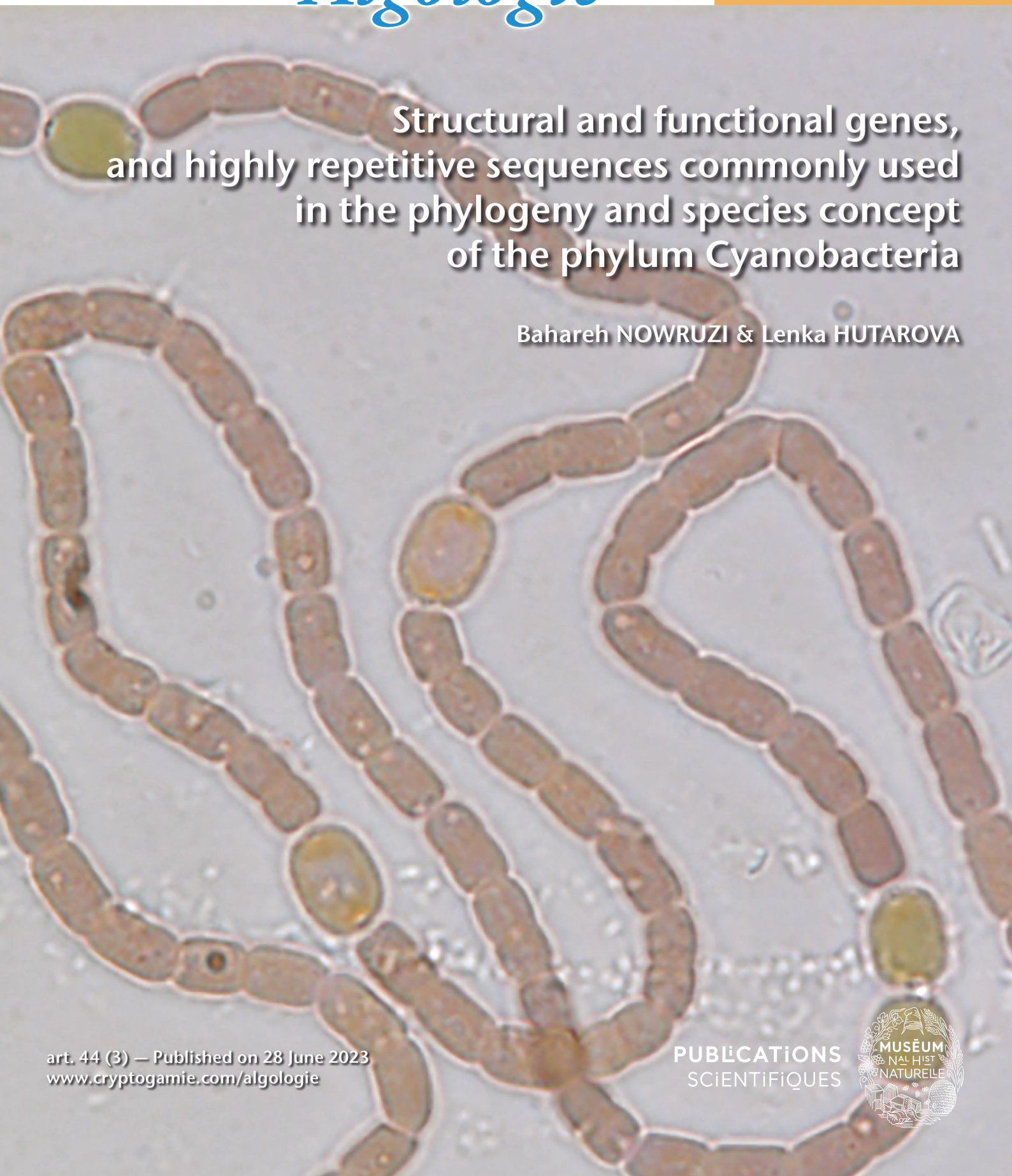
cryptogamie
Algologie
2023 • 44 • 3

Structural and functional genes, and highly repetitive sequences commonly used in the phylogeny and species concept of the phylum Cyanobacteria

Bahareh NOWRUZI & Lenka HUTAROVA



art. 44 (3) — Published on 28 June 2023
www.cryptogamie.com/algologie

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

Couverture / *Cover*:
Cyanobactérie *Aliinostoc* sp. 1 isolée d'une rizière en Iran / *Aliinostoc* sp. 1 cyanobacteria isolated from a paddy field of Iran

Cryptogamie, Algologie est indexé dans / Cryptogamie, Algologie *is indexed in*:
– Aquatic Sciences & Fisheries Abstracts Part I.
– Biological Abstracts
– Chemical Abstracts
– Current Contents
– Marine Science Contents Tables (FAO)
– Science Citation Index
– Publications bibliographiques du CNRS (Pascal)

Cryptogamie, Algologie est distribué en version électronique par / Cryptogamie, Algologie *is distributed electronically by*:
– BioOne® (http://www.bioone.org/loi/crya)

Cryptogamie, Algologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Cryptogamie, Algologie *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish*: ***Adansonia***, ***Geodiversitas***, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Comptes Rendus Palévol***, ***Cryptogamie*** **sous-sections** ***Bryologie***, ***Mycologie***.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 0181-1568 / ISSN (électronique / *electronic*) : 1776-0984

Structural and functional genes, and highly repetitive sequences commonly used in the phylogeny and species concept of the phylum Cyanobacteria

Bahareh NOWRUZI
Department of Biotechnology, Science and Research Branch,
Islamic Azad University, Tehran (Iran)
bahareh.nowruzi@srbiau.ac.ir (corresponding author)

Lenka HUTAROVA
Department of Biology, Faculty of Natural Sciences,
University of Saints Cyril and Methodius, Trnava (Slovakia)

Submitted on 4 May 2022 | Accepted on 22 February 2023 | Published on 28 June 2023

Nowruzi B. & Hutarova L. 2023. — Structural and functional genes, and highly repetitive sequences commonly used in the phylogeny and species concept of the phylum Cyanobacteria. *Cryptogamie, Algologie* 44 (3): 59-84. https://doi.org/10.5252/cryptogamie-algologie2023v44a3. http://cryptogamie.com/algologie/44/3

ABSTRACT
Cyanobacteria are a lineage of Eubacteria that have long captured the attention of scientists. Approximately 5310 species of cyanobacteria have been hitherto described and new species are continually being found, named and described according to established rules. The correct determination of cyanobacteria strains concerns new biotechnological applications as well as ecological studies. There are many situations where it is crucial to recognise distinct algae species, however methods for doing so vary greatly. The aim of this review is to summarize the state of the art of the main and most recent molecular studies focusing on the phylum Cyanobacteria, with particular attention to the most frequently used gene markers. For a long time, the classification method used for cyanobacteria as well as traditionally described species was mainly based on morphology. Over time, integrative taxonomy, which involves the inclusion of many characters and comprehensive taxa sampling, has become the rule as it provides a better resolution of species relationships. For a better resolution of the phylogenies of the phylum Cyanobacteria, it is usually necessary to focus on different genetic markers: from the most common, like the 16S and 23S rRNA, ITS, *rbc*LXS and *rpo*C genes, to genes not so widely used, such as *het*R, *psb*A, *tuf*A, *gyp* and *cpc*BA. Also, the highly repetitive sequences often used for the symbiotic cyanobacteria represent an important factor in the inference of the phylogenetic relationships.

KEY WORDS
Cyanobacteria,
functional genes,
structural genes,
highly repetitive sequences,
phylogeny.

RÉSUMÉ

Gènes structurels, fonctionnels, et séquences hautement répétitives couramment utilisés pour la phylogénie et concept d'espèces dans le phylum des cyanobactéries.

Les cyanobactéries sont une lignée d'eubactéries qui attirent depuis longtemps l'attention des scientifiques. Environ 5 310 espèces de cyanobactéries ont été décrites jusqu'à présent et de nouvelles espèces sont continuellement découvertes, généralement nommées et décrites d'après des règles précises. La détermination correcte des souches de cyanobactéries a des répercussions sur de nouvelles applications biotechnologiques ainsi que sur des études écologiques. Dans de nombreuses situations, il est crucial de reconnaître des espèces d'algues distinctes, mais les méthodes pour y parvenir varient considérablement. L'objectif de cette revue est de faire le point sur les principales et les plus récentes études moléculaires portant sur le phylum des cyanobactéries, en accordant une attention particulière aux marqueurs génétiques les plus fréquemment utilisés. Pendant longtemps, la méthode de classification utilisée pour les cyanobactéries et les espèces traditionnellement décrites était principalement basée sur la morphologie. Au fil du temps, la taxonomie intégrative, qui implique l'inclusion de nombreux caractères et un échantillonnage complet des taxons, est devenue la règle car elle permet une meilleure résolution des relations entre espèces. Pour une meilleure résolution des phylogénies du phylum des cyanobactéries, il est généralement nécessaire de se concentrer sur différents marqueurs génétiques : des plus courants, comme les gènes ARNr 16S et 23S, ITS, *rbc*LXS et *rpo*C, aux gènes moins utilisés, comme *het*R, *psb*A, *tuf*A, *gyp* et *cpc*BA. De plus, les séquences hautement répétitives souvent utilisées pour les cyanobactéries symbiotiques représentent un facteur important dans la construction des relations phylogénétiques.

MOTS CLÉS
Cyanobacteria, gènes fonctionnels, gènes structurels, séquences hautement répétitives, phylogénie.

INTRODUCTION

Cyanobacterial taxonomy has been significantly modified by data from ultrastructural studies, ecological analyses, and, in particular, molecular assisted taxonomy. Indeed, the modern combined approach allows broader recognition and more exact definition of the range of cyanobacterial diversity (Oren 2011). This has led to the concept of "polyphasic approach", which is the most recognised method for the practical determination and description of cyanobacterial taxa (Casamatta *et al*. 2005; Siegesmund *et al*. 2008). The use of this approach has resulted in the creation and definition of many new genera. Their description was based exclusively on their isolated and separated positions in phylogenetic trees (Komárek 2020). Nowadays, the taxonomy of cyanobacteria, due to the rapid increase of these new genera, is unclear and confused. Hence, the constantly evolving cyanobacterial system needs to be clarified (Turner 1997; Komárek 2020). The most problematic issue in the current taxonomy of cyanobacteria might be the authors' different approaches in describing new species. Most characters used previously for species description were challenged by molecular phylogenies which revealed that they are rarely synapomorphic. Description of species based only on the topology of a phylogenetic tree of strains, without observation of morphological characters precludes comparaison with species described on the basis of anatomical features for which molecular data are still lacking (Komárek 2020).

There are three alternative proposals to amend the Rules of the *International Code of Nomenclature of Prokaryotes* (ICNB) to resolve the status of the Cyanobacteria in the prokaryotic nomenclature. Two were earlier published (Oren & Garrity 2014; Pinevich 2015). The third proposal is based on the *International Code of Nomenclature for algae, fungi, and plants* (ICN) (Oren 2020). A summary of the status of cyanobacteria taxonomy and the integration between the ICNB and ICN codes can be found in Wilmotte *et al*. 2017. According to Algae Base, till now we have recognized more than 5000 species belonging to the phylum Cyanobacteria, which are classified into more than 290 genera (Guiry & Guiry 2021). The present review focuses on the phylogenetic evolution of Cyanobacteria, their relationships inferred from molecular studies, as well as on the choice of molecular markers commonly used in the reconstruction of evolutionary relationships (Fig. 1).

RESULTS AND DISCUSSION

Phylogeny of cyanobacteria

Cyanobacteria are referred to as one of the earliest branching bacterial lineages (Pace 2009; Hug *et al*. 2016). A phylogenetic tree has been reconstructed from sequences that are derived from extant species (Valerio *et al*. 2009). For the discovery of phylogenetic relationships among the phylum Cyanobacteria, molecular markers and molecular phylogeny have become powerful tools. Recent research indicates that the phylum Cyanobacteria is related to the nonphotosynthetic groups Sericytochromatia (Soo *et al*. 2017) and Vampirovibrionia (Grettenberger *et al*. 2020), formally Melainabacteria (Di Rienzi *et al*. 2013), and that they share an ancestor. The Silva database, as well as NCBI, recognised the relationship between Melainabacteria and Cyanobacteria and separated them together into still non-defined phyla (Garcia-Pichel *et al*. 2019). Still, molecular phylogeny seems to be necessary for resolving deep-branching relationships within the Cyanobacteria. Cyanobac-

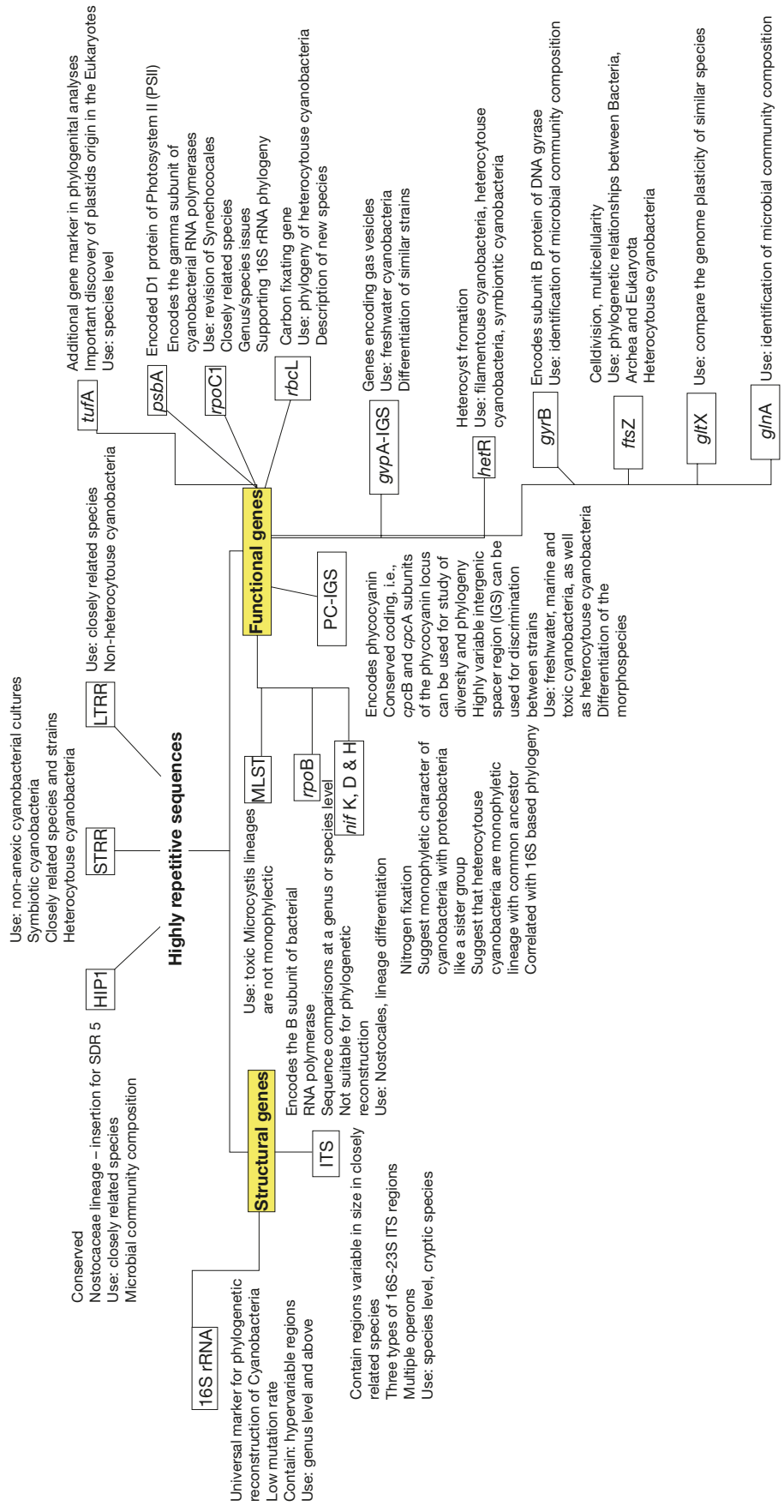


Fig. 1. — A summary of structural and functional genes, and highly repetitive sequences commonly used in the phylogeny of cyanobacteria.

teria as a phylum first evolved in freshwater and colonised benthic and terrestrial habitats during the Proterozoic. It also seems that cyanobacteria evolved from benthic marine environment and some diverged from freshwater ancestors during the Neoproterozoic (1000-542 Mya) (Sánchez-Baracaldo 2015). Within the Cyanobacteria, molecular clock analyses also infer that the marine planktonic cyanobacteria evolved sometime near the end of the Pre-Cambrian (Sánchez-Baracaldo *et al*. 2014). For heterocyte-forming cyanobacteria, these analyses suggested their appearance during the Proterozoic (*c*. 2211-2057 Mya) (Falcón *et al*. 2011).

