper 'The concept of a bacterium' that 'The distinctive property of bacteria and blue–green algae is the prokaryotic nature of their cells'. The Stanier *et al.* (1978) paper raised nomenclatural issues that still have not been resolved today. No cyanobacteria featured in the *Approved Lists of Bacterial Names* (Skerman *et al.*, 1980).

After this late start, the number of papers dealing with cyanobacteria published in the journal is still small: in the 32 years that have passed since the two above-mentioned short articles appeared, no more than 41 articles on cyanobacteria have been published in the journal, or 42 if a paper on their phages (Johnson & Potts, 1985) is also included. This list does not include minutes of the meetings of the ICSB/ICSP or their subcommittees in which cyanobacteria featured on the agenda, unless the

discussion was entirely devoted to cyanobacterial nomenclature (Trüper, 1986).

The articles can be classified in three categories. First, there are descriptions of new taxa. These are so far very few, and this is understandable in view of the current difficulty in validly publishing new names of cyanobacteria under the rules of the ICNP. Most descriptions of new taxa are therefore published in the botanical literature. A second group of papers discusses the problems of the nomenclature of the cyanobacteria/cyanophyta under the ICNB/ICNP and the ICBN. The third and largest group consists of articles on systematics, in which isolates are compared using different taxonomic approaches without any implications for the nomenclature of the group under either Code. The first of those papers, a chemotaxonomic study of *Anabaena* and *Nostoc* on the basis of fatty acid composition, was published only 18 years ago (Caudales & Wells, 1992).

On the occasion of the 60th anniversary of IBBNT/IJSB/IJSEM, I here present an overview of the papers published on cyanobacteria by the journal and of the involvement of the journal in the discussions to solve the nomenclature problems connected with the group, as well as some information on the key characteristics suitable for classification and identification of cyanobacteria.

Nomenclature of cyanobacteria and description of new taxa of cyanobacteria in IBBNT/IJSB/IJSEM

The number of descriptions of novel species and genera of cyanobacteria in the journal has been very small. This is not surprising as IJSEM and its predecessors have thus far published species descriptions of cyanobacteria under the rules of the ICNB/ICNP only. As the ICNP is not independent of the ICBN, it is formally impossible to describe species under the rules of the ICNP within genera previously named under the botanical rules. The ICBN has a statement in Article 45.4 that 'if the taxon is treated as belonging to the algae, any of its names need satisfy only the requirements of the pertinent non-botanical *Code* for status equivalent to valid publication under the present *Code*'. The ICSP thus far has not reciprocated this article in the rules of the ICNP. Therefore it is possible to validly publish names of novel species only when the genus name has not earlier been used in the botanical nomenclature. Examples are rare: only four new genera have thus been added: *Prochlorothrix* (Burger-Wiersma *et al.*, 1989), *Halospirulina* (Nübel *et al.*, 2000), *Planktotricoides* (Suda *et al.*, 2002) and a recent addition to the list, *Rubidibacter* (Choi *et al.*, 2008).

As a result of technical errors in the past, a considerable number of the names of cyanobacterial taxa published in IJSEM and its predecessor IJSB are problematic. More information on the status of these names under the ICNP can be found in Oren & Tindall (2005) and in the List of Prokaryotic Names with Standing in Nomenclature (http://www.bacterio.cict.fr; Euzéby, 1997). Here is, in alphabetical order, the list of names of cyanobacteria included in the pages of IJSEM/IJSB:

- The species name *Crinalium epipsammum* included in Validation List no. 38 (De Winder *et al.* 1991).
- The genus *Halospirulina* and the species *Halospirulina tapeticola* (Nübel *et al.*, 2000).
- The proposed emendation of *Limnothrix redekei* (Suda *et al.*, 2002).
- The species name *Microcystis aeruginosa* (Otsuka *et al.*, 2001).
- The genus name *Planktotricoides* with the species *Planktotricoides raciborskii* (Suda *et al.*, 2002).
- Two novel species within the genus *Planktothrix*: *Planktothrix mougeotii* and *Planktothrix pseudagardhii* (Suda *et al.*, 2002). The authors also proposed emendation of *Planktothrix aghardii* and *Planktothrix rubescens*.
- The names of the order *Prochlorales*, family *Prochloraceae*, genus *Prochloron* and species *Prochloron didemni* (Florenzano *et al.*, 1986; Pinevich *et al.*, 1997).
- The subspecies name *Prochlorococcus marinus* subsp. *pastoris* (Rippka *et al.*, 2000).
- The names for the family *Prochlorotrichaceae*, the genus *Prochlorothrix* and the species *Prochlorothrix hollandica* (Burger-Wiersma *et al.*, 1989).
- The new genus *Rubidibacter* and the species *Rubidibacter lacunae* (Choi *et al.*, 2008).
- The emendation of *Tychonema bourrellyi* (Suda *et al.*, 2002).

