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Validation of the generic name *Gloeobacter* Rippka *et al.* 1974, Cyanophyceae

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Abstract – The genus name *Gloeobacter* with the single (= type) species *Gloeobacter violaceus* (Cyanophyta, Cyanoprokaryota, Cyanobacteria) was described by Rippka, Waterbury *et* Cohen-Bazire (*Arch. Microbiol.* 100: 419-436, 1974). However, this is not a validly published name and so it currently has no standing under the botanical International Code of Nomenclature (ICN, Mc Neil *et al.* 2012) or the International Code of Nomenclature of Prokaryotes (ICNB/ICNP, Lapage *et al.* 1992). The lack of valid publication of the genus name causes many problems in the taxonomy of this phylogenetically and experimentally important cyanophyte/cyanobacterium. The lack of thylakoids, a feature unique among all known cyanobacteria, as well as the phylogenetic position of the representative of this genus, warrant valid publication of this generic name. The type strain was deposited in the collection PCC in Paris under the number PCC 7421 and later introduced into numerous other strain collections; however, the dried specimens were not yet conserved. The type strain is cited as holotype in Castenholz (Bergey's Manual, 2001). We here propose validation of the names *Gloeobacter* Rippka *et al.* 1974, gen. nov (type: *Gloeobacter violaceus*) and *Gloeobacter violaceus* Rippka *et al.* 1974, sp. nov., utilising the description by Rippka *et al.* reproduced here, and supported by the exsiccate BRNM No. HY 2366 (under the rules of the botanical Code of Nomenclature - ICN), using exsiccate from the type strain 7421 (PCC 7421^T = ATCC 29082^T).

Cyanophyceae / Cyanobacteria / Gloeobacter / taxonomy / validation

Résumé – **Validation du nom *Gloeobacter* Rippka *et al.* 1974, Cyanophycées** – Le genre *Gloeobacter*, avec l'unique espèce *G. violaceus* a été décrit par Rippka, Waterbury *et* Cohen-Bazire en 1974. Cependant, ce n'est pas un nom validement publié et, en conséquence, il n'a pas de statut sous le Code International de Nomenclature botanique ni sous le Code International de la Nomenclature des Prokaryotes. Le fait que ces deux noms ne soient pas validement publiés cause de nombreux problèmes dans la taxonomie de ces cyanophycées/cyanobactéries phylogénétiquement et expérimentalement importantes. Ce genre est caractérisé par l'absence de thylakoïdes, un caractère unique parmi toutes les cyanophycées connues et il a une position phylogénétique unique, ce qui justifie la

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validation de son nom. La souche « type » est déposée dans la collection PCC de Paris, sous le n° PCC 7421 et a été distribuée ensuite à de nombreuses autres collections de cultures. Cette souche originale a été citée comme « holotype » par Castenholz (Bergey's Manual, 2001). Nous proposons ici de valider les noms *Gloeobacter* gen. nov. et *G. violaceus* sp. nov., utilisant la description de Rippka *et al.* reproduite ici et supportée par l'exsiccata BRNM n° HY 2366 (conformément aux règles du Code de Nomenclature botanique – ICN) utilisant un exsiccata de la souche originale PCC 7421 (PCC 7421^T = ATCC 29082^T).

Cyanophycées / Cyanobactéries / Gloeobacter / taxonomie / validation

INTRODUCTION

In 1974, Rippka, Waterbury and Cohen-Bazire described the genus *Gloeobacter* with a single species, *Gloeobacter violaceus*, a unicellular cyanobacterium that lacks thylakoids (Rippka *et al.*, 1974). These names were not included in the *Approved List of Bacterial Names* of 1980 (Skerman *et al.*, 1980) or in later validation lists. The 'form-genus' *Gloeobacter* as cited later for the same cyanobacterial species (Herdman *et al.*, 2001) can equally not be considered effective publication as the term 'form-genus' has neither standing under the International Code of Nomenclature of Bacteria/International Code of Nomenclature of Prokaryotes (the Bacteriological Code ICNP; Lapage *et al.*, 1992), nor do the names have standing under the botanical International Code of Nomenclature ICN (McNeill *et al.*, 2012), as in violation of Article 8.4 the type material was designated exclusively a living culture, and, in addition, only an English description was provided, not one in Latin as required at that time (Art. 44.1).