One of the most widely used phylogenetic trees in the past was the Universal Tree of Life (Forterre 2015). In this tree the length of each branch corresponds quantitatively to the number of base sequence changes that have occurred in that lineage since its divergence from its nearest neighbour. The original definition of the Universal Tree of Life, proposes only vertical evolution through a branching lineage of ancestors and descendants (Strunecký, Wachtlova and Koblizek pers. comm.). The best documented early branch of this tree is the cyanobacterial lineage (Schopf *et al*. 2006). The study based on 16S rRNA sequences also suggested that cyanobacterial species producing baeocytes, heterocytes and true branching filaments are each phylogenetically coherent (Tomitani *et al*. 2006). On the other hand, acquisition of suitable 16S rRNA cyanobacterial sequences is limited by the ability of cyanobacterial strains to grow in culture, which is a prerequisite allowing DNA isolation from unique cyanobacterial taxa. Nevertheless, scepticism over resolving the branching of large clusters by sequencing of 16S rRNA has arisen (Casamatta *et al*. 2005).

It was suggested that, on this basis, all branches diverged within a very short interval of evolutionary distance (Giovannoni *et al*. 1988). Later, authors hypothesised that this topology may reflect the evolutionary development of oxygenic photosynthesis, which allowed an explosive radiation of cyanobacteria in a short time span. No clearly resolved relationships among the clusters may be explained by this rapid radiation or by recombination within 16S rRNA (Yap *et al*. 1999; Boucher *et al*. 2004; Miller *et al*. 2005; Morandi *et al*. 2005).

Therefore, by this approach, reconstruction of the phylogeny of cyanobacteria using only 16S rRNA is very difficult. However, the relationships within the largest monophyletic groups (e.g. heterocyte-forming cyanobacteria) can be potentially misinterpreted by a lot of scattered sequences from databases. Their unstable place in the tree can be caused by their relatively large evolutionary distances from the other investigated cyanobacteria and their consecutive attraction to unrelated sequences ("long branches attraction"). This could be linked to the fact that these false similarities commonly arise between different groups without real phylogenetic affinities, by chance (Korelusová 2008; Baldev *et al*. 2015). In fact, despite three to four billion years of evolution, the phylogenetic information content of 16S rRNA is limited. Consequently, this marker allows only a spot check of the evolutionary history of microorganisms. This is often indicated by locally different topologies of trees based on different markers, data sets, or the application of different phylogenetic approaches. Other issues, such as uneven G + C content distribution, differencing transition-transversion ratios, correlated positions, and the chimera problem with environmental sequences, should be thoroughly investigated in the future.

The absence of organisms at intermediate levels of relatedness prevents researchers from inferring which identities are real and which have occurred accidentally. The unrelated sequences, casually grouped, cause the occurrence of distinctively lower bootstrap values all over the phylogenetic tree. Still, based on the 16S rRNA phylogenetic tree, it is possible to hypothesize that filamentous morphology has a polyphyletic origins within the cyanobacteria and the heterocyte and akinetes forming taxa have a monophyletic origin (Tomitani *et al*. 2006).

Phylogenetic reconstruction based on different molecular markers is also possible, but the number of these sequences is subsequently lower. In the Table 1, we present 16 molecular markers used for reconstruction of phylogenetic relationships within the Cyanobacteria, with the most common primers for them.

Based on multi-gene analyses of four different markers such as 16S rRNA, *het*R, *nif*H and *rpo*C1, the monophyly of Synechococcales, Chroococcales, Oscillatoriales (excluding the *Phormidium*-like lineage) and the Nostocales (including the *Phormidium*-like lineage) were suggested (Thomazeau *et al*. 2010). For nitrogen fixing species of cyanobacteria, phylogenies reconstructed by using *nif*H and *nif*D genes show differently supported branches within the cyanobacterial phylogenetic tree. Contrary to *nif*H and *nif*D gene markers, heterocyte-forming genera form a monophyletic lineage (Henson *et al*. 2004).

The use of several genes with a presumed vertical evolution (Komárek *et al*. 2014) leads to a possible bias towards well established patterns, which could omit the large number of genes needed for evolutionary success. This selective approach could lead to misunderstanding of phylogenetic relationships, as well as a wrong interpretation of the evolutionary history of the phylum Cyanobacteria. The phylogenetic trees of cyanobacteria obtained from conservative core genes (e.g. *rpo*C1, *rbc*L and *tuf*A) with relatively slow evolutionary rates (like the 16S rRNA), are typologically similar to trees based on 16S rRNA genes (Strunecký, Wachtlova and Koblizek pers. comm.). When compared to multilocus analyses based on whole genomes of cyanobacteria, the use of 16S based trees is a better solution at the genera rank (Mareš 2018). Also, the first attempt to use a multilocus analysis for cyanobacterial taxonomy by Komárek *et al*. 2014 have shown that some cyanobacterial orders are polyphyletic and have leaded to the description of some new orders and families. In the multilocus based tree, the mixed group of filamentous and unicellular species is evident. This supports the hypothesis that multicellularity represents a trait which had multiple sequential origins or the trait was lost during the long evolution of the cyanobacteria (Schirrmeister *et al*. 2013; Dvořák *et al*. 2014b). The analyses of these trees also showed us that both the botanical and bacterial codes used for cyanobacteria are not sufficient for their taxonomy and must be changed

Table 1. — Target genes and oligonucleotide primers used in phylogeny of cyanobacteria.

Target gene/ sequence	Type of gene	Sequence 5' 3'	Reference
*rpo*B	Functional: the *rpo*B gene encodes the β subunit of bacterial RNA polymerase	F GTAGTTGTARCCNTCCCA R RCMGCMGACGAAGAAGACG	Rajaniemi *et al*. 2005
16S rRNA	Structural: the 16S rRNA gene (small subunit of the ribosome) is the most conserved DNA in all cells. It has a universal distribution in prokaryotes	27F1 5'-AGAGTTTGATCCTGGCTCAG (8-27) (30-52) 23S30Ra 5'-CTTCGCCTCTGTGTGCCTAGGT	Neilan *et al*. 1997 Lepère *et al*. 2000
*nif*D	Functional: nitrogenase is an α2β2 tetramer encoded by *nif*K (β subunits) and *nif*D (α subunits), while the reductase is a α2 dimer encoded by *nif*H	*nif*D552-F (5'-TCCGKGGKGTDTCTCAGTC-3') *nif*D861-R (5'-CGRCWGATRTAGTTCAT-3')	Roeselers *et al*. 2007
*nif*H		2F (5'-CGTAGGTTGCGACCCTAAGGCTGA-3') 2R (5'-GCATACATCGCCATCATTTCACC-3')	Gaby & Buckley 2012
*rpo*C1	Functional: encodes the gamma subunit of cyanobacterial RNA polymerases and is homologous to the chloroplast RNA polymerase C1 subunit	Rcf (5'-TGGGGHGAAAGNACAYTNCCTAA-3') Rcr (5'-GCAAANCGTCCNCCATCYAAYTGBA-3')	Rantala *et al*. 2004
PC-IGS	Functional: the gene encoding of the major light-harvesting accessory pigment proteins, particularly the phycocyanin operon (*cpc*), including the intergenic spacer (IGS) between two phycobilisome (bilin) subunits *cpc*B and *cpc*A and the corresponding flanking regions (cpcBA-IGS), have also been targeted for phylogenetic studies of cyanobacteria	*cpc*B (5'-GGCTGCTTGTTTACGCGACA-3') *cpc*A (5'-CCAGTACCACCAGCAACTAA-3')	Neilan *et al*. 1995
16S-23S ITS	Structural: this region is another useful marker in the taxonomy of cyanobacteria. It is an internally transcribed spacer between genes for small (16S) and large (23S) ribosomal subunits	16SF (5'TGTACACACCGGCCCGTC3') 23SR (5'-CTCTGTGCCTAGGTATCC-3')	Iteman *et al*. 2000
*rbc*L	Functional: this gene is encoding large subunit D-ribulose 1,5-bisphosphate carboxylase-oxygenase	F (5'-GACTTCACCAAAGAYGACGAAAACAT-3') R (5'-GAACTCGAACTTRATYTCTTTCCA-3')	Fewer *et al*. 2007
*tuf*A	Functional: the *tuf*A gene which encodes the elongation factor Tu has a central role in protein synthesis	F (5'-CACGTDGAYTGYCCNGGNCACGCTG-3') R (5'-ATNCGRTCNCCDGGCATAACCATTTC-3')	Fewer *et al*. 2007
*psb*A	Functional: the D1 protein of Photosystem II (PSII), encoded by the *psb*A genes, is an indispensable component of oxygenic photosynthesis	*psb*A86F (5'-TTTATGTGGGTTGGTTCGG-3') *psb*A980R4 (5'-TGAGCATTACGCTCGTGC-3')	Junier *et al*. 2007
ERIC1A	Highly repetitive genes: they are located in extragenic regions and can be transcribed and their distribution in eubacteria has revealed their application to fingerprinting of bacterial genomes	(5'-ATGTAAGCTCCTGGGGATTCAC-3')	De Bruijn 1992
ERIC1B		(5'-AAGTAAGTGACTGGGGTGAGCG-3')	De Bruijn 1992
STRR1a	Highly repetitive genes: these sequences consist of three different simple tandem heptanucleotide sequence repeats	(5'-CCARTCCCCARTCCCC-3')	Rasmussen & Svenning 1998
HIP-TG	Highly repetitive genes: the palindrome that was being explored was an octameric (8-nucleotides long) palindrome known as a highly iterated palindrome 1 (HIP1) and have been considered as the most accepted tool for assessing microbial diversity	(5'-GCGATCGCTG-3')	Smith *et al*. 1998
HIP-GC		(5'-GCGATCGCGC-3')	Smith *et al*. 1998
HIP-CA		(5'-GCGATCGCCA-3')	Smith *et al*. 1998

(Mareš 2018). According to (Mareš 2018), the orders Gloeobacterales, Spirulinales, Chroococcidiopsidales, and Nostocales represent probably monophyletic lineages. Pleurocapsales and Chroococcales represent intermixed but relatively compact lineages, which need to be taxonomically solved in the future. Synechococcales and Oscillatoriales seem to be exclusively polyphyletic and need to be revised. The main issue with this taxonomic approach is a lack of whole genomic data, and reference strains and sequences are required for future analyses (Mareš 2018).

Whole genome phylogeny of cyanobacteria

Until quite recently, the most available genome data from Cyanobacteria belonged to marine unicellular taxa (*Synechococcus* Nägeli and *Prochlorococcus* Chisholm *et al*.) (Sánchez-Baracaldo & Cardona 2020). The increase in sequencing of cyanobacterial genomes from different environments like soil (Churro *et al*. 2020), freshwater (Tanabe *et al*. 2018; Teikari *et al*. 2019; Boden *et al*. 2021) and different extreme environments (Stucken *et al*. 2013; Urrejola *et al*. 2019), help to resolve deep-branching relationships within the phylum Cyanobacteria (Schirrmeister *et al*. 2015). The size of the cyanobacterial genomes directly correlates with their habitat adaptation (Prabha *et al*. 2016). Recent studies show that the size of the genomes of terrestrial and freshwater strains is larger than marine ones (Chen *et al*. 2021). In fact, we can assume that species that colonise rapidly changing environments, often with harsh conditions and unstable environment, have larger genomes (Bentkowski *et al*. 2017; Chen *et al*. 2021).

The main problem with the analysis of whole genomes lies in the fact that the genome database is still considerably smaller in term of taxa sampling than the 16S rRNA database (Strunecký, Wachtlova and Koblizek pers. comm.). While the phylogeny of Cyanobacteria based on 16S rRNA or core genes shows a similar topology based on their similar slow evolutionary rate (Strunecký, Wachtlova and Koblizek pers. comm.), where the genus *Gloeobacter* Rippka, Waterbury & Cohen-Bazire and thermophilic *Synechococcus* species often represent the group as the most primitive cyanobacteria (Mareš *et al*. 2013). Another hypothesis presented phylogenomic tree based on the whole genome (at least 1000 genes), where the species from *Prochlorococcus*, marine *Synechococcus* and *Cyanobium* Rippka & Cohen-Bazire form a separate clade (Strunecký, Wachtlova and Koblizek pers. comm.). Outgroups in the trees are related to other eubacteria, so it does not affect the clustering within Cyanobacteria (Strunecký, Wachtlova and Koblizek pers. comm.; Strunecký *et al*. 2022).

Recently, Strunecký, Wachtlova and Koblizek, proposed ten new orders and fifteen new families based on 120 concatenated genes. Moreover, they found that phylogenetic evidence supports merging several intermixed groups, such as the orders Chroococcales and Pleurocapsales, or several families of heterocytous cyanobacteria fused into Scytonemataceae, Hapalosiphonaceae, Tolypotrichaceae, and Aphanizomenonaceae. Moreover, besides Cyanophyceae, another class, Vampirovibriophyceae is proposed to belong to the Cyanophyta phylum.

As mentioned above, they introduced 10 orders: Aegeococcales with new family Aegeococcaceae O.Strunecký & J.Mareš; Acaryochloridales with families Acaryochloridaceae J.Komárek, J.Kaštovský, J.Mareš & J.R.Johansen and Thermosynechococcaceae J.Strunecký & J.R.Johansen; Prochlorotrichales with family Prochlorotrichaceae Burger-Wiersma L.J.Stal & L.R.Mur; Nodosilineales with families Nodosilineaceae O.Strunecký & J.Mareš, Cymatolegaceae O.Strunecký & J.Mareš and Persinemataceae O.Strunecký & J.Mareš; Oculatellales with family Oculatellaceae T.Mai & J.R.Johansen; Leptolyngbyales with families Leptolyngbyaceae J.Komárek, J.Kaštovský, J.Mareš & J.R.Johansen, Trichocoleusaceae T.Mai & J.R.Johansen and Neosynechococcaceae O.Strunecký & J.Mareš; Geitlerinematales with family Geitlerinemataceae O.Strunecký & J.Mareš; Desertifilales O.Strunecký & J.Mareš with family Desertifilaceae P.Hašler, D.Casamatta, P.Dvořák & A.Poulíčková; Coleofasciculales O.Strunecký & J.Mareš with families Coleofasciculaceae J.Komárek, J.Kaštovský, J.Mareš & J.R.Johansen and Wilmottiaceae O.Strunecký & J.Mareš; and Gomontiellales O.Strunecký & J.Mareš with families Gomontiellaceae A.AElenkin ex L.Geitler, Chamaesiphonaceae M.Borzì, Cyanothecaceae J.Komárek, J.Kaštovský, J.Mareš & J.R.Johansen and Konicacronemataceae O.Strunecký & J.Mareš. In existing orders they described new families Anthocerotibacteraceae O.Strunecký & J.Mareš in Gloeobacterales; Thalassoporaceae O.Strunecký & J.Mareš in Pseudanabaenales; Aerosakkonemataceae O.Strunecký & J.Mareš in Oscillatoriales; Lusitaniellaceae O.Strunecký & J.Mareš in Spirulinales; and Halothecacae O.Strunecký & J.Mareš in Chroococcales.

Based on the study of the genomes, we could predict, that within the Oxyphotobacteria, the first diverse are the Gloeobacterales, closely followed by the early branching Synechococcales with Gloeomargaritales branching in a successive pattern (Chen *et al*. 2021). The PSC clade (marine species *Prochlorococcus* spp., marine *Synechococcus* species and species from the genus *Cyanobium*), which contained species from marine picocyanobacteria, formed a separate clade from other cyanobacterial lineages. Studies suggest that the phylogenetic position of the PSC clade is due to historical separation (Dvořák *et al*. 2014b). Species from these clades also contained noticeably smaller genomes compared to other cyanobacteria, caused by reduced rates of mutation and specialisation in genomes due to high selection pressure in the environment (Strunecký, Wachtlova and Koblizek pers. comm.). If focused on selected groups, such as *Leptolyngbya* Anagnostidis & Komárek, *Oscillatoria* Vaucher ex Gomont, *Synechococcus*, the phylogenetic trees constructed based on whole genome sequencing as well as multigene analyses suggested some changes in the position of traditionally described species (Walter *et al*. 2017).