In 2002, Cavalier-Smith proposed names of the division *Cyanobacteria*, the subdivisions *Gloeobacteria* and *Phycobacteria*, the classes *Chroobacteria*, *Gloeobacteria* and *Hormogoneae*, and the orders *Chroococcales*, *Gloeobacterales*, *Nostocales*, *Oscillatoriales*, *Pleurocapsales* and *Stigonematales*. Most of these names are problematic for different reasons (List Editor, 2002), including the fact that most are based on genus names that have no standing under the ICNP.

Finally, there is a delightful little paper by Potts (1997), disclosing the etymology of the cyanobacterial genus name *Nostoc* (validly published under the ICBN), showing that 'Nostoch', the name used by Paracelsus in the 16th century for the slimy colonies of this genus, was a combination of 'Nostril' and its German equivalent 'Nasenloch'.

Cyanobacterial nomenclature under the rules of the ICSB/ICSP

When, in 1978, Stanier and his colleagues proposed that the nomenclature of the Cyanobacteria shall be governed by the provisions of the International Code of Nomenclature of Bacteria, they obviously chose to publish their proposal in IJSB, the official journal of the ICSB. This paper was preceded by a short article in which Gibbons & Murray (1978) requested the validation of the order *Cyano-*

bacteriales, even though there was (and still is) no corresponding genus in the order. As there is no corresponding genus, there can be no type genus and hence the name would be illegitimate. Many discussions have since been devoted to the problems connected with the treatment of cyanobacterial nomenclature under the ICNB/ICBP and the ICBN, and the journal has always been an excellent framework for the publication of views, workshop summaries etc. related to this issue (Trüper, 1986; Oren, 2004). These include a paper presenting the opposing view that cyanobacterial nomenclature should be covered by the ICBN alone as 'the fact that cyanobacteria can now be grown in pure culture does not necessarily mean that their nomenclature should be dealt with by the Bacteriological Code' (Lewin, 1979).

As a result of the proposal by Stanier *et al.* (1978) and the subsequent discussions in the ICSB/ICSP, a nomenclatural system has emerged in which Cyanophyta/Cyanobacteria have been named according to the provisions of either Code. This is where the major problems lie because the two Codes handle various aspects differently. One of the critical issues is that valid publication of names under the ICNP includes a formal act of registration/indexing, centralized in IJSB/IJSEM, whereas few restrictions exist on the journal in which names may be validly published under the ICBN. Under current revisions of the ICNP, the nomenclatural type of a species is a viable type strain maintained in pure culture, while under the ICBN, non-living type specimens must be preserved permanently, although algal cultures preserved in a metabolically inactive state are acceptable as types. Oren & Tindall (2005) provided an overview of the current status of the problem and of the current nomenclature status of those few cyanobacterial taxa described in IJSB/IJSEM in the past. Discussions on the harmonization of the nomenclature of the Cyanobacteria/Cyanophyta under the ICBN and the ICNP are continuing, but little progress has been made thus far.

Studies on the molecular taxonomy and chemotaxonomy of cyanobacteria

By far the largest category of cyanobacteria papers in IJSB/IJSEM (28 of 43 papers) consists of molecular phylogenetic studies, using 16S rRNA genes and other relevant genes as markers to obtain information to be used in the systematics of the group. No formal proposals for the establishment of new taxa were made in any of these papers and the nomenclature used is that governed by the ICBN.

The studies in this group include DNA–DNA reassociation experiments for the characterization of strains of heterocystous cyanobacteria (Lachance, 1981) and *Microcystis* (Kondo *et al.*, 2000), and comparisons of the guanine+cytosine content of the genomic DNA of *Microcystis* strains (Fahrenkrug *et al.*, 1992).