Gloeobacter violaceus strain PCC 7421 (designated as type strain; = ATCC 29082) has been deposited in several culture collections, and much information has been obtained on this organism (see e.g. Bryant *et al.*, 1981; Guglielmi *et al.*, 1981; Schneider & Jürgens, 1991; Selstam & Campbell, 1996; Turner, 1997; and numerous others). Its complete genome sequence was published by Nakamura *et al.* (2003). The 16S rRNA gene sequence of the strain PCC 7421 is commonly used as an outgroup in phylogenetic trees in cyanobacterial studies. Moreover, *Gloeobacter* is an extremely important and widely used model organism for the study of photosynthesis and evolution of plant life (Mimuro *et al.*, 2008, Williamson *et al.*, 2011).

The name of the genus *Gloeobacter* with the type *Gloeobacter violaceus* Rippka, Waterbury *et* Cohen-Bazire is therefore validated in this article according to the botanical ICN (McNeill *et al.*, 2012) by designating a permanently preserved specimen as type, instead of the living strain originally designated by Rippka *et al.* (1974). The reasons for validation of the genus name and following conservation of the name of its single species will be further explained in a proposal to conserve the name *Gloeobacter violaceus*) to be published subsequently in Taxon (Mareš *et al.*, submitted; cf. also www.CyanoDb.cz). We want to keep the names of the original authors in the validated name, because they have the principal merit for discovering of this remarkable and phylogenetically important type of cyanobacteria/cyanoprokaryotes/cyanophytes. The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequence and the genome sequence of the type strain of *Gloeobacter violaceus* are AF 132790 and BA 000045, respectively.

RESULTS AND DISCUSSION

Based on cell morphology and ecology, *Gloeobacter violaceus* resembles *Gloeothece coerulea* (Geitler, 1928), found in dolomite rock samples from Lunz (Austria). The name *G. coerulea* was validly published under the provisions of the botanical International Code of Nomenclature (see also Komárek & Anagnostidis, 1998). Already the original authors of *Gloeobacter* wrote (Rippka *et al.*, 1974, p. 434) that "the size of its cells and their polar granules fit the description by Geitler (1928) of the species *G.* [= *Gloeothece*] *coerulea*". Castenholz (2001) suggests (p. 503) that "*Gloeobacter violaceus* conforms to the botanical species *Gloeothece coerulea* Geitler 1928, but with minor discrepancies in color". However, the compared *Gloeothece* strains, which are cited as different from *Gloeobacter violaceus* (as arguments of different characters between *Gloeobacter* and *Gloeothece coerulea*) do not correspond with *Gloeothece coerulea* morphologically and ecologically. These data, their comparison, and presupposition of difference between *Gloeothece coerulea* and *Gloeobacter* are therefore irrelevant. Moreover, no type material of *Gloeothece coerulea* is available for a comparative study, so that there is no way to ascertain whether this botanical species may indeed have exhibited the ultra-structural features and phylogenetic position that define the genus *Gloeobacter*.

Up to now, there has been no strain of *Gloeothece coerulea* in culture collections, and the question if cytomorphology, ecology and life cycles of this species fully agree with *Gloeobacter violaceus* is still open. Several populations of typical *Gloeothece* were in fact designated as *Gloeothece coerulea* by later authors; however, this identification is *sine typo*. The similar concept was used also in the study of Golubić & Campbell (1979). Komárek & Anagnostidis (1998) designated the similar, but typical *Gloeothece* species (with blue envelopes) as *Gloeothece cyanochroa*. As previously reported, the protoplast color of *Gloeobacter* can change in certain degree in dependence of the life cycle (Mareš *et al.*, 2013). The respective priority of the epithet "*coeruleus*" for *Gloeobacter violaceus* is therefore unclear.

More strains of *Gloeobacter* (similar to PCC 7421) were isolated and studied later:

(i) two strains, namely "*Gloeobacter violaceus* PCC 8105" isolated by S. Campbell from Wolfenschiessen, Nierwolden, Switzerland (Turner *et al.*, 1999), and "PCC 9601" isolated by M. Gugger and A. Caltreau from a hill scraping and freshwater molasse in the Alpine region of Switzerland (Herdman *et al.*, 2001), both deposited also in PCC collection (http://www.crbip.pasteur.fr/onglet.jsp?tab=cyano).