The positions of major cyanobacterial taxonomical groups deduced from phylogenomic analyses correspond with their phylogenetic positions based on 16S rRNA, except for selected genera, which seem to be polyphyletic. Also, the use of multigene analyses seems to be insufficient for distinguishing very closely related species (Mareš 2018). The increase of metagenomic and whole genome sequencing of cyanobacteria brings new data, which can enlighten the cyanobacterial taxonomy in the future. Nevertheless, known genomes usually represent one of the 100 genera, with more represented taxa from *Nostoc* Vaucher ex Bornet & Flahault, *Leptolyngbya*, *Prochlorococcus*, *Synechococcus*, *Planktothrix* Anagnostidis & Komárek, *Microcystis* Lemmermann and *Calothrix* Bornet & Flahault (Dextro *et al*. 2021).

Horizontal gene transfer and its significance in molecular phylogeny

Horizontal gene transfer (HTG), potentially followed by recombination with or replacement of resident homologs,

represents an important factor in the phylogeny of prokaryotic organisms such as cyanobacteria and shapes their evolutionary history (Koonin *et al.* 2001). For example, studies of atypical nucleotides in individual cyanobacteria genomes indicate that cyanobacteria acquired between 9.5-16.6% of their genes through HGT (Nakamura *et al.* 2004) and *c.* 50% of extended gene families putatively have a history of HGT (Zhaxybayeva *et al.* 2006).

Primarily, HGT is accomplished with plasmid transposons, as well as other mobile elements and viruses (Avni & Snir 2020). For cyanobacteria, the main vectors in gene transfer are cyanophages (Sabehi *et al.* 2012; Shestakov & Karbysheva 2015; Nowruzi & Blanco 2019). They can move genes (for example, photosynthesis-related genes), which play an important role in cyanobacterial adaptation and survival (Kloub *et al.* 2021). Also, the integration of cyanobacterial genes in cyanophages suggests that the gene transfer occurred in both directions (Papini, Falsini and Karssa pers. comm.). According to a genomic study (Kang *et al.* 2014), the cyanobacterial genome can be divided into two sets of genes: 1) "stable core genes", which have a common evolutionary history and are usually not transferred too much; and 2) "variable shell", which contains genes that are not common for every strain of cyanobacteria, and are present in no or various numbers of copies in the genome. These are often targeted by horizontal gene transfer or homology recombination (Shi & Falkowski 2008). The genes suitable for transfer can be divided into four categories, as genes responsible for: 1) information, storage and processing; 2) cellular processes and signalling; 3) metabolism; and 4) poorly characterised genes (Zhaxybayeva *et al.* 2006). Horizontal transfer usually occurs between housekeeping genes such as 16S, *fts*Z, *glt*X and *rec*A (Thompson *et al.* 2009; Hoffmann *et al.* 2012; Meyer *et al.* 2017).

The transfer of core genes, which are involved in transcription, translation and related processes and are rarely horizontally transferred, has a greater impact on phylogenetic relationships (Woese 2004). Also, multigene transfer can occur among cyanobacteria and fungi (Szöllősi *et al.* 2015).

Nowadays, HGT seems to be a major factor in species delimitation in cyanobacteria (Papini, Falsini and Karssa pers. comm.) and plays a key role in the selection pressure leading to cyanobacterial diversification (Willis & Woodhouse 2020). Shestakov & Karbysheva 2015 discovered that coevolution of the cyanobacterial genome and cyanophages, as well as a strict cyanophage-host relationship, could have a significant impact on cyanobacterial species delimitation. This could be due to some cyanophages' affinity for specific strains of cyanobacteria. In fact, HGT occurs in the same environment within the species with higher phylogenetic affinity (Dvořák *et al.* 2018). The species could then evolve in two ways. If the frequency of homologue recombination (HR) is higher than the mutation rate, this species will evolve in a similar mode to that due to sexual exchange of genetic material. If the frequency of HR is lower than the mutation rate, the population will remain clonal (Fraser *et al.* 2007). The evidence for the impact of HGT on prokaryotic evolution is significant. It was suggested that between Bacteria and

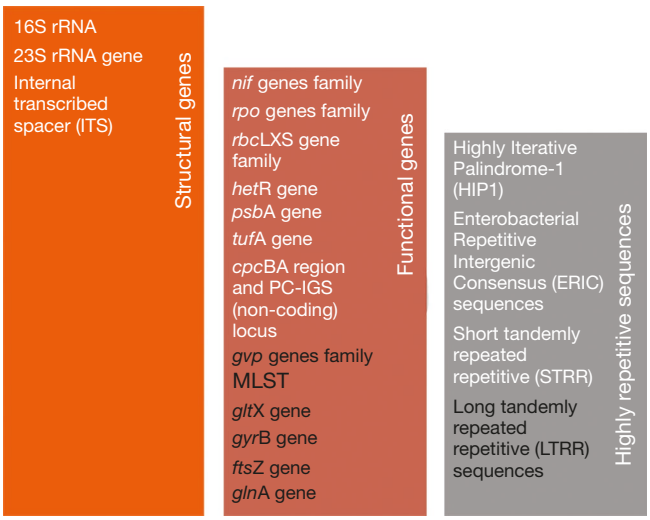


Fig. 2. — Phylogeny of common or less studied genetic markers. According to the literature review, less common studied genetic marker has been highlighted.

Archaea there exists the HGT barrier, which is responsible for the rare transfer of genes between these organisms (Avni & Snir 2020). On the other hand, it was also discovered, that HGT between two strains of bacteria is the most common type of gene transfer. With the discovery that 16S rRNA and other "housekeeping" core genes are also capable, though in limited ways, of being transferred by HGT, their use for proper phylogenetic reconstruction may be questioned.

Structural and functional genes

A structural gene codes for ribosomal or transfer RNA or for proteins (such as enzymes) other than a regulatory factors. Functional genes are involved in transcription, translation, regulation of gene expression, and protein-protein interactions, as opposed to the static aspects of genomic information, such as DNA sequences or structures. The best use of these genes in phylogenetics is shown in Table 2 and Figure 2.

16S rRNA and 23S rRNA gene

Phylogenetic analyses are used to estimate the evolutionary relationships among organisms, and the phylogenetic analysis of the 16S rRNA gene has revealed close relationships among cyanobacteria, and it has a central role in inferring phylogenetic relationships and in the identification of bacteria (Edwards *et al.* 1989; Lepère *et al.* 2000; Vaz *et al.* 2015; Jahodářová *et al.* 2018). The 23S rRNA gene is longer than the 16S rRNA gene and, consequently, it contains more informative sites and leads to better resolution, but the sequence database of the 23S rRNA gene is smaller in comparison to the 16S rRNA gene (Turner 1997; Garrity *et al.* 2005). The 16S rRNA gene is the most used for cyanobacterial phylogeny. This marker is universal in prokaryotes and eukaryotes, is stable, contains nine informative variable regions, and the occurrence of these sequences in the databases is relatively large (Johansen *et al.* 2017a; Johnson *et al.* 2019).

The nature of this sequence, with a mosaic of highly conserved regions interspersed with variable and hypervariable

Table 2. — Application of structural and functional genes in taxonomy and molecular phylogeny.

Genes	Taxa	References
Structural genes		
16S rRNA	Confirmation monophyletic in the orders of Nostocales and Pleurocapsales and polyphyletic in the order of Chroococcales, Oscillatoriales, and Stigonematales	Wanigatunge *et al*. 2014
	Calothrix	Sihvonen *et al*. 2007
	Calothrix, *Gloeotrichia* and *Tolypothrix*	Johansen *et al*. 2017b
	Anabaena, *Aphanizomenon*, *Oscillatoria* and picocyanobacterial genera such as *Synechococcus* and *Synechocystis*	Lyra *et al*. 2001; Wilmotte & Herdman 2001; Gugger *et al*. 2002; Suda *et al*. 2002
	Planktothrix agardhii, *Nodularia* and *Microcystis*	Otsuka *et al*. 2000; Lyra *et al*. 2001; Humbert *et al*. 2013
	Azolla and *Anabaena*	Svenning *et al*. 2005
ITS	*Scytonema hyalinum*	Johansen *et al*. 2017b
	Strain *Anabaena* sp. PCC 7120	Katoh *et al*. 2003
	Discrimination of a variety of cyanobacteria by means of DGGE analysis	Janse *et al*. 2003
	Leptolyngbya corticola	Johansen *et al*. 2011
	Prochlorococcus and *Synechococcus*	Rocap *et al*. 2002
	Roholtiella	Bohunická *et al*. 2015
	Microcoleus vaginatus	Boyer *et al*. 2002
	Oxynema aestuarii	Mahansaria *et al*. 2018
	Dapisostemon and *Streptostemon*	Hentschke *et al*. 2016
	Mojavia pulchra and *Trichocoleus desertorum*	Řeháková *et al*. 2007; Muhlsteinova *et al*. 2014
	Ancylothrix as a new genus of *Phormidiaceae*	Martins *et al*. 2016
	Cephalothrix komarekiana and *Cephalothrix lacustris*	León-Tejera *et al*. 2016
	Pleurocapsales *Hyella patelloides* LEGE 07179	Brito *et al*. 2017
	Oculatella	Osorio-Santos *et al*. 2014
	Revise the genus *Geitlerinema* and a description of the genus *Anagnostidinema* (Oscillatoriophycidae, Cyanobacteria)	Strunecký *et al*. 2016
	Nostoc commune and *Nostoc punctiforme*	Řeháková *et al*. 2007
	Pantanalinema and *Alkalinema*	Vaz *et al*. 2015
	Mastigoteuthis psychrophila	Berrendero Gómez *et al*. 2016
	Phyllonema (Rivulariaceae, Cyanobacteria)	González-Resendiz *et al*. 2018
	Elainella	Jahodářová *et al*. 2018
	Brasilonema geniculatum and *Calothrix dumus*	Villanueva *et al*. 2019
	Roholtiella fluviatilis, *Roholtiella bashkiriorum*, *R. fluviatilis* and *R. bashkiriorum*	Bohunická *et al*. 2015
	Kyrtuthrix	León-Tejera *et al*. 2016
	Desmonostoc danxiaense (Nostocales, Cyanobacteria)	Cai *et al*. 2018
	Nunduva	González-Resendiz *et al*. 2018
	Rivularia halophila (Nostocales, Cyanobacteria)	Shalygin *et al*. 2018
Functional genes		
nif K, D and H	*Plectonema boryanum* and *Anabaena torulosa*	Apte & Thomas 1987
	Anabaena, *Aphanizomenon* and *Nostoc*	Gaby & Buckley 2012
	Cylindrospermopsis raciborskii	Dyble *et al*. 2002
	Trichodesmium thiebautii	Zehr *et al*. 2008
	Anabaena, *Aphanizomenon* and *Nostoc*	Galhano *et al*. 2011
	Nostoc and *Anabaena*	Henson *et al*. 2004
	Gloeothece sp., *Calothrix* sp. and *Anabaena* sp.	Kallas *et al*. 1983
	Azolla and *Anthoceros*	Meeks *et al*. 1988
*het*R	*Anabaena*, *Aphanizomenon*, and *Nostoc*	Galhano *et al*. 2011
*tuf*A	*Synechococcus*	Honda *et al*. 1999
PC-IGS region	*Nodularia spumigena*, *Anabaena circinalis* and *Microcystis aeruginosa*	Miller & McMahon 2011
	Nodularia	Bolch *et al*. 1999
	Arthrospira	Lyra *et al*. 2001
	Geitlerinema and *Microcystis*	Piccin-Santos *et al*. 2014
	Nodularia	Barker *et al*. 2000
	Synechococcus	Robertson *et al*. 2001
	Arthrospira	Kumar *et al*. 2017
	Oscillatoriales	Premanandh *et al*. 2006
*gvp*A-IGS	*N. spumigena*	Barker *et al*. 1999
	Nodularia	Barker *et al*. 2000
	Arthrospira	Miklaszewska *et al*. 2012
*rbc*L	*Aphanizomenon*	Gugger *et al*. 2002
	Anabaena, *Aphanizomenon*, *Nostoc* and *Trichormus*	Rajaniemi *et al*. 2005
	Anabaena	Katrianna *et al*. 2008

Table 2. — Continuation.

Genes	Taxa	References
*rpo*C1	*Anabaena* sp. PCC 7120	Bergsland & Haselkorn 1991
	Cylindrospermum raciborskii	Wilson *et al*. 2000
	C. raciborskii	Morozova *et al*. 2002
*rpo*B	*Anabaena*/*Aphanizomenon*	Rajaniemi *et al*. 2005
*psb*A	*Synechococcus* sp.	Garczarek *et al*. 2008
	Cylindrospermopsis and *Raphidiopsis*	Wu *et al*. 2011
MLST	*M. aeruginosa*	Tanabe *et al*. 2007
*glt*X	*Gloeobacter violaceus* GluRS	Luque *et al*. 2008
	Microcystis cf. *aeruginosa* CV01	El Alaoui *et al*. 2003
	M. aeruginosa	Humbert *et al*. 2013
*gyr*B	*Phormidium*	Sciuto *et al*. 2012
*fts*Z	Archaea, Bacteria and Eukaryota	Demchuk & Blium 2005
*gln*A	*Prochlorococcus*	El Alaoui *et al*. 2003
	Sulfolobus solfataricus	Sanangelantoni *et al*. 1990
Highly repetitive genes		
HIP1	*Synechococcus* PCC 6301	Gupta *et al*. 1993
STRR	*Calothrix* and *Microcystis*	Mazel *et al*. 1990; Asayama *et al*. 1996
	Azolla	Zheng *et al*. 1999
	Cylindrospermopsis raciborskii	Wilson *et al*. 2000
	Gunnera and *Azolla*	Bergman *et al*. 2008
	Nostoc and *Anabaena*	Shukla *et al*. 2013
	Westiellopsis	Selvakumar & Gopalaswamy 2008
	C. raciborskii	Chonudomkul *et al*. 2004
LTRR	*Anabaena strain* PCC7120	Masepohl *et al*. 1996
	Anabaena	Prasanna *et al*. 2006
	Anabaena	Ezhilarasi & Anand 2016

stretches, makes it extremely convenient for PCR primer design (García-Martínez *et al*. 1999). In addition, the vast database of sequences available for this gene makes it possible to search for cultivated close relatives.

However, the usage of 16S rRNA for the study of biodiversity can be tricky. One of the problems reflects the fact that the genes for 16S rRNA are extremely constant in size. The 16S rRNA gene sequence is about 1550 bp long and is composed of both variable and conserved regions (García-Martínez *et al*. 1999). The problem arises from the fact that 16S, 23S, and 5S with at least one tRNA and internal transcribed spaces are usually linked in one operon. In bacterial genomes, these operons can be found in multiple copies (between one and fifteen), and the 16S rRNA can differ between these operons. Although intragenomic divergence of the 16S rRNA genes can be as high as 11.6%, generally it seems to be lower than 1% (Case *et al*. 2007; Sun *et al*. 2013). This caused problems in the identification of closely related species (Acinas *et al*. 2004). Based on 16S rRNA, traditionally, the identity of sequences > 95% represents a new genus, whereas sequences with a similarity > 97% represent the same species (Schloss & Handelsman 2005; Johnson *et al*. 2019).

However, usage of this marker has some opponents, and doubts regarding its credibility were raised very early after the expansion of molecular methods in the taxonomy of bacteria. The similarity of some bacterial genomes based on DNA-DNA hybridisation to the similarity of 16S rRNA sequences from the same strains was compared (Fox *et al*. 1992). Results showed that the similarity between genomes does not always correlate with the similarity between 16S rRNA sequences. For example, when the 16S rRNA sequence similarity is smaller than 97.5%, the similarity by DNA-DNA hybridization is smaller than 70% (Stackebrandt & Goebel 1994).