16S rRNA gene-based phylogenetic studies have been published on the genera *Microcystis* (Neilan *et al.*, 1997; Lyra *et al.*, 2001), *Nodularia* (Lehtimäki *et al.*, 2000; Moffitt *et al.*, 2001), *Anabaena*, *Aphanizomenon*, *Planktothrix* (Lyra *et al.*, 2001), on symbiotic *Nostocaceae* (Papaefthimiou *et al.*, 2008) and on the true branching *Stigonematales* (Gugger & Hoffmann, 2004). In some studies, attempts have been made to correlate the phylogenetic position as determined on the basis of 16S rRNA gene sequences with other properties such as the production of toxins. A 16S rRNA-based study of special interest is the phylogenetic evaluation of cyanobacteria preserved as historic herbarium exsiccata. Such studies may prove of importance in the future when attempts will be made to link 'botanical' names based on type specimens preserved in herbaria with living organisms of similar morphology (Palinska *et al.*, 2006).

Other molecular markers generally used in systematic studies to complement 16S rRNA gene sequence information include the phycocyanin operon and its intergenic spacer (*cpcBA*-IGS) in the genera *Synechococcus*, *Arthrospira*, *Rivularia*, *Calothrix*, *Nodularia* and *Aphanizomenon* (Robertson *et al.*, 2001; Janson & Granéli, 2002; Manen & Falquet, 2002; Berrendero *et al.*, 2008); the β-subunit of RNA polymerase (*rpoB*) in the genera *Nodularia*, *Anabaena*, *Aphanizomenon*, *Trichormus* and *Nostoc* (Lyra *et al.*, 2005; Rajaniemi *et al.*, 2005), a sigma factor (*rpoD*) in the genus *Microcystis* (Sakamoto *et al.*, 1993), ribulose bisphosphate carboxylase/oxygenase (*rbcLX*) in the genera *Aphanizomenon*, *Trichormus*, *Nostoc* and *Nodularia* (Gugger *et al.*, 2002b; Lyra *et al.*, 2005; Rajaniemi *et al.*, 2005), the gene *ndaF* involved in polyketide peptide synthesis and the gas vesicle protein gene *gvpA* and its intergenic spacer in the genus *Nodularia* (Lyra *et al.*, 2005), the nitrogenase gene *nifD* in heterocystous cyanobacteria (Henson *et al.*, 2004), *hetR* involved in heterocyst differentiation in the genera *Nodularia* and *Aphanizomenon* (Janson & Granéli, 2002), RNase P (*rnpB*) in the genus *Prochlorococcus* (Schön *et al.*, 2002), the introns of $tRNA^{LEU}$ in heterocystous cyanobacteria (Wright *et al.*, 2001; Oksanen *et al.*, 2004) and a large number of other marker genes (Gupta *et al.*, 2003).

Finally, a number of papers have centred on fatty acids as chemotaxonomic markers in the taxonomy of unicellular cyanobacteria of the order *Pleurocapsales* (Caudales *et al.*, 2000) and of the genus *Microcystis* (Gugger *et al.*, 2002a) and of free-living (Caudales & Wells, 1992) and the symbiotic heterocystous filamentous genera *Anabaena*, *Nostoc* and other filamentous types (Caudales *et al.*, 1995; Gugger *et al.*, 2002a).

The impact of papers on cyanobacteria in IJSEM and its predecessors

Almost without exception, papers on cyanobacteria published in the journal have been extensively cited. Based on information retrieved on August 26, 2009 from the database of the ISI Web of Knowledge, the cyanobacteria papers published between 1978 and 2006 have been cited on average 28 times. The ten top scorers are the papers on evolutionary relationships among toxic and non-toxic

Microcystis strains by Neilan *et al.* (1997), the description of *Prochlorococcus marinus* subsp. *pastoris* by Rippka *et al.* (2000), the molecular characterization of *Anabaena*, *Aphanizomenon*, *Microcystis* and *Planktothrix* by Lyra *et al.* (2001), the proposal to place the nomenclature of the cyanobacteria under the rules of the ICNB by Stanier *et al.* (1978), the DNA reassociation studies on heterocystous cyanobacteria by Lachance (1981), the phylogenetic and morphological evaluation of *Anabaena*, *Aphanizomenon*, *Trichormus* and *Nostoc* by Rajaniemi *et al.* (2005), the phylogenetic analysis of the genus *Synechococcus* by Robertson *et al.* (2001), the characterization of *Nodularia* strains by Lehtimäki *et al.* (2000) and of *Anabaena* and *Aphanizomenon* by Gugger *et al.* (2002b), and the description of *Prochlorothrix hollandica*, the family *Prochlorotrichaceae* and the order *Prochlorales* (Burger-Wiersma *et al.*, 1989). These papers have accumulated 120, 74, 69, 59, 57, 53, 53, 53, 51 and 48 citations, respectively, numbers far higher than most articles in IJSEM and its predecessors.