(ii) Mareš *et al.* (2013) isolated two strains of the cyanobacterial species identified as *Aphanothece caldariorum* Richter *ex* Hansgirg 1892, from two different tropical greenhouses of the botanical gardens in Liberec and Teplice, Czech Republic. The type of *A. caldariorum* is not available any more (it was destroyed in the past), however this species is commonly identified and understood by most authors as described by Geitler (1932, p. 169-170, Fig. 76). The species in this widely used sense was clearly identified on the basis of habitat, cell morphology and formation of nanocytes (small reproduction cells resulting from rapid and repeating fission of cells). Both these newly isolated strains exhibited exactly the main key cytomorphological characters of *Gloeobacter violaceus* (only with a little larger dimensions of cells in natural material) and very similar ecology (comp. also Hansgirg, 1892, Geitler, 1932, 1960, and others) to *A. caldariorum sensu* Geitler (1932).

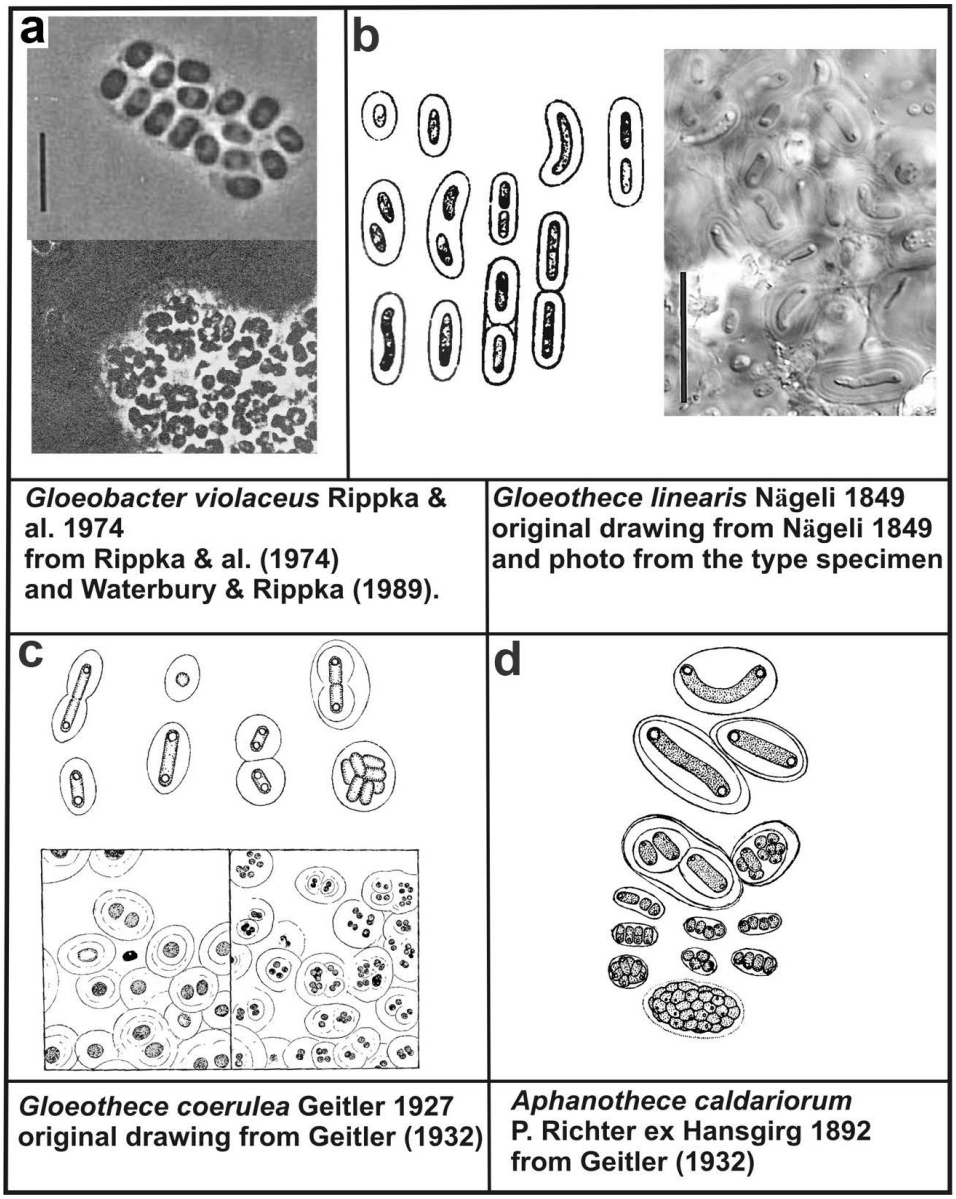

Fig. 1. Cyanobacterial taxa, morphologically corresponding to *Gloeobacter violaceus*, described under various names. Scale bars: *a* – 5 μm; *b* – 20 μm. The magnification of drawings in *c* and *d* was not specified in the original sources.

From the detailed polyphasic analyses (Mareš *et al.*, 2013) clearly follows that *A. caldariorum* in the sense of Geitler (1932) is identical to *Gloeobacter violaceus* strain PCC 7421. Nevertheless, since the type of *Aphanothece caldariorum* no longer exists and cannot be examined, the priority against *Gloeobacter violaceus* under the ICN is unclear, similarly to *Gloeothece coerulea*.

It is possible that some other small-celled species of *Gloeothece*, including *G. linearis*, the type of that generic name, and *Aphanothece* described in botanical papers may be assigned to the genus *Gloeobacter*, though confirmation of this will require more isolates of these two genera and a comparison with their corresponding exsiccates (if available). For instance, *Aphanothece caldariorum* is possibly (according to Drouet & Daily, 1956) based on taxonomically unclear *Aphanothece nebulosa* A. Braun in Rabenhorst, Alg. Eur. 246-248: 5454, 1876.