It is found that only trees based on three metabolic genes (Enolase, UppS, and HemB) were incongruent with the other gene trees, which is probably due to HGT, gene duplication, or long-branch attraction (Sanchez-Baracaldo *et al*. 2005). The main disadvantage of marker genes other than 16S rRNA genes is that their sequence databases are currently rather small (Ludwig *et al*. 2009). Still, the 16S rRNA represents the most common genetic marker for cyanobacterial taxonomy. The significance and expansion of 16S rRNA are shown in the statistics for the number of 16S rRNA sequences deposited in GenBank (http://www.ncbi.nlm.nih.gov), which list *c*. 306 875 sequences from cyanobacteria on 4 April 2022 (http://www.ncbi.nlm.nih.gov).

The phylogenetic analysis of the 16S rRNA gene has revealed close relationships among cyanobacteria, indicating that the diversification of cyanobacteria happened within a short period of time (Giovannoni *et al*. 1988; Wilmotte & Herdman 2001), probably between 2450 and 2100 Ma (Tomitani *et al*. 2006). Based on the phylogeny of the 16S rRNA genes, chlorophyll-a/b-containing Prochlorales (Prochlorophyta) were shown to be polyphyletic (Urbach *et al*. 1992) and to cluster with Cyanobacteria (Wilmotte 1994; Palenik & Swift 1996). This suggests that the Prochlorales and Cyanobacteria shared a common ancestor, and that the Prochlorales are not a valid phylogenetic group. The 16S rRNA sequence analysis data confirmed that the order Nostocales and the order Pleurocapsales are monophyletic, while the orders Chroococcales, Oscillatoriales, and Stigonematales are polyphyletic (Wanigatunge *et al*. 2014). The 16S rRNA genes from 42 cyanobacterial cultures and environmental samples belonging to the genus

Calothrix and the morphologically similar genera *Rivularia* C.Agardh ex Bornet et Flahault, *Gloeotrichia* J.Agardh ex Bornet & Flahault, and *Tolypothrix* Kützing ex Bornet & Flahault were sequenced. The results showed large sequence diversity among the same morphotype within the *Calothrix* strains. Moreover, it was discovered that the *Calothrix*, *Gloeotrichia*, and *Tolypothrix* lineages are not monophyletic; on the other hand, they contain a high level of genetic diversity (Sihvonen *et al*. 2007). However, the cyanobacterial orders/subsections have not been supported by the 16S rRNA gene sequence analysis (Giovannoni *et al*. 1988; Turner 1997; Gugger *et al*. 2002; Ishida *et al*. 2009). Only heterocytous cyanobacteria belonging to the two orders/subsections appear to be monophyletic in the 16S rRNA gene analysis (Wilmotte & Herdman 2001; Gugger *et al*. 2002).

At the species level, the usage of this marker is quite problematic. Also, the phylogenetic position of several cyanobacterial strains seems to be incongruent with their morphology and does not correspond to their current classification as species from the genera *Anabaena* Bory de Saint-Vincent, *Aphanizomenon* Morren ex Bornet & Flahault (Lyra *et al*. 2001; Gugger *et al*. 2002), *Oscillatoria* (Suda *et al*. 2002), and picocyanobacteria such as *Synechococcus* and *Synechocystis* Sauvageau (Wilmotte & Herdman 2001). In some cases, strains of a genus or species formed a monophyletic cluster in the 16S rRNA gene analysis, e.g. *Planktothrix agardhii* (Gomont) Anag. & Komar, *Nodularia* (Mertens in Jürgens) ex Bornet & Flahault (Lyra *et al*. 2001) and *Microcystis* (Otsuka *et al*. 2000; Lyra *et al*. 2001; Humbert *et al*. 2013; Nowruzi & Lorenzi 2021).

However, the morphologically distinguished *Microcystis* species were found to be genetically very closely related to each other (Otsuka *et al*. 2000). Unification of different *Microcystis* species into a single species has been proposed (Otsuka *et al*. 2000). The work focused on the phylogeny of symbiotic cyanobacteria within the genus *Nostoc* and, based on 16S rRNA sequence analyses, related the affiliation of the higher plant *Azolla* Lam. with the species from the genus *Anabaena*. This showed that the strains within this genus can form symbioses within the additional hosts (Svenning *et al*. 2005). These phenomena were described by the discovery of five operons containing 16S rRNA in the species *Scytonema hyalinum* N.L.Gardner, *Scytonema* sp. (NIES-4075) and *Scytonema* sp. (HK-05). Four of them were more similar than 99.5% and were able to be distinguished by the divergent 16S-23S ITS between each other. The other type of operon shows 96% sequence identity to 16S rRNA with *Scytonema sensu stricto* and 94-95% sequence similarity with sequences outside the Scytonemataceae. This seems to be caused by HGT, and it is proof of the ability of core genes to undergo HGT (Johansen *et al*. 2017a).

The sequence of the genomes of strains from culture collections around the world, built phylogenetic trees and compared them with trees built based on 16S rRNA, show that the taxonomic inconstancies in cyanobacterial taxonomy are caused by the morphological plasticity of cyanobacteria to some extent. Also, results show an irregularity between different databases regarding cyanobacterial taxonomy. The commonly used databases, CyanoDB and AlgaeBase, whose taxonomy is based on 16S rRNA data, have different phylogenetic positions for some strains at the family level than the Silva database, commonly used in genomic research (Hirose *et al*. 2021). An example could be the genus *Phormidesmis* Turicchia, Ventura, Komárková & Komárek, which is based on 16S taxonomically assigned to Leptolyngbyaceae (Raabova *et al*. 2019) in the CyanoDB as well as AlgaeBase (Guiry & Guiry 2021) and NCBI database (Schoch *et al*. 2020). In the Silva database, these strains belong to Phormidiaceae, which is not validated in any of the 16S-based databases (Hirose *et al*. 2021).

The 16S rRNA as a marker represents, in the near past, the best marker widely used for phylogenetics and for describing new species and genera within the phylum Cyanobacteria. Also, a cryptic species was discovered due to its use (Komárek *et al*. 2014). Nowadays, new genera are still described based on this marker, such as *Alborzia* Nowruzi & Soares (Nowruzi & Soares 2021), *Cryptochroococcus* Y.Wang, N.Jia & R.Li (Wang *et al*. 2021), *Waterburya* Bonthond & Shalygin (Bonthond *et al*. 2021), *Vermifilum* D.E.Berthold, Lefler & Laughinghouse (Berthold *et al*. 2021), *Microcoleusiopsis* R.Geng & G.Yu (Geng *et al*. 2021), *Pseudochroococcus* (Duval *et al*. 2022) and much more. Although this marker seems to be no longer exclusively sufficient for phylogenetic reconstruction, it remains an invaluable tool for basic classification of cyanobacterial strains at the genus level and is still widely used.

Internal transcribed spacer (ITS) between 16S and 23S rRNA

With a few exceptions, different subunits within the operon commonly follow the gene arrangement of order 16S-23S-5S. The typical number of copies of operons in cyanobacteria is one to five. This number depends on morphological complexity and usually increases with it (Iteman *et al*. 2000; Schirrmeister *et al*. 2015). The small genome bacteria are associated with the most deviations in these types of structures. This suggests that intergenic spacer regions with variable length could be found between the 16S and 23S genes, as well as between the 23S and 5S. This concrete region shows extreme variability in size, even within the closely related taxa (García-Martínez *et al*. 1999). Size patterns can be used to characterise different communities of bacteria or archaea, and the widely divergent sequence allows the detection of species-like units very precisely by PCR, oligo-probe, or even long DNA probe (using the whole spacer region) hybridisation (Berrendero Gómez *et al*. 2016).

The internally transcribed spacer between genes for small (16S) and large (23S) ribosomal subunits represents a useful marker in cyanobacterial taxonomy. In the case of discrete species or OTU (operational taxonomic units) of closely related taxa, the spacer region seems to be highly conserved. While the ITS regions of cyanobacteria vary in length from 283 to 545 nucleotides and contain both tRNA-Ile and tRNAAla genes, or neither, there is no correlation between ITS size and tRNASB coding capacity (Iteman *et al*. 2000). However, occasionally longer ITS sequences, longer than

1000 bp, can be found (Rocap *et al*. 2002). The average length of ITS is between 442 and 694 nt for species that belong to the Cyanobacteria (Marquardt & Palinska 2007). In taxonomy and population genetics, the ITS region is worth applying at the species level in population genetics because it possesses sufficient variability. This has an advantage over 16S rRNA, which seems to have a more suitable resolution for genus level or above. The total generated amplicon then needs to be cloned (Nowruzi *et al*. 2016), and then the individual clones are sequenced separately (Boyer *et al*. 2001).

Sequences of the ITS region are used for reconstruction of phylogenetic trees or for comparison of RNA secondary structures among studied strains (Boyer *et al*. 2001, 2002; Siegesmund *et al*. 2008; Perkerson *et al*. 2011). Moreover, the ITS showed marked differences that are consistent between operons among numerous strains of *Scytonema hyalinum* (Johansen *et al*. 2017a). For different species that contain multiple operons, the spacer may considerably vary in size, even among the different operons in a single cell. The ITS sequence and secondary structures were used for recognition of intrageneric and intergeneric limits within the cyanobacterial taxa *Leptolyngbya corticola* Johansen & Kováčik. Results showed that the structure and sequence of these ITS regions were highly congruent with the phylogeny that was determined from 16S rRNA gene sequence data (Johansen *et al*. 2011). This consensus provides a quick and sufficient way to recognize intrageneric and possibly intergeneric taxonomic diversity. The usage of ITS in resolution of closely related taxa can be seen in work regarding *Nostoc* and *Scytonema* Agardh ex Bornet & Flahault (Boyer *et al*. 2001), *Phormidium* Kützing ex Gomont (Marquardt & Palinska 2007), *Synechocystis* (Kaneko *et al*. 1996), *Dulcicalothrix* Saraf *et al*. (Nowruzi & Shalygin 2021), *Reptodigitus* Casamatta *et al*. (Casamatta *et al*. 2020), *Myxacorys* Pietrasiak & J.R.Johansen (Pietrasiak *et al*. 2019), *Roholtiella* Bohunická, Pietrasiak & J.R.Johansen (Bohunická *et al*. 2015), *Dapisostemon* Hentschke, Sant'Anna & J.R.Johansen, *Streptostemon* Sant'Anna, Azevedo, Kaštovský & Komárek (Hentschke *et al*. 2016), *Anagnostidinema* Strunecký *et al*. (Strunecký *et al*. 2016), *Oculatella* Zammit, Billi & Albertano (Osorio-Santos *et al*. 2014), *Elainella* Jahodářová, Dvorák & Hasler (Jahodářová *et al*. 2018), *Roholtiella* (Bohunická *et al*. 2015) and many more works. Moreover, on the basis of the 16S-23S ITS region, the *Rivularia halophila* Shalygin & Pietrasiak (Nostocales, Cyanobacteria) as an independent lineage in the evolutionary tree was described for the first time (Shalygin *et al*. 2018). However, because the species contains multiple and variable copies of ITS within the 16S rRNA, this marker is not able to distinguish closely related strains. These could be observed in the genera *Moorea* Engene *et al*. (Engene *et al*. 2012), *Leptolyngbya* (Marquardt & Palinska 2007) and *Nostoc* (Iteman *et al*. 2000). The heterogeneity and variability of the ITS in some genera seems to discredit its usage as a suitable molecular marker for large-scale, closely related species, as well as large taxonomic studies.

nif genes family

The molybdenum dependent nitrogenase (*nif*) genes seem to have a single origin in cyanobacteria. They are responsible for nitrogen fixation and are highly conserved (Thiel 2019), and it is assumed, that they were inherited from a common cyanobacterial ancestor (Watanabe & Horiike 2021). Totally, 16 *nif* genes can be identified in cyanobacteria. They form a different operon (*nif*BSU, *nif*ENXW, *nif*HDK and *nif*VZT) (Esteves-Ferreira *et al*. 2017; Watanabe & Horiike 2021). Eight *nif* genes are regarded as core to the N2 fixation pathway (Esteves-Ferreira *et al*. 2017). The *nif* operons are able to be duplicated or horizontally transferred and they could even be lost during the long evolutionary history in different lineages (Peters *et al*. 2013; Mus *et al*. 2019). Evolutionary, the *nif* gene cluster and N2 fixation appeared around three billion years ago. It seems that N2 fixation traits are not ancestral in cyanobacteria, but they were gained only once in evolutionary history. These occurred probably just after the split between *Gloeobacter violaceus* Rippka, Waterbury & Cohen-Bazire and the rest of the remaining cyanobacteria. These splits indeed slightly support the possibility that this trait was obtained by HGT (Latysheva *et al*. 2012). The HGT of *nif* operons, occurred from a common cyanobacterial ancestor of diazotrophic cyanobacteria and none of the *nif* genes comprising operons were obtained by HGT outside of this phylum (Watanabe & Horiike 2021). Also, the HGT of these operons is restricted, and independent gene loss may occur in each lineage of the non-diazotrophic cyanobacteria.

From a taxonomic point of view, these gene clusters are represented not only in cyanobacteria which form heterocyte and are able to fix nitrogen, but also in picocyanobacteria from freshwater lakes (Zani *et al*. 2000). From recent studies focused on cyanobacterial genomes, the operons *nif*BSW, *nif*HDK, *nif*ENXW and *nif*VZT are essentially conserved with minimum translocation and insertions (Watanabe & Horiike 2021). Some cyanobacteria, such as *Anabaena* sp. (YBS01), *Anabaena variabilis* Bory ex Bornet & Flahault (ATCC 29413) (Bolhuis *et al*. 2010), *Anabaena laxa* N.L.Gardner (NIES-50), *Calothrix brevissima* Bornet & Flahault ex Bomet & Flahault (NIES-22), *Calothrix* sp. (NIES-2098), *Calothrix* sp. (NIES-2100), *Tolypothrix tenuis* Kützing ex Bornet & Flahault (PCC 7101), *Tolypothrix variabilis* Kützing ex Bornet & Flahault (0441), *Nostoc carneum* C.Agardh ex Bornet & Flahault (NIES-2107) (Watanabe & Horiike 2021), and *Anabaena* sp. (PCC 7120) (Mulligan & Haselkorn 1989), contain two *nif* gene operons, which were probably obtained by HGT (Watanabe & Horiike 2021). Cyanobacteria phylogeny based on *nif* gene clusters corresponds to 16S rRNA phylogeny, but comparisons of *nif*H and 16s rRNA phylogenies have provided additional insight into cyanobacterial classification and nitrogenase evolution (Zehr *et al*. 1997). As a molecular marker, the *nif* gene operons, are useful for characterization of diazotrophic communities and characterisation of their properties. These operons were used in phylogenetic analyses of *Raphidiopsis raciborskii* (Woloszynska) Aguilera *et al*. (formerly known as *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya & Subba Raju) (Dyble *et al*. 2002; Gaby & Buckley 2012),

Anabaena, *Aphanizomenon* and *Nostoc* (Apte & Prabhavathi 1994; Galhano *et al*. 2011), and *Trichodesmium* Ehrenberg ex Gomont (Ben-Porath & Zehr 1994). Based on analyses of the *nif*H sequences, the heterocyte forming cyanobacteria appear to be monophyletic (Zehr *et al*. 2001, 2008).

Inheritance of *nif*D appears to occur through vertical transfer for most cyanobacteria, except for a possible lateral transfer in *Anabaena variabilis*. The *nif*D also provides phylogenetic signal (Henson *et al*. 2004), and has been used to help elucidate evolutionary relationships among the heterocyte forming cyanobacteria (Roeselers *et al*. 2007). It also proved useful in discriminating between two genera of heterocyte-forming cyanobacteria *Nostoc* and *Anabaena* (Henson *et al*. 2004), where *nif*H failed (Tamas *et al*. 2000). In the comparison of phylogenetic trees based on *nif*K and *nif*D genes, it seems that heterocytous strains have a stable position, except for strains from the genus *Scytonema* and *Calothrix*. In phylogenetic tree based on the *nif*K gene, *Scytonema* has a stable position as sister to other Nostocales. However, in phylogenetic tree based on the *nif*D gene, strains from the genus *Scytonema* have an unresolved position near Stigonematales and near the strains from the genus *Fischerella* (Bornet & Flahault) Gomont (Hartmann & Barnum 2010). The main advantage of their usage in taxonomy is that they are not present in all cyanobacterial genera. For example, they are usually absent in strains from the order Pleurocapsales (Jung *et al*. 2021).