Genotypic, chemotaxonomic and other phenotypic markers useful for the description and classification of cyanobacteria

For the characterization, description and classification of cyanobacteria, morphological, physiological, chemotaxonomic and genotypic characters are all important. Basically, the guidelines for the characterization of prokaryote strains for taxonomic purposes (Tindall *et al.*, 2010) can and should also be applied to the description of cyanobacteria.

The current approaches towards the classification and identification of cyanobacteria are mainly based on morphological and, to a lesser extent, on the analysis of gene or protein sequence data (Castenholz, 2001; Waterbury, 2006). Due to the tremendous variation in shape and size among the cyanobacteria, morphological features are much more useful classification criteria than for any other group of prokaryotes. Properties of interest are the occurrence of branching and the formation of heterocysts (cells specialized for nitrogen fixation), hormogonia (short segments of trichomes that function to disseminate the species) and akinetes (thick-walled survival forms) for filamentous species and the generation of baeocytes (small cells formed by multiple fissions of a parent cell) for some unicellular forms. Motility by gliding or, in rare cases, by swimming (not mediated by flagella) is another property of interest.

Features of the photosynthetic system in which variations exist among the different groups of cyanobacteria include the arrangement of the thylakoids and the types of pigments present in addition to chlorophyll *a*: chlorophyll *b* and divinyl derivatives of chlorophyll *b* and *a* in the order *Prochlorales* and in the genus *Prochlorococcus* and related organisms, and chlorophyll *d* (in the genus *Acaryochloris*), and phycobilins (phycocyanin, phycoerythrin) that in some taxa may be present in different ratios depending on the quality of the light (complementary chromatic adaptation). Most cyanobacteria are obligate phototrophs, but some have the ability to grow photoheterotrophically or even grow on simple organic compounds in the dark.

Lipid and fatty acid analyses provide useful chemotaxonomical information that can be used for classification and identification of cyanobacteria (Sato & Murata, 1988). Some types only contain saturated and monounsaturated fatty acids, while others also have di- and tri-unsaturated fatty acids (Kenyon, 1972; Kenyon *et al.*, 1972). Polyunsaturated fatty acids can only be synthesized from their saturated derivatives in an oxygen-dependent pathway. In those species that lack polyunsaturated fatty acids, the monounsaturated acids are made by the same mechanism, but in others the 'bacterial', oxygen-independent pathway is used. This is especially the case in cyanobacteria that live in sulfide-rich environments. The two pathways can be discriminated by the position of the double bond in the monounsaturated fatty acids (Ionescu *et al.*, 2007).

16S rRNA gene sequences are used extensively in the characterization and classification of cyanobacteria. Often there is little correspondence between the morphology-based classification of the organisms and the 16S rRNA gene sequence-based phylogeny. Notably the orders *Chroococcales*, *Pleurocapsales* and *Oscillatoriales* do not form coherent phylogenetic lineages (Wilmotte & Herdman, 2001). When the 16S rRNA gene sequences do not provide sufficient resolution to reconstruct phylogenetic trees, the much more variable intergenic transcribed spacer between the 16S and the 23S rRNA genes can be used. For nitrogen-fixing species, *nifH* and other components of the nitrogenase system can be used as phylogenetic markers in studies of cyanobacterial characterization.

Final comments

The above survey shows that, in spite of the relatively low number of articles on cyanobacteria published in IJSEM and its predecessors, the journal has proved to be an excellent framework for such papers, not only for the description of new taxa but also for phylogenetic, chemotaxonomic and other studies of species named under the provisions of the ICBN. Most of these papers have been highly cited.

Aspects of cyanobacterial systematics and nomenclature (both under the provisions of the ICNP and the ICBN) deserve to be covered in IJSEM. Therefore the journal should remain the perfect framework for the publication of high quality papers on cyanobacteria in the future.

Note added in proof

An additional paper describing the use of an *rpoB* signature sequence for molecular typing of cyanobacteria is included in this issue of IJSEM. See the paper by Gaget *et al.* (2011) for more details.

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