We therefore propose the validation of the genus name *Gloeobacter* Rippka *et al.*, gen. nov. (type: *Gloeobacter violaceus*) and *Gloeobacter violaceus* Rippka *et al.*, sp. nov. (with exsiccatum no. BRNM HY 2366 deposited in Moravian Museum Brno, Czech Republic as type [derived from the originally designated type strain PCC7421^T = ATCC 29082]) in accordance with article 32-45 of the botanical ICN (McNeill *et al.*, 2012). As a description or diagnosis in Latin is no longer required, the names are validated by the inclusion here of the English description provided by Rippka *et al.* (Art. 38.1(a) and Art. 38.5), thereby allowing the names to be attributed to these authors (Art. 46.2).

The acceptance of our proposal has become of great importance, since several additional independent isolates assignable to the same genus and species are now available and can be used in relevant evolutionary and experimental studies. *Gloeobacter* is also extremely significant from the phylogenetic point of view and has been widely cited under this generic name in numerous experimental works and in basic manuals concerning Cyanobacteria/Cyanophytes for the last 38 years (Bryant, 1981, Guglielmi *et al.*, 1981; Schneider & Jürgens, 1991; Selstam & Campbell, 1996; Turner, 1997; Komárek & Anagnostidis, 1998; Turner *et al.*, 1999; Castenholz, 2001; Herrero & Flores edit., 2008; Schirmeister *et al.*, 2011; and many others).

We append to this article the formal publication of this generic name and that of its type species:

***Gloeobacter* Rippka, Waterbury *et* Cohen-Bazire gen. nov.**

Gloeobacter (Gloe.o.bac'ter. Gr. masc. n. *gloios* glutinous substance, gum; N.L. masc. n. *bacter* equivalent of Gr. neut n. *bacterion* rod, staff; N.L. masc. n. *Gloeobacter* glutinous rod).

Validating description: "Unicellular, rod-shaped cyano bacteria which multiply by binary transverse fission. The cells being held together by thin multilayered sheaths as in the genus *Gloeothece*. Thylakoids and phycobilisomes absent. A cytoplasmic membrane which follows the contour of the cell wall is the only unit membrane system in the cell. Immediately underlying it is an electron-dense, cortical layer about 80 μm wide, completely enclosing other cytoplasmic structures. The GC content of the DNA is approx. 65 moles percent". Rippka, Waterbury, & Cohen-Bazire.