The *nif* gene operons seem to be ideal molecular markers for the study of diazotrophic communities, as well as strains in which some are able to fix nitrogen and some are not. In phylogeny, they show relatively good results in taxonomy on the genus level in heterocyte forming cyanobacteria. The results of different phylogenetic trees based on the *nif* gene operons and 16S rRNA gene indicate congruence between them.

Gene hetR

The *het*R gene is highly conserved and can be found exclusively in Cyanobacteria (Kim *et al*. 2011). This gene encodes a serine-type protease with a regulatory role in the differentiation process and pattern formation of heterocyte (Thomazeau *et al*. 2010). Multiple copies of these genes in the cyanobacterial genome can cause an increase in the formation of heterocyte. If this gene is absent, the strains are unable to form heterocyte (Kumar *et al*. 2010). The function of these genes predicts the taxonomic usage of this marker mostly on heterocyte-forming cyanobacterial strains. But, this gene was also isolated from non-heterocyte strains able to fix nitrogen in the genus *Katagnymene* Lemmermann, *Trichodesmium* (Lundgren *et al*. 2005) and *Leptolyngbya* (Tomitani *et al*. 2006).

The unique distribution of the *het*R gene among filamentous cyanobacteria and its relatively high sequence variation between closely related strains also makes it a powerful gene marker for discriminating filamentous cyanobacteria (Galhano *et al*. 2011).

These gene markers were used in strains that showed low genetic diversity and needed more variable genes for the differentiation and analysis of intergeneric phylogeny. These approaches were used in the genera *Trichodesmium* (Janson *et al*. 1999), *Katagnymene* (Lundgren *et al*. 2005), symbiotic *Nostoc* strains (Rasmussen & Svenning 1998), *Calothrix* (Foster & Zehr 2006), *Aphanizomenon*, *Nodularia* and *Anabaena* (Janson & Granéli 2002). Based on phylogenetic trees constructed from *het*R gene sequences, the results support the theory of the monophyletic character of Stigonematales (Tomitani *et al*. 2006). The gene *het*R is a significant molecular marker for heterocyte-forming species as well as those capable of nitrogen fixation in symbiotic cyanobacteria (Warshan *et al*. 2017).

rbcLXS gene family

This operon encoding the large and small Rubisco (D-ribulose 1,5-bisphosphate carboxylase/oxygenase) subunits also includes two intergenic spacers and gene *rbc*X encoding a putative Rubisco chaperonin (Singh *et al*. 2015; Teneva *et al*. 2019). This operon, containing functional genes, is occasionally dispersed throughout the phylum Cyanobacteria in different taxa. This patchy distribution, where operons flow across different phylogenetical lineages, suggests a vertical inheritance of this cluster from a common cyanobacterial ancestor (Zhang & Yang 2019). Also, this operon is not expressed in the heterocyte (Elhai & Wolk 1990; Gugger *et al*. 2002; Rajaniemi *et al*. 2005). This region of the genome is also subjected to HGT and that makes it unable to be suitable for strain differentiation (Rudi *et al*. 1998). In taxonomy, genes from this operon are usually used in multi-locus analyses, which play an important role in understanding the evolution of cyanobacterial lineages. The *rbc*L, as well as other genes from this operon, are suitable for phylogenetical analyses due to less ambiguous conservative nature. Also, this gene is in the genome of cyanobacteria in a single copy and is free from length mutation except at the far end (Singh *et al*. 2015). For taxonomical evaluation of the order level, this marker did not work. In the study of the heterocytous Nostocales and Stigonematales (Singh *et al*. 2015), this marker did not distinguish these orders from each other. On the other hand, it provides evidence for Stigonematales polyphyletic origin. These gene regions were used for description of genera *Anabaena* (Gugger *et al*. 2002; Rajaniemi *et al*. 2005; Katrianna *et al*. 2008), *Aphanizomenon* (Gugger *et al*. 2002; Rajaniemi *et al*. 2005), *Nostoc* and *Trichormus* (Ralfs ex Bornet & Flahault) Komárek & Anagnostidis (Rajaniemi *et al*. 2005), *Phormidium* (Sciuto *et al*. 2012), *Aliinostoc* S.N.Bagchi, N.Dubey & P.Singh (Bagchi *et al*. 2017), *Neosynechococcus* Dvorák, Hindák, Hasler & Hindáková (Dvořák *et al*. 2014a), *Desikacharya* Saraf & Prashant Singh (Saraf *et al*. 2019), *Pycnacronema* M.D.Martins & Branco (Martins *et al*. 2019), *Leptothoe* D.Konstantinou & S.Gkelis (Konstantinou *et al*. 2019), *Altericista* Averina, E.Polyakova, Senetskaya & Pinevich (Averina *et al*. 2021), *Perforafilum* Zimba, Shalygin & I.-S. Huang (Zimba *et al*. 2021) and more.

The genes from operon *rbc*LXS are suitable for usage in multi-loci analyses, but as single markers, they are not suitable for evolutionary distant species or closely related strains. Also, the phylogenetic tree constructed based on them is not usually coherent with the phylogenetical tree based on 16S rRNA for strains within the clustered groups.

The rpo genes family

The most important genes from the rpo gene family for the taxonomy of cyanobacteria are the *rpo*C1 and *rpo*B genes. In cyanobacteria, the *rpo*C and *rpo*B genes are transcribed separately from each other. Still, they represent important housekeeping genes and have significant importance in phylogenetic analyses.

The *rpo*B gene in cyanobacteria encodes the subunit of RNA polymerase. This gene is well conserved within the cyanobacteria and in the study of its evolution, the HGT was not observed (Gaget *et al*. 2011). However, in Nostocaceae, the insertion and deletion of this gene were observed (Rajaniemi *et al*. 2005). The lack of evidence for HGT indicates probable vertical inheritance (Gaget *et al*. 2011). This molecular marker is suitable for sublevel identification of strains (Gaget *et al*. 2011). This can be used in studies with large datasets of sequences from natural communities (Ogier *et al*. 2019), following the seasonal abundance of species in these communities over time (Gaget *et al*. 2011). In genus evaluation, it is usually used in the discrimination of potentially toxigenic cyanobacteria such as *Anabaena*, *Aphanizomenon*, *Nostoc* (Nowruzi *et al*. 2012), *Stigonema* C.Agardh ex Bornet & Flahault (Nowruzi *et al*. 2013), *Fischerella* (Nowruzi & Lorenzi 2021), *Trichormus* (Rajaniemi *et al*. 2005), marine filamentous genera *Arthrospira*, *Leptolyngbya*, *Oscillatoria*, *Phormidium* (Cheon *et al*. 2011), *Microcystis* (Lee *et al*. 2020) and *Nodularia* (Lyra *et al*. 2005). This gene is often used in microbial community analysis (Case *et al*. 2007; Ogier *et al*. 2019) and is suitable for estimation of microbial abundance. The use of this gene in larger phylogenetic analyses is not recommended, but it can be used as one of the genes in multi-loci analyses.

In cyanobacteria, the gene *rpo*C1, which encodes the unique subunit gamma of RNA polymerases, together with gene *rpo*C2, corresponds to the single *rpo*C gene in other bacteria (Xie *et al*. 1989). In the cyanobacterial genome, they are in a single copy (Bergsland & Haselkorn 1991). In Eubacteria, the RNA polymerase holoenzyme plays a central role in gene transcription. This subunit is a common and unique feature of the core RNA polymerase of cyanobacteria and plastids, hence the *rpo*C1 gene coding for this subunit is a good molecular marker for the detection and identification of these microorganisms. The sequence of this gene could be easily and specifically PCR amplified. In phylogenetic studies, distantly related cyanobacterial groups can be evaluated. An important property in the analyses using the *rpo*C1 gene is the presence or absence of the third codon position. Phylogenetic trees derived with *rpo*C1 data match those derived with 16S rRNA data (Palenik & Swift 1996). When the third codon is included, the analyses show greater divergence between related strains (Toledo & Palenik 1997).

As a molecular marker, *rpo*C1 is more discriminating for species differentiation than 16S rRNA (Wilson *et al*. 2000) and can better diverge closely related species, making it a more appropriate candidate for resolving questions at the genus/species-level issues (Valerio *et al*. 2009). The major taxonomic use of this marker was in the revision of Synechococcales (Mai *et al*. 2018). In this work, the Oculatellaceae and Trichocoleusaceae (formerly known as Trichocoleaceae) were described, as well as Leptolyngbyaceae and Prochlorotrichaceae were studied. The analyses based on the *rpo*C1 gene were in agreement with the 16S rRNA-based analyses. In the phylogenetic reassessment of the Synechococcales, the Oculatellaceae show the most divergent and cohesive group based on the *rpo*C1 gene analyses, and appear to be the sister group of the Leptolyngbyaceae. This marker can be used for species identification of close related species like *Raphidiopsis* F.E.Fritsch & M.F.Rich (Wilson *et al*. 2000; Gugger *et al*. 2005), *Nostoc* (Xie *et al*. 1989), *Synechococcus*, *Prochlorococcus* (Toledo & Palenik 1997), *Anabaena* (Bergsland & Haselkorn 1991), *Planktothrix* (Lin *et al*. 2010), *Minunostoc* F.Cai & R.Li (Cai *et al*. 2019, 2020), *Pegethrix* Mai, J.R.Johansen & Bohunická, *Drouetiella* J.R.Johansen & Pietrasiak, *Timaviella* Sciuto & Moro, *Cartusia* Mai, J.R.Johansen & Pietrasiak, *Tildeniella* Mai, J.R.Johansen & Pietrasiak, *Komarkovaea* Mai, J.R.Johansen & Pietrasiak, *Kaiparowitsia* Mai, J.R.Johansen & Bohunická (Mai *et al*. 2018), *Calothrix*, *Tolypothrix*, *Scytonema* (Morales *et al*. 2017), thin species from thermal springs like *Leptolyngbya*, *Phormidium*, *Geitlerinema* (Anagnostidis & Komárek) Anagnostidis (Moro *et al*. 2010), *Chrysosporum* E.Zapomelová, O.Skaácelová, P.Pumann, R.Kopp & E.Janecek, *Cuspidothrix* Rajaniemi *et al*., *Raphidiopsis*, *Sphaerospermopsis* Zapomelová *et al*. (Kim *et al*. 2020). *Rpo*C1 usually supports the phylogenetic position of strains based on 16S rRNA and ITS analyses. In closely related species, it shows higher diversification and may represent a suitable marker in multi-loci analyses.

The psbA gene family

The *psb*A, a significant functional gene, plays an important role in oxygenic photosynthesis in cyanobacteria (Mulo *et al*. 2009). It encodes the D1 protein of the Photosystem II (PSII) reaction centre (Junier *et al*. 2007). Multiple copies of this genus can be found in cyanobacteria, such as Synechococcus (Sullivan *et al*. 2006). Some cyanobacteria can have up to eight copies of this gene (Sheridan *et al*. 2020). The different *psb*A genes in cyanobacteria encode more than one type of D1 protein (Sicora *et al*. 2009). Also, several diazotrophic cyanobacteria, such as *Xenococcus* sp. (PCC 9228), *Pseudanabaena* sp. (PCC 6802), *Trichodesmium erythraeum* Ehrenberg ex Gomont, and *Lyngbya* sp. (PCC 8106), lack this gene (Sheridan *et al*. 2020). The main problem in using this gene as a molecular marker is differences in primer specificity. Due to this, the results might not be comparable at all in community studies (Junier *et al*. 2007).

This gene was used to assess the community structure of marine picocyanobacteria (Zeidner *et al*. 2003) and the community structure of freshwater lakes dominated by the genera *Synechococcus*, *Prochlorococcus*, *Aphanizomenon*, *Chroococcus* N.L.Gardner, and *Schizothrix* Kützing ex Gomont (Junier *et al*. 2007). In *Raphidiopsis* (formally known as *Cylindrospermopsis* G.Seenayya & N.Subba Raju) (Wu *et al*. 2011) and *Synechococcus* (Singh & Bhadury 2019), this gene was used to distinguish closely related strains. The result of phylogenetic analyses based on *psb*A and the *nif*D gene are relatively similar (Singh *et al*. 2015). Also, the results of the analyses of

*psb*A compared with the 16S rRNA phylogenetic tree show the polymorphic character of Stigonematales.

For species with multiple copies (heterocyte-forming species) or no copies (some unicellular and filamentous species) in the cyanobacterial genome, as well as differences in length, this molecular marker is not suitable for use as a single marker for phylogenetic analyses. It is only suitable for studies of closely related species or community structure.

tufA genes

The *tuf*A gene encodes the elongation factor Tu and plays a central role in protein synthesis in prokaryotic organisms (Delwiche *et al*. 1995). Usually, gram-negative bacteria have two tuf genes. Two copies of the *tuf*A gene were observed in *Spirulina platensis* (Gomont) Geitler (Tiboni *et al*. 1984). The *tuf*A gene represents a potentially good candidate for phylogenetic analyses because it is well conserved, and homologous genes are present in a wide range of organisms (Honda *et al*. 1999). However, in taxonomical research, this gene is not usually used. This gene was used for the study of evolutionary lineages in *Synechococcus* (Honda *et al*. 1999) *Leptolyngbya* group, Synechococcus and *Thermosynechococcus* H.Katoh, S.Itoh, J.-R.Shen & M.Ikeuchi (Sanchez-Baracaldo *et al*. 2005). Nowadays, the *tuf*A gene is used as an additional molecular marker in describing new species such as *Neowestiellopsis persica* Kabirnataj, Nematzadeh, Talebi, Tabatabaei & P.Singh (Kabirnataj *et al*. 2018) or *Aliinostoc morphoplasticum* Bagchi, Dubey & P.Singh (Bagchi *et al*. 2017). This marker could be used as an additional gene for an analysis of the taxonomical position of distant species.

Phycocyanin coding cpcBA region and PC IGS (non coding) locus

This marker represents a phycocyanin intergenic spacer based on phycocyanin loci, including the noncoding intergenic spacer between *cpc*B and *cpc*A genes (Piccin-Santos *et al*. 2014), which encode phycocyanin b and phycocyanin a (Bolch *et al*. 1999). The phycocyanin operon is conserved (MacGregor *et al*. 2001), and contains five open reading frames (ORFs), separated by noncoding intergenic spacers (IGS), which are usually highly variable. In the Cyanobacteria, this spacer has a mosaic distribution. This suggests the possible HGT of this region (Cadel-Six *et al*. 2008), as well as the possible intragenic recombination close to stop codon of the *cpc*B genes (Manen & Falquet 2002). The locus *cpc*BA-IGS displayed length heterogeneity from 629 to 910 bp (Shukla *et al*. 2021), but the length is highly conserved within the genus (Baker *et al*. 2001). This region was used to investigate the genetic diversity of cyanobacteria in four eutrophic lakes (Miller & McMahon 2011).

This marker was used in multi-loci studies in phylogenetic analyses. The marker topologies and similarities were studied in the genera *Arthrospira* Stizenberger ex Gomont and *Microcystis* (Manen & Falquet 2002; Dadheech *et al*. 2010; Choi *et al*. 2012; Kumar *et al*. 2017), *Geitlerinema* and *Microcystis* (Piccin-Santos *et al*. 2014), *Nostoc* (Hong *et al*. 2018), *Nodularia* (Laamanen *et al*. 2001), *Microcystis* (Schatz *et al*. 2005; Tan *et al*. 2010; Otten & Paerl 2011), *Anabaenopsis* V.V.Miller (Ballot *et al*. 2008), *Raphidiopsis* (Dyble *et al*. 2002) and more.

Analyses based on this marker showed a clear separation of true branching strains from unbranched heterocyte forming cyanobacteria. Also, phylogeny based on this marker supported the polyphyletic origin of the order Nostocales. It can be used in the separation of freshwater planktic cyanobacteria species (Shukla *et al*. 2021).