A more thorough description on the basis of our investigations is:

Colonial, unicellular cyanobacteria with oval or rod-like cells, enveloped by thin, homogeneous up to layered mucilaginous sheath; layers of the sheath are more or less concentrical around cells, colourless or slightly yellowish coloured. Cells multiply by binary transverse fission in one plane, the cells being held together by thin multi-layered sheaths, and by occasional rapid division in nanocytes, 0.7-2.5 μm in diameter. Thylakoids are absent. The cytoplasmic membrane, the only unit membrane system of the cell, follows the contour of the cell wall and contains the oxygenic photosynthetic apparatus with chlorophyll a and carotenoids as associated pigments. Phycobilisomes, composed of the colored

phycobiliproteins and uncolored linker proteins, are present. These water-soluble pigment complexes are bundle-shaped and form an electron-dense, cortical layer, about 50-80 nm wide, at the inner surface of the cytoplasmic membrane, completely enclosing other cytoplasmic components, except at the cross walls of dividing cells.

Type: *Gloeobacter violaceus* Rippka, Waterbury *et* Cohen-Bazire, sp. nov.

Validating description that by Rippka, Waterbury, and Cohen-Bazire for the genus (above).

Gloeobacter violaceus (vi.o.la'ce.us. L. masc. adj. *violaceus*, violet-colored).

A more thorough description on the basis of our investigations is:

Individual cells oval to cylindrical, 2-12 × 0.8-1.5 mm, with pale blue-green, sometimes slightly violet up to almost colourless cell content. Cortical layer in cells about 80 nm wide. Cells contain unusually large polyphosphate granules, typically located at both poles of the cells. As a result of formation of multiple sheaths, the cells tend to remain associated after division to form irregular masses of variable size. Larger aggregates of cells have a characteristic violet color, which may turn bluish gray under sub-optimal growth conditions. Cells are non-motile. Pigmented by chlorophyll a, different carotenoids, allophycocyanin, phycocyanin and phycoerythrin. The phycoerythrin contains two types of chromophores, phycoerythrobilin and phycourobilin, absorbing at 564 nm and 498 nm, respectively. The organism is an obligate photoautotroph, does not fix N_2, aerobically or anaerobically, and is incapable of performing complementary chromatic adaptation. No growth is observed at 37°C. The major lipids are monogalactosyl diacylglycerol, digalactosyl diacylglycerol, phosphatidyl glycerol and phosphatidic acid. Sulfoquinovosyl diacylglycerol is lacking. Major fatty acids are C16:0, C18:3, and C18:2 with minor amounts of C18:0 and C18:1. The genome size of the type strain is 4,649,019 bp. DNA G + C content is 62-65 mol %, based on the genome sequence of different strains, including the type strain (64 mol% G+C of the DNA; Herdman *et al.* 2001).

Holotype: Exsiccatum no. BRNM HY 2366 (deposited in Moravian Museum Brno, Czech Republic).

Reference strain: PCC 7421 (PCC 7421^T = ATCC 29082^T), isolated from the surface of a limestone rock collected in 1972 in Canton Obwalden, Switzerland. Position in the phylogenetic tree: Cuzman *et al.*, 2010, Mareš *et al.*, 2013.

Other strains: PCC 8105, PCC 9601, CCALA 979, CCALA 980, CCALA 981

Habitat: Subaerophytic, surfaces of the limestone rocks. Probably more distributed on subaerophytic alkaline substrates; known from European temperate zone, sometimes on other substrates in greenhouses.

Etymology: Both the generic and specific names express the main cytomorphological characters (common mucilage around cells, bacterial structure of cells, colour of cell content).

Synonymous species:

? *Aphanocapsa nebulosa* A. Braun *in* Rabenhorst, *Alg. Eur.* 246-248: 2454, 1876.

? *Gloeothece coerulea* Geitler, *Arch. Protistenk.* 60: 440, 1928.

? *Gloeothece linearis* Nägeli, *Gatt. Einzell. Alg.*: 58, 1849.

? *Aphanothece caldariorum* Richter *ex* Hansgirg, *Prodr. Algenfl. Böhmen* 2:136, 1892.

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