The best possible way to use this marker seems to be in environmental studies, for the quick identification of species at genus level as well as in multi-loci analyses.

gvp genes family

The gvp is a conserved gene cluster of 8-14 genes, coding for proteins responsible for gas vesicle formation (Albouy *et al*. 2001). Gas vesicles are composed of proteins, mainly by *gvp*A, coded by the gene *gvp*A. This protein is highly conserved and hydrophobic, and it is responsible for the formation of conical and cylindrical parts of the gas vesicles (Powell *et al*. 1991). The durability and strength of vesicles under high pressure is caused by the protein *gvp*C, coded by the *gvp*C gene (Hayes *et al*. 1992). This structural gene cluster is highly conserved, but it could be present in more copies in the genome of cyanobacteria. They also display a variation in the length of the *gvp*C gene (Beard *et al*. 1999). The presence of this gene family in different strains is highly irregular. The number of copies usually depends on the ability to form gas vesicles as well as the size and position of vesicles in filaments. In the case of *Pseudanabaena* sp., this strain forms small gas vesicles only next to the cell septa. This is co-related with the presence of only one copy of the *gvp*A gene and the absence of the *gvp*C gene (Damerval *et al*. 1991). In *Calothrix* sp., the genes *gvp*A1, *gvp*A2 and *gvp*C form an operon, where *gvp*A1 and *gvp*A2 are 99% identical. They also have two copies of this operon (Damerval *et al*. 1987). The two copies of operon *gvp*AC were also detected in *Plantothrix* sp., where the *gvp*C gene displays a variation in length (Beard *et al*. 1999). In *Microcystis aeruginosa* (Kützing) Kützing (Mlouka *et al*. 2004), three gene copies of *gvp*A were detected. From these analyses, there seems to be higher abundance and differentiation in gene *gvp*A than in *gvp*C, and the expression of this gene cluster is regulated at low light intensity or high growth temperature (Cai *et al*. 2020). At the taxonomic level, these genes were used as markers in multi-loci studies of *Nodularia* (Barker *et al*. 2000), *Nostoc spumigena* (Barker *et al*. 1999), *Arthrospira* Stizenberger ex Gomont (Miklaszewska *et al*. 2012; Misztak *et al*. 2021), *Synechococcus*, *Planktothrix*, *Pseudanabaena* Lauterborn, Nodularia, *Nostoc*, *Calothrix* (Miklaszewska *et al*. 2012), *Anabaena* (Buchholz *et al*. 1993), *Planktothrix* (Pancrace *et al*. 2017), *Microcystis* (Min *et al*. 2007), *Dolichospermum* (Ralfs ex Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek, and *Aphanizomenon* (Driscoll *et al*. 2018). As a molecular marker for phylogenetical analyses, this gene cluster is not suitable based on the large variability of length (*gvp*C gene) and non-consistent number of copies (*gvp*A gene) in the genome, even in species from one genus.

Highly repetitive sequences

Highly Iterative Palindrome-1 (HIP1)

Highly Iterative Palindrome-1 (HIP1) represents the octameric palindrome (GCGATCGC). This concrete palindrome has not been observed in genomes outside of cyanobacteria, but within cyanobacteria, it appears quite frequently (Xu *et al*. 2018). In the context of genetics, palindromes are nucleotide sequences that are read with the same 5' (prime) to 3' on one strand or 5' to 3' on the complementary strand (Xu *et al*. 2018). They can play a role as restriction enzyme sites (Delaye & Moya 2011). These sequences were first identified in a cadmium-tolerant strain of *Synechococcus* (PCC 6301) (Gupta *et al*. 1993). Thus, repetitive sequences have been considered as the most accepted tool for assessing microbial diversity (Garcia-Pichel *et al*. 2001; Gugger *et al*. 2002; Roeselers *et al*. 2007; Valerio *et al*. 2009; Shokraeia *et al*. 2019). This sequence was unique since it was highly represented among many cyanobacteria genomes, meaning that it has a very high occurrence rate. Not surprisingly, HIP1 was the most abundant sequence with 7356 matches in the cyanobacterial genome (Vuong 2014). Every sequence afterwards, in terms was represented by HIP1 with one or two different nucleotides at the beginning or end of the sequence (Tompa 1999). For example, HIP1, the second most found octameric sequence, "GGCGATCG", was essentially without the cytosine at the end of the sequence and with a guanine added to the beginning of the sequence. This pattern occurred for multiple cyanobacteria, which suggests that HIP1 should have a significant impact and role in these organisms.

These sequences were used to study closely related strains of *Trichodesmium* (Orcutt *et al*. 2002), *Raphidiopsis raciborskii* (Neilan *et al*. 2003), *Nostoc linckia* Bornet ex Bornet & Flahault (Krugman *et al*. 2001), *Microcystis panniformis* Komárek, Komárková-Legnerová, Sant'Anna, M.T.P.Azevedo & P.A.C.Senna (Bittencourt-Oliveira *et al*. 2007), *Oscillatoria*, *Anabaenopsis*, *Symploca* Kützing ex Gomont (Smith *et al*. 1998), *Nostoc*, *Fischerella*, *Anabaena* (Smith *et al*. 1998; Comte *et al*. 2004), *Synechococcus*, *Pseudanabaena*, *Planktothrix*, *Microcystis* (Comte *et al*. 2004), and *Leptolyngbya* (Bruno *et al*. 2006). From a phylogenetic point of view, these sequences are not suitable for use in phylogenetic analyses due to the relatively low information content of the data (Smith *et al*. 1998), but are excellent for distinguishing closely related species isolated from environmental samples. This method is also usable on non-axenic strains with contamination by non-phototrophic bacteria (Comte *et al*. 2004).

Enterobacterial Repetitive Intergenic Consensus (ERIC) sequences

The Enterobacterial Repetitive Intergenic Consensus (ERIC) sequences are highly conserved at the nucleotide sequence level and are approximately 126 bp long. However, in different species, their chromosomal locations can be different. They seem to be located in non-coding transcribed regions of the chromosome, usually in the met E-metR region (Hulton *et al*. 1991), in either orientation with respect to transcription or including a conserved inverted repeat. Moreover, REP elements and or ERIC sequences have been used for the identification of symbiotic and free-living cyanobacteria (Rasmussen & Svenning 1998; Lehtimäki *et al*. 2000).

In phylogenetic studies, these sequences were used in the determination of closely related species in the genus *Nostoc*, *Nodularia* (Rasmussen & Svenning 1998), *Anabaena*, *Aphanizomenon*, *Microcystis*, *Planktothrix* (Lyra *et al*. 2001), *Microcystis aeruginosa*, *Planktothrix agardhii*, *Oscillatoria neglecta* H.C.Wood, nom. inval., and genus *Aphanizomenon* (Valério *et al*. 2005). These highly conserved sequences seem to be suitable for close-related species identification, as well as the rapid identification of species in samples from nature.

Short tandemly repeated repetitive (STRR) and long tandemly repeated repetitive (LTRR) sequences

In the particular case of cyanobacteria, a distinct family of repetitive sequences has been described (Prabha & Singh 2019), and a PCR-based fingerprinting method was developed for cyanobacteria using short tandemly repeated repetitive (STRR) sequences as primers in *Calothrix* (Mazel *et al*. 1990) and *Microcystis* strains (Asayama *et al*. 1996). These sequences consist of three different simple tandem heptanucleotide sequence repeats that were initially described for *Calothrix* species, where the copy number was estimated at about 100 per genome (Valerio *et al*. 2009). The STRR sequences have been identified in several other cyanobacterial genera and species, to date mostly in heterocyte forming cyanobacteria but also in some non-heterocyte forming cyanobacteria (Liaimer *et al*. 2016). The specificity of these sequences has made the STRRs useful even for non-axenic cyanobacterial cultures (Anand *et al*. 2019). They are suitable for being used as an oligonucleotide probe or as primers in the generation of PCR-amplified DNA profiles (Wilson *et al*. 2000). In phylogenetic studies, these sequences were used in studies of symbiotic cyanobacteria from the genera *Anabaena* (Zheng *et al*. 1999), *Nostoc* (Zheng *et al*. 1999; Nilsson *et al*. 2002; *Thajuddin et al*. 2010), and *Calothrix* (Mazel *et al*. 1990, 1991; Thajuddin *et al*. 2010). For the identification of closely related species and strains, these markers were used in *Raphidiopsis raciborskii* (Wilson *et al*. 2000), *Anabaena*, *Hapalosiphon* Nägeli ex Bornet & Flahault, *Cylindrospermum* Kützing ex Bornet & Flahault (Shukla *et al*. 2013), *Westiellopsis* Janet (Selvakumar & Gopalaswamy 2008; Shukla *et al*. 2013), *Synechococcus* (Rasmussen & Svenning 1998; Muralitharan & Thajuddin 2011), *Plectonema* Thuret ex Gomont, *Microcoleus* Desmaziéres ex Gomont, *Phormidium* (Rasmussen & Svenning 1998), *Plectonema*, *Microcystis* (Rouhiainen *et al*. 1995). Also, these markers were used for analyses of relationships between Stigonematales and Nostocales. They discovered a close association between these two orders (Shukla *et al*. 2013). The LTRR sequence has also been identified in some cyanobacterial species (Valerio *et al*. 2009), for the first time in *Anabaena* sp. (PCC 7120) (Masepohl *et al*. 1996). The size of this fragment is 37 bp and could be present in the genome in multiple copies (Rasmussen & Svenning 1998). In the phylogenetic studies, this marker was used in the identification of strains from the genera *Nostoc* (Rasmussen & Sven-

ning 1998; Guevara *et al*. 2002), *Anabaena* (Prasanna *et al*. 2006; Ezhilarasi & Anand 2009), and *Leptolyngbya* (Bruno *et al*. 2005). This marker is, however, usually used for quick identification of strains from environmental samples such as freshwater (Valerio *et al*. 2009), symbionts (Lyra *et al*. 2001; Nilsson *et al*. 2002). These highly conserved STRR and LTRR sequences appear to be suitable for identifying closely related species as well as identifying species in natural samples quickly. Also, they are necessary for the identification of symbiotic cyanobacteria from different hosts. They can be used to identify strains at the species and genus levels, as well as to solve phylogenetic relationships within problematic orders with a shared evolutionary history. However, the LTRR sequences seem to be suitable for identification of non-axenic cultures; this method sometimes identifies their contaminants but not the real cyanobacteria (Bruno *et al*. 2005). The last analyses based on these markers also show that the LTRR sequences are not suitable for distinct populations of cyanobacteria with similar morphology (Negi *et al*. 2019).

CONCLUSION

Until now, the 16S rRNA with ITS has been the most powerful tool for describing new species and phylogenetical analyses, together with the other structural and functional genes such as 23S rRNA, *nif* gene operon, *het*R, *rpo*C, *rbc*LX, etc. These genes have a relatively low mutation rate, and they are usually suitable for the description of new taxa at genus level. If the new species needs to be described, the most useful seems to be the ITS region in combination with 16S rRNA analyses. Usage of ITS region can be controversial due to the multiple copies in the genomes and its high variability among some closely related species. Molecular markers like *rpo*C1, *psb*A, and short repetitive sequences like HIP1, ERIC, STRR, and LTRR appear to be useful for identifying closely related species. For the multi-locus analyses the genes *rbc*lXS, *rpo*C1, *rpo*B, *gyr*B, *tuf*A, *cpc*AB, and *nif*KDH are the suitable candidates. These genes are also important in the study of community's structure and the identification of species in samples from nature. On the other hand, *psb*A, *tuf*A, *gvp* genes and short repetitive sequences HIP1, seem to be potentially not suitable for phylogenetic analyses. For identification of new species within the nitrogen fixating species, or heterocyte forming species, the genes from the *nif* operon, *het*R gene and HIP1, and STRR sequences are suitable. Concerning the obtained results from recent works, we propose to identify new species or toxin-producing strains by standardising folding procedures and structural data labelling used in the analysis for ITS comparisons as a complement to the functional and structural genes in the future. Moreover the use of environmental DNA (eDNA) in the ecology, mitigation, and prediction of freshwater harmful algae could be helpful. Objective results of the study require quantifying the relationship between ITS secondary structures and taxonomy. Further studies are needed to determine the importance and tuning of lateral gene transfer in the evolutionary history of new cyanobacteria strains.

REFERENCES

Acinas S. G., Marcelino L. A., Klepac-Ceraj V. & Polz M. F. 2004. — Divergence and redundancy of 16S rRNA sequences in genomes with multiple rrn operons. *Journal of bacteriology* 186 (9): 2629-2635. https://doi.org/10.1128/JB.186.9.2629-2635.2004

Albouy D., Castets A.-M. & de Marsac N. T. 2001. — The gas vesicle gene (*gvp*) cluster of the cyanobacterium *Pseudanabaena* sp. strain PCC 6901. *DNA Sequence* 12 (5-6): 337-344.

Anand N., Thajuddin N. & Dadheech P. 2019. — Cyanobacterial taxonomy: Morphometry to molecular studies, *in* Mishra A. K., Tiwari D. N. & Rai A. N. (eds), *From Basic Science to Applications*. Academic Press, Cambridge: 43-64. https://doi.org/10.1016/B978-0-12-814667-5.00003-9

Apte S. & Prabhavathi N. 1994. — Rearrangements of nitrogen fixation (*nif*) genes in the heterocystous cyanobacteria. *Journal of Biosciences* 19 (5): 579-602. https://doi.org/10.1007/BF02703204

Apte S. K. & Thomas J. 1987. — Nitrogen fixation genes (*nif* K, D, H) in the filamentous nonheterocystous cyanobacterium *Plectonema boryanum* do not rearrange. *Journal of Genetics* 66 (2): 101. https://doi.org/10.1007/BF02931656

Asayama M., Tanaka K., Takahashi H., Sato A., Aida T. & Shirai M. 1996. — Cloning, sequencing and characterization of the gene encoding a principal sigma factor homolog from the cyanobacterium *Microcystis aeruginosa* K-81. *Gene* 181 (1-2): 213-217.

Averina S., Polyakova E., Senatskaya E. & Pinevich A. 2021. — A new cyanobacterial genus *Altericista* and three species, *A. lacusladogae* sp. nov., *A. violacea* sp. nov., and *A. varichlora* sp. nov., described using a polyphasic approach. *Journal of Phycology* 57 (5): 1517-1529. https://doi.org/10.1111/jpy.13188

Avni E. & Snir S. 2020. — A new phylogenomic approach for quantifying horizontal gene transfer trends in prokaryotes. *Scientific reports* 10 (1): 1-14. https://doi.org/10.1038/s41598-020-62446-5

Bagchi S. N., Dubey N. & Singh P. 2017. — Phylogenetically distant clade of *Nostoc*-like taxa with the description of *Aliinostoc* gen. nov. and *Aliinostoc morphoplasticum* sp. nov. *International Journal of Systematic and Evolutionary Microbiology* 67 (9): 3329-3338. https://doi.org/10.1099/ijsem.0.002112

Baker J. A., Neilan B. A., Entsch B. & McKay D. B. 2001. — Identification of cyanobacteria and their toxigenicity in environmental samples by rapid molecular analysis. *Environmental Toxicology* 16 (6): 472-482. https://doi.org/10.1002/tox.10010

Baldev E., Mubarakali D., Kumar R. D. & Thajuddin N. 2015. — Molecular phylogeny of morphologically diverse cyanobacteria based on ribosomal conserved sequence. *Journal of Environmental Science and Technology* 8 (5): 188-197. https://doi.org/10.3923/jest.2015.188.197

Ballot A., Dadheech P. K., Haande S. & Krienitz L. 2008. — Morphological and phylogenetic analysis of *Anabaenopsis abijatae* and *Anabaenopsis elenkinii* (Nostocales, Cyanobacteria) from tropical inland water bodies. *Microbial Ecology* 55 (4): 608-618. https://doi.org/10.1007/s00248-007-9304-4

Barker G. L., Hayes P. K., O'mahony S. L., Vacharapiyasophon P. & Walsby A. E. 1999. — A molecular and phenotypic analysis of *Nodularia* (cyanobacteria) from the Baltic Sea. *Journal of Phycology* 35 (5): 931-937. https://doi.org/10.1046/j.1529-8817.1999.3550931.x

Barker G. L., Handley B. A., Vacharapiyasophon P., Stevens J. R. & Hayes P. K. 2000. — Allele-specific PCR shows that genetic exchange occurs among genetically diverse *Nodularia* (Cyanobacteria) filaments in the Baltic Sea. *Microbiology* 146 (11): 2865-2875. https://doi.org/10.1099/00221287-146-11-2865

Beard S., Handley B., Hayes P. & Walsby A. 1999. — The diversity of gas vesicle genes in *Planktothrix rubescens* from Lake Zürich. *Microbiology* 145 (10): 2757-2768. https://doi.org/10.1099/00221287-145-10-2757

Ben-Porath J. & Zehr J. 1994. — Detection and characterization of cyanobacterial *nif*H genes. *Applied and Environmental Microbiology* 60 (3): 880-887. https://doi.org/10.1128/aem.60.3.880-887.1994

Bentkowski P., Van Oosterhout C., Ashby B. & Mock T. 2017. — The effect of extrinsic mortality on genome size evolution in prokaryotes. *The ISME Journal* 11 (4): 1011-1018. https://doi.org/10.1038/ismej.2016.165

Bergman B., Zheng W.-W., Klint J. & Ran L. 2008. — On the origin of plants and relations to contemporary cyanobacterial-plant symbioses. *Plant Biotechnology* 25 (3): 213-220. https://doi.org/10.5511/plantbiotechnology.25.213

Bergsland K. J. & Haselkorn R. 1991. — Evolutionary relationships among eubacteria, cyanobacteria, and chloroplasts: evidence from the *rpo*C1 gene of *Anabaena* sp. strain PCC 7120. *Journal of Bacteriology* 173 (11): 3446-3455. https://doi.org/10.1128/jb.173.11.3446-3455.1991

Berrendero Gómez E., Johansen J. R., Kaštovský J., Bohunická M. & Čapková K. 2016. — *Macrochaete* gen. nov.(Nostocales, Cyanobacteria), a taxon morphologically and molecularly distinct from *Calothrix*. *Journal of Phycology* 52 (4): 638-655. https://doi.org/10.1111/jpy.12425

Berthold D. E., Lefler F. W. & Laughinghouse I. H. D. 2021. — Untangling filamentous marine cyanobacterial diversity from the coast of South Florida with the description of Vermifilaceae fam. nov. and three new genera: *Leptochromothrix* gen. nov., *Ophiophycus* gen. nov., and *Vermifilum* gen. nov. *Molecular Phylogenetics and Evolution* 160: 107010. https://doi.org/10.1016/j.ympev.2020.107010

Bittencourt-Oliveira M. D. C., Moura A. D. N., Gouvêa-Barros S. & Pinto E. 2007. — HIP1 DNA fingerprinting in *Microcystis panniformis* (Chroococcales, Cyanobacteria). *Phycologia* 46 (1): 3-9. https://doi.org/10.2216/06-01.1

Boden J. S., Konhauser K. O., Robbins L. J. & Sánchez-Baracaldo P. 2021. — Timing the evolution of antioxidant enzymes in cyanobacteria. *Nature Communications* 12 (1): 1-12. https://doi.org/10.1038/s41467-021-24396-y

Bohunická M., Pietrasiak N., Johansen J. R., Gómez E. B., Hauer T., Gaysina L. A. & Lukešová A. 2015. — *Roholtiella*, gen. nov. (Nostocales, Cyanobacteria) – a tapering and branching cyanobacteria of the family Nostocaceae. *Phytotaxa* 197 (2): 84-103. https://doi.org/10.11646/phytotaxa.197.2.2

Bolch C. J., Orr P. T., Jones G. J. & Blackburn S. I. 1999. — Genetic, morphological, and toxicological variation among globally distributed strains of *Nodularia* (Cyanobacteria). *Journal of Phycology* 35 (2): 339-355. https://doi.org/10.1046/j.1529-8817.1999.3520339.x

Bolhuis H., Severin I., Confurius-Guns V., Wollenzien U. I. & Stal L. J. 2010. — Horizontal transfer of the nitrogen fixation gene cluster in the cyanobacterium *Microcoleus chthonoplastes*. *The ISME Journal* 4 (1): 121-130. https://doi.org/10.1038/ismej.2009.99

Bonthond G., Shalygin S., Bayer T. & Weinberger F. 2021. — Draft genome and description of *Waterburya agarophytonicola* gen. nov. sp. nov.(Pleurocapsales, Cyanobacteria): a seaweed symbiont. *Antonie van Leeuwenhoek* 114 (12): 2189-2203. https://doi.org/10.1007/s10482-021-01672-x

Boucher Y., Douady C. J., Sharma A. K., Kamekura M. & Doolittle W. F. 2004. — Intragenomic heterogeneity and intergenomic recombination among haloarchaeal rRNA genes. *Journal of Bacteriology* 186 (12): 3980-3990. https://doi.org/10.1128/JB.186.12.3980-3990.2004

Boyer S. L., Flechtner V. R. & Johansen J. R. 2001. — Is the 16S-23S rRNA internal transcribed spacer region a good tool for use in molecular systematics and population genetics? A case study in cyanobacteria. *Molecular Biology and Evolution* 18 (6): 1057-1069. https://doi.org/10.1093/oxfordjournals.molbev.a003877

Boyer S. L., Johansen J. R., Flechtner V. R. & Howard G. L. 2002. — Phylogeny and genetic variance in terrestrial *Microcoleus* (cyanophyceae) species based on sequence analysis of the 16s rRna gene and associated 16S-23S ITS region 1. *Journal of Phycology* 38 (6): 1222-1235. https://doi.org/10.1046/j.1529-8817.2002.01168.x

Brito A., Ramos V., Mota R., Lima S., Santos A., Vieira J., Vieira C. P., Kaštovský J., Vasconcelos V. M. & Tamagnini P. 2017. — Description of new genera and species of marine cyanobacteria from the Portuguese Atlantic coast. *Molecular Phylogenetics and Evolution* 111: 18-34. https://doi.org/10.1016/j.ympev.2017.03.006

Bruno L., Billi D. & Albertano P. 2005. — Optimization of molecular techniques applied to the taxonomy of epilithic *Leptolyngbya* strains. *Archiv für Hydrobiologie. Supplementband. Algological Studies* 117: 197-207.

Bruno L., Billi D., Albertano P. & Urzí C. 2006. — Genetic characterization of epilithic cyanobacteria and their associated bacteria. *Geomicrobiology Journal* 23 (5): 293-299. https://doi.org/10.1080/01490450600760732

Buchholz B., Hayes P. & Walsby A. 1993. — The distribution of the outer gas vesicle protein, *Gvp*C, on the *Anabaena* gas vesicle, and its ratio to *Gvp*A. *Microbiology* 139 (10): 2353-2363.

Cadel-Six S., Dauga C., Castets A. M., Rippka R., Bouchier C., de Marsac N. T. & Welker M. 2008. — Halogenase genes in nonribosomal peptide synthetase gene clusters of *Microcystis* (Cyanobacteria): Sporadic distribution and evolution. *Molecular Biology and Evolution* 25 (9): 2031-2041. https://doi.org/10.1093/molbev/msn150

Cai F., Yang Y., Wen Q. & Li R. 2018. — *Desmonostoc danxiaense* sp. nov.(Nostocales, Cyanobacteria) from Danxia mountain in China based on polyphasic approach. *Phytotaxa* 367 (3): 233-244. https://doi.org/10.11646/phytotaxa.367.3.3

Cai F., Li X., Geng R., Peng X. & Li R. 2019. — Phylogenetically distant clade of *Nostoc*-like taxa with the description of *Minunostoc* gen. nov. and *Minunostoc cylindricum* sp. nov. *Fottea* 19 (1): 13-24. https://doi.org/10.5507/fot.2018.013

Cai K., Xu B.-Y., Jiang Y.-L., Wang Y., Chen Y., Zhou C.-Z. & Li Q. 2020. — The model cyanobacteria *Anabaena* sp. PCC 7120 possess an intact but partially degenerated gene cluster encoding gas vesicles. *BMC Microbiology* 20 (1): 1-11. https://doi.org/10.1186/s12866-020-01805-8

Casamatta D. A., Johansen J. R., Vis M. L. & Broadwater S. T. 2005. — Molecular and morphological characterization of ten polar and near-polar strains within the Oscillatoriales (Cyanobacteria) 1. *Journal of Phycology* 41 (2): 421-438. https://doi.org/10.1111/j.1529-8817.2005.04062.x

Casamatta D. A., Villanueva C. D., Garvey A. D., Stocks H. S., Vaccarino M., Dvořák P., Hašler P. & Johansen J. R. 2020. — *Reptodigitus chapmanii* (Nostocales, Hapalosiphonaceae) gen. nov.: a unique Nostocalean (Cyanobacteria) genus based on a polyphasic approach 1. *Journal of Phycology* 56 (2): 425-436. https://doi.org/10.1111/jpy.12954

Case R. J., Boucher Y., Dahllöf I., Holmström C., Doolittle W. F. & Kjelleberg S. 2007. — Use of 16S rRNA and *rpo*B genes as molecular markers for microbial ecology studies. *Applied and Environmental Microbiology* 73 (1): 278-288. https://doi.org/10.1128/AEM.01177-06

Chen M.-Y., Teng W.-K., Zhao L., Hu C.-X., Zhou Y.-K., Han B.-P., Song L.-R. & Shu W.-S. 2021. — Comparative genomics reveals insights into cyanobacterial evolution and habitat adaptation. *The ISME Journal* 15 (1): 211-227. https://doi.org/10.1038/s41396-020-00775-z

Cheon J.-Y., Lee M.-A. & Ki J.-S. 2011. — Analysis of RNA polymerase beta subunit (*rpo*B) gene sequences for the discrimination of cyanobacteria *Anabaena* species. *Korean Journal of Microbiology* 47 (3): 268-274.

Choi G.-G., Ahn C.-Y. & Oh H.-M. 2012. — Phylogenetic relationships of *Arthrospira* strains inferred from 16S rRNA gene and *cpc*BA-IGS sequences. *Algae* 27 (2): 75-82. https://doi.org/10.4490/algae.2012.27.2.075

Chonudomkul D., Yongmanitchai W., Theeragool G., Kawachi M., Kasai F., Kaya K. & Watanabe M. M. 2004. — Morphology, genetic diversity, temperature tolerance and toxicity of *Cylindrospermopsis raciborskii* (Nostocales, Cyanobacteria) strains from Thailand and Japan. *FEMS Microbiology Ecology* 48 (3): 345-355. https://doi.org/10.1016/j.femsec.2004.02.014

Churro C., Semedo-Aguiar A. P., Silva A. D., Pereira-Leal J. B. & Leite R. B. 2020. — A novel cyanobacterial geosmin producer, revising *Geo*A distribution and dispersion patterns in Bacteria. *Scientific Reports* 10 (1): 1-18. https://doi.org/10.1038/s41598-020-64774-y

Comte K., Rippka R., Friedl T., Day J. G., de Marsac N. T. & Herdman M. 2004. — Assessment of genotypic identity of cyanobacterial strains in culture collections using HIP1-based primers. *Nova Hedwigia* 79 (1): 293-312. https://doi.org/10.1127/0029-5035/2004/0079-0293

Dadheech P. K., Ballot A., Casper P., Kotut K., Novelo E., Lemma B., Pröschold T. & Krienitz L. 2010. — Phylogenetic relationship and divergence among planktonic strains of *Arthrospira* (Oscillatoriales, Cyanobacteria) of African, Asian and American origin deduced by 16S-23S ITS and phycocyanin operon sequences. *Phycologia* 49 (4): 361-372. https://doi.org/10.2216/09-71.1

Damerval T., Castets A. M., Houmard J. & de Marsac N. T. 1991. — Gas vesicle synthesis in the cyanobacterium *Pseudanabaena* sp.: occurrence of a single photoregulated gene. *Molecular Microbiology* 5 (3): 657-664. https://doi.org/10.1111/j.1365-2958.1991.tb00737.x

Damerval T., Houmard J., Guglielmi G., Csiszàr K. & de Marsac N. T. 1987. — A developmentally regulated *gvp*ABC operon is involved in the formation of gas vesicles in the cyanobacterium *Calothrix* 7601. *Gene* 54 (1): 83-92. https://doi.org/10.1016/0378-1119(87)90350-7

De Bruijn F. J. 1992. — Use of repetitive (repetitive extragenic palindromic and enterobacterial repetitive intergeneric consensus) sequences and the polymerase chain reaction to fingerprint the genomes of *Rhizobium meliloti* isolates and other soil bacteria. *Applied and Environmental Microbiology* 58 (7): 2180-2187. https://doi.org/10.1128/aem.58.7.2180-2187.1992

Delaye L. & Moya A. 2011. — Abundance and distribution of the highly iterated palindrome 1 (HIP1) among prokaryotes. *Mobile Genetic Elements* 1 (3): 159-168. https://doi.org/10.4161/mge.1.3.18300

Delwiche C. F., Kuhsel M. & Palmer J. D. 1995. — Phylogenetic analysis of *tuf*A sequences indicates a cyanobacterial origin of all plastids. *Molecular Phylogenetics and Evolution* 4 (2): 110-128. https://doi.org/10.1006/mpev.1995.1012

Demchuk O. & Blium I. 2005. — Phylogenetic tree of bacterial and eucaryotic FtsZ-proteins based on the homology of their primary sequences. *TSitologiia i genetika* 39 (4): 3-12.

Dextro R. B., Delbaje E., Cotta S. R., Zehr J. P. & Fiore M. F. 2021. — Trends in Free-access Genomic Data Accelerate Advances in Cyanobacteria Taxonomy. *Journal of Phycology* 57 (5): 1392-1402. https://doi.org/10.1111/jpy.13200

Di Rienzi S. C., Sharon I., Wrighton K. C., Koren O., Hug L. A., Thomas B. C., Goodrich J. K., Bell J. T., Spector T. D. & Banfield J. F. 2013. — The human gut and groundwater harbor non-photosynthetic bacteria belonging to a new candidate phylum sibling to Cyanobacteria. *eLife* 2: e01102. https://doi.org/10.7554/eLife.01102

Driscoll C. B., Meyer K. A., Šulčius S., Brown N. M., Dick G. J., Cao H., Gasiūnas G., Timinskas A., Yin Y. & Landry Z. C. 2018. — A closely-related clade of globally distributed bloom-forming cyanobacteria within the Nostocales. *Harmful Algae* 77: 93-107. https://doi.org/10.1016/j.hal.2018.05.009

Duval C., Hamlaoui S., Piquet B., Toutirais G., Yéprémian C., Reinhardt A., Duperron S., Marie B., Demay J. & Bernard C. 2022. — Diversity of cyanobacteria from thermal muds (Balaruc-Les-Bains, France) with the description of *Pseudochroococcus coutei* gen. nov., sp. nov. *FEMS Microbes* 2: xtab006.

Dvořák P., Hindák F., Hašler P., Hindakova A. & Poulíčková A. 2014a. — Morphological and molecular studies of *Neosynechococcus sphagnicola*, gen. et sp. nov.(Cyanobacteria, Synechococcales). *Phytotaxa* 170 (1): 24-34. https://doi.org/10.11646/phytotaxa.170.1.3

Dvořák P., Casamatta D. A., Poulíčková A., Hašler P., Ondřej V. & Sanges R. 2014b. — Synechococcus: 3 billion years of global dominance. *Molecular Ecology* 23 (22): 5538-5551.

Dvořák P., Jahodářová E., Casamatta D., Hašler P. & Poulíčková A. 2018. — Difference without distinction? Gaps in cyanobacterial systematics; when more is just too much. *Fottea* 18 (1): 130-136. https://doi.org/10.5507/fot.2017.023

Dyble J., Paerl H. W. & Neilan B. A. 2002. — Genetic characterization of *Cylindrospermopsis raciborskii* (Cyanobacteria) isolates from diverse geographic origins based on *nif*H and *cpc*BA-IGS nucleotide sequence analysis. *Applied and Environmental Microbiology* 68 (5): 2567-2571. https://doi.org/10.1128/AEM.68.5.2567-2571.2002

Edwards U., Rogall T., Blöcker H., Emde M. & Böttger E. C. 1989. — Isolation and direct complete nucleotide determination of entire genes. Characterization of a gene coding for 16S ribosomal RNA. *Nucleic Acids Research* 17 (19): 7843-7853. https://doi.org/10.1093/nar/17.19.7843

El Alaoui S., Diez J., Toribio F., Gómez-Baena G., Dufresne A. & García-Fernández J. M. 2003. — Glutamine synthetase from the marine cyanobacteria *Prochlorococcus* spp.: characterization, phylogeny and response to nutrient limitation. *Environmental Microbiology* 5 (5): 412-423. https://doi.org/10.1046/j.1462-2920.2003.00433.x

Elhai J. & Wolk C. 1990. — The genes for nitrogenase are developmentally regulated and exhibit a spatial pattern of expression in the cyanobacterium *Anabaena*. *EMBO Journal* 9: 3379-3388. https://doi.org/10.1002/j.1460-2075.1990.tb07539.x

Engene N., Rottacker E. C., Kaštovský J., Byrum T., Choi H., Ellisman M. H., Komárek J. & Gerwick W. H. 2012. — *Moorea producens* gen. nov., sp. nov. and *Moorea bouillonii* comb. nov., tropical marine cyanobacteria rich in bioactive secondary metabolites. *International Journal of Systematic and Evolutionary Microbiology* 62 (5): 1171. https://doi.org/10.1099/ijs.0.033761-0

Esteves-Ferreira A. A., Cavalcanti J. H. F., Vaz M. G. M. V., Alvarenga L. V., Nunes-Nesi A. & Araújo W. L. 2017. — Cyanobacterial nitrogenases: phylogenetic diversity, regulation and functional predictions. *Genetics and Molecular Biology* 40 (1): 261-275. https://doi.org/10.1590/1678-4685-gmb-2016-0050

Ezhilarasi A. & Anand N. 2009. — Phylogenetic analysis of the genus *Anabaena* based on PCR fingerprinting. *African Journal of Biotechnology* 8 (24): 6756-6763.

Ezhilarasi A. & Anand N. 2016. — Phylogenetic Analysis of the Genus *Anabaena* by Single Randomly Amplified Polymorphic DNA (RAPD) Fingerprinting. *Biosciences Biotechnology Research Asia* 6 (2): 733-738.

Falcón L. I., Magallón S. & Castillo A. 2011. — Dating the cyanobacterial ancestor of the chloroplast. *The ISME Journal* 5 (2): 366. https://doi.org/10.1038/ismej.2010.98

Fewer D. P., Rouhiainen L., Jokela J., Wahlsten M., Laakso K., Wang H. & Sivonen K. 2007. — Recurrent adenylation domain replacement in the microcystin synthetase gene cluster. *BMC Evolutionary Biology* 7 (1): 183. https://doi.org/10.1186/1471-2148-7-183

Forterre P. 2015. — The universal tree of life: an update. *Frontiers in Microbiology* 6: 717. https://doi.org/10.3389/fmicb.2015.00717

FOSTER R. A. & ZEHR J. P. 2006. — Characterization of diatom–cyanobacteria symbioses on the basis of *nif*H, *het*R and 16S rRNA sequences. *Environmental Microbiology* 8 (11): 1913-1925. https://doi.org/10.1111/j.1462-2920.2006.01068.x

FOX G. E., WISOTZKEY J. D. & JURTSHUK JR P. 1992. — How close is close: 16S rRNA sequence identity may not be sufficient to guarantee species identity. *International Journal of Systematic and Evolutionary Microbiology* 42 (1): 166-170.

FRASER C., HANAGE W. P. & SPRATT B. G. 2007. — Recombination and the nature of bacterial speciation. *Science* 315 (5811): 476-480. https://doi.org/10.1126/science.1127573

GABY J. C. & BUCKLEY D. H. 2012. — A comprehensive evaluation of PCR primers to amplify the *nif*H gene of nitrogenase. *PLoS ONE* 7 (7): e42149. https://doi.org/10.1371/journal.pone.0042149

GAGET V., GRIBALDO S. & DE MARSAC N. T. 2011. — An *rpo*B signature sequence provides unique resolution for the molecular typing of cyanobacteria. *International Journal of Systematic and Evolutionary Microbiology* 61 (1): 170-183. https://doi.org/10.1099/ijs.0.019018-0

GALHANO V., DE FIGUEIREDO D. R., ALVES A., CORREIA A., PEREIRA M. J., GOMES-LARANJO J. & PEIXOTO F. 2011. — Morphological, biochemical and molecular characterization of *Anabaena*, *Aphanizomenon* and *Nostoc* strains (Cyanobacteria, Nostocales) isolated from Portuguese freshwater habitats. *Hydrobiologia* 663 (1): 187-203. https://doi.org/10.1007/s10750-010-0572-5

GARCÍA-MARTÍNEZ J., ACINAS S. G., ANTON A. I. & RODRÍGUEZ-VALERA F. 1999. — Use of the 16S-23S ribosomal genes spacer region in studies of prokaryotic diversity. *Journal of Microbiological Methods* 36 (1-2): 55-64.

GARCIA-PICHEL F., LÓPEZ-CORTÉS A. & NÜBEL U. 2001. — Phylogenetic and morphological diversity of cyanobacteria in soil desert crusts from the Colorado Plateau. *Applied and Environmental Microbiology* 67 (4): 1902-1910. https://doi.org/10.1128/AEM.67.4.1902-1910.2001

GARCIA-PICHEL F., LOMBARD J., SOULE T., DUNAJ S., WU S. H. & WOJCIECHOWSKI M. F. 2019. — Timing the evolutionary advent of cyanobacteria and the later great oxidation event using gene phylogenies of a sunscreen. *mBio* 10 (3): e00561-00519. https://doi.org/10.1128/mBio.00561-19

GARCZAREK L., DUFRESNE A., BLOT N., COCKSHUTT A. M., PEYRAT A., CAMPBELL D. A., JOUBIN L. & SIX C. 2008. — Function and evolution of the *psb*A gene family in marine *Synechococcus*: *Synechococcus* sp. WH7803 as a case study. *The ISME Journal* 2 (9): 937-953. https://doi.org/10.1038/ismej.2008.46

GARRITY G. M., BRENNER D. J., KRIEG N., STALEY J. & MANUAL B. S. 2005. — The Alpha-, Beta-, Delta-, and Epsilonproteobacteria, *in* BRENNER D. J., KRIEG N. & STALEY J. (eds), *Bergey's Manual of Systematic Bacteriology*. Vol. 2: *The Proteobacteria*. Springer, New York, 1388 p.

GENG R., LI W., CHAO A., GUO X., LI H., YU G. & LI R. 2021. — Establishment of a new filamentous cyanobacterial genus, *Microcoleusiopsis* gen. nov.(microcoleaceae, cyanobacteria), from benthic mats in open channel, Jiangxi Province, China. *Diversity* 13 (11): 548. https://doi.org/10.3390/d13110548

GIOVANNONI S., TURNER S., OLSEN G., BARNS S., LANE D. & PACE N. 1988. — Evolutionary relationships among cyanobacteria and green chloroplasts. *Journal of Bacteriology* 170 (8): 3584-3592. https://doi.org/10.1128/jb.170.8.3584-3592.1988

GONZÁLEZ-RESENDIZ L., JOHANSEN J. R., ESCOBAR-SÁNCHEZ V., SEGAL-KISCHINEVZKY C., JIMÉNEZ-GARCÍA L. F. & LEÓN-TEJERA H. 2018. — Two new species of *Phyllonema* (Rivulariaceae, Cyanobacteria) with an emendation of the genus. *Journal of Phycology* 54 (5): 638-652. https://doi.org/10.1111/jpy.12769

GRETTENBERGER C. L., SUMNER D. Y., WALL K., BROWN C. T., EISEN J. A., MACKEY T. J., HAWES I., JOSPIN G. & JUNGBLUT A. D. 2020. — A phylogenetically novel cyanobacterium most closely related to *Gloeobacter*. *The ISME Journal* 14 (8): 2142-2152. https://doi.org/10.1038/s41396-020-0668-5

GUEVARA R., ARMESTO J. J. & CARU M. 2002. — Genetic diversity of *Nostoc* microsymbionts from *Gunnera tinctoria* revealed by PCR-STRR fingerprinting. *Microbial Ecology* 44 (2): 127-136. https://doi.org/10.1007/s00248-002-1019-y

GUGGER M., LYRA C., HENRIKSEN P., COUTE A., HUMBERT J.-F. & SIVONEN K. 2002. — Phylogenetic comparison of the cyanobacterial genera *Anabaena* and *Aphanizomenon*. *International Journal of Systematic and Evolutionary Microbiology* 52 (5): 1867-1880.

GUGGER M., MOLICA R., LE BERRE B., DUFOUR P., BERNARD C. & HUMBERT J.-F. 2005. — Genetic diversity of *Cylindrospermopsis* strains (Cyanobacteria) isolated from four continents. *Applied and Environmental Microbiology* 71 (2): 1097-1100. https://doi.org/10.1128/AEM.71.2.1097-1100.2005

GUIRY M. D. & GUIRY G. M. 2021. — AlgaeBase. World-Wide Electronic Publication, National University of Ireland, Galway. Available from: http://www. algaebase.org.

GUPTA A., MORBY A. P., TURNER J. S., WHITTON B. A. & ROBINSON N. J. 1993. — Deletion within the metallothionein locus of cadmium-tolerant *Synechococcus* PCC 6301 involving a highly iterated palindrome (HIP1). *Molecular Microbiology* 7 (2): 189-195.

HARTMANN L. S. & BARNUM S. R. 2010. — Inferring the evolutionary history of Mo-dependent nitrogen fixation from phylogenetic studies of *nif*K and *nif*DK. *Journal of Molecular Evolution* 71 (1): 70-85. https://doi.org/10.1007/s00239-010-9365-8

HAYES P., BUCHHOLZ B. & WALSBY A. 1992. — Gas vesicles are strengthened by the outer-surface protein, *Gvp*C. *Archives of Microbiology* 157 (3): 229-234. https://doi.org/10.1007/BF00245155

HENSON B. J., HESSELBROCK S. M., WATSON L. E. & BARNUM S. R. 2004. — Molecular phylogeny of the heterocystous cyanobacteria (subsections IV and V) based on *nif*D. *International Journal of Systematic and Evolutionary Microbiology* 54 (2): 493-497. https://doi.org/10.1099/ijs.0.02821-0

HENTSCHKE G. S., JOHANSEN J. R., PIETRASIAK N., FIORE M. D. F., RIGONATO J., SANT'ANNA C. L. & KOMAREK J. 2016. — Phylogenetic placement of *Dapisostemon* gen. nov. and *Streptostemon*, two tropical heterocytous genera (Cyanobacteria). *Phytotaxa* 245 (2): 129-143. https://doi.org/10.11646/phytotaxa.245.2.4

HIROSE Y., OHTSUBO Y., MISAWA N., YONEKAWA C., NAGAO N., SHIMURA Y., FUJISAWA T., KANESAKI Y., KATOH H. & KATAYAMA M. 2021. — Genome sequencing of the NIES Cyanobacteria collection with a focus on the heterocyst-forming clade. *DNA Research* 28 (6): dsab024. https://doi.org/10.1093/dnares/dsab024

HOFFMANN M., MONDAY S. R., ALLARD M. W., STRAIN E. A., WHITTAKER P., NAUM M., MCCARTHY P. J., LOPEZ J. V., FISCHER M. & BROWN E. W. 2012. — *Vibrio caribbeanicus* sp. nov., isolated from the marine sponge Scleritoderma cyanea. *International Journal of Systematic and Evolutionary Microbiology* 62 (8): 1736-1743. https://doi.org/10.1099/ijs.0.032375-0

HONDA D., YOKOTA A. & SUGIYAMA J. 1999. — Detection of seven major evolutionary lineages in cyanobacteria based on the 16S rRNA gene sequence analysis with new sequences of five marine *Synechococcus* strains. *Journal of Molecular Evolution* 48 (6): 723-739. https://doi.org/10.1007/PL00006517

HONG J., KIM O., JO S., KIM H., JEONG M. & YOON H. 2018. — Characterization of alkane-producing *Nostoc* sp. isolated from a summer bloom for biofuel potential. *Journal of Biobased Materials and Bioenergy* 12 (3): 244-251. https://doi.org/10.1166/jbmb.2018.1757

HUG L. A., BAKER B. J., ANANTHARAMAN K., BROWN C. T., PROBST A. J., CASTELLE C. J., BUTTERFIELD C. N., HERNSDORF A. W., AMANO Y. & ISE K. 2016. — A new view of the tree of life. *Nature Microbiology* 1 (5): 1-6. https://doi.org/10.1038/nmicrobiol.2016.48

HULTON C., HIGGINS C. & SHARP P. 1991. — ERIC sequences: a novel family of repetitive elements in the genomes of *Escherichia coli*, *Salmonella typhimurium* and other enterobacteria. *Molecular Microbiology* 5 (4): 825-834. https://doi.org/10.1111/j.1365-2958.1991.tb00755.x

Humbert J.-F., Barbe V., Latifi A., Gugger M., Calteau A., Coursin T., Lajus A., Castelli V., Oztas S. & Samson G. 2013. — A tribute to disorder in the genome of the bloom-forming freshwater cyanobacterium *Microcystis aeruginosa*. *PLoS ONE* 8 (8): e70747. https://doi.org/10.1371/journal.pone.0070747

Ishida K., Welker M., Christiansen G., Cadel-Six S., Bouchier C., Dittmann E., Hertweck C. & de Marsac N. T. 2009. — Plasticity and evolution of aeruginosin biosynthesis in cyanobacteria. *Applied and Environmental Microbiology* 75 (7): 2017-2026. https://doi.org/10.1128/AEM.02258-08

Iteman I., Rippka R., de Marsac N. T. & Herdman M. 2000. — Comparison of conserved structural and regulatory domains within divergent 16S rRNA-23S rRNA spacer sequences of cyanobacteria. *Microbiology* 146 (6): 1275-1286. https://doi.org/10.1099/00221287-146-6-1275

Jahodářová E., Dvořák P., Hašler P., Holušová K. & Poulíčková A. 2018. — *Elainella* gen. nov.: a new tropical cyanobacterium characterized using a complex genomic approach. *European Journal of Phycology* 53 (1): 39-51. https://doi.org/10.1080/09670262.2017.1362591

Janse I., Meima M., Kardinaal W. E. A. & Zwart G. 2003. — High-resolution differentiation of cyanobacteria by using rRNA-internal transcribed spacer denaturing gradient gel electrophoresis. *Applied and Environmental Microbiology* 69 (11): 6634-6643. https://doi.org/10.1128/AEM.69.11.6634-6643.2003

Janson S. & Granéli E. 2002. — Phylogenetic analyses of nitrogen-fixing cyanobacteria from the Baltic Sea reveal sequence anomalies in the phycocyanin operon. *International Journal of Systematic and Evolutionary Microbiology* 52 (4): 1397-1404.

Janson S., Bergman B., Carpenter E. J., Giovannoni S. J. & Vergin K. 1999. — Genetic analysis of natural populations of the marine diazotrophic cyanobacterium *Trichodesmium*. *FEMS Microbiology Ecology* 30 (1): 57-65. https://doi.org/10.1111/j.1574-6941.1999.tb00635.x

Johansen J. R., Kovacik L., Casamatta D. A., Iková K. F. & Kaštovský J. 2011. — Utility of 16S-23S ITS sequence and secondary structure for recognition of intrageneric and intergeneric limits within cyanobacterial taxa: *Leptolyngbya corticola* sp. nov.(Pseudanabaenaceae, Cyanobacteria). *Nova Hedwigia* 92 (3-4): 283-302.

Johansen J. R., Mareš J., Pietrasiak N., Bohunická M., Zima Jr J., Štenclová L. & Hauer T. 2017a. — Highly divergent 16S rRNA sequences in ribosomal operons of *Scytonema hyalinum* (Cyanobacteria). *PLoS ONE* 12 (10): e0186393.

Johansen J. R., Strunecký O., Bohunická M., Čapková K. Č., Raabová L., Dvořák P. & Komárek J. 2017b. — A revision of the genus *Geitlerinema* and a description of the genus *Anagnostidinema* gen. nov.(Oscillatoriophycidae, Cyanobacteria). *Fottea* 17 (1): 114-126.

Johnson J. S., Spakowicz D. J., Hong B.-Y., Petersen L. M., Demkowicz P., Chen L., Leopold S. R., Hanson B. M., Agresta H. O. & Gerstein M. 2019. — Evaluation of 16S rRNA gene sequencing for species and strain-level microbiome analysis. *Nature Communications* 10 (1): 1-11. https://doi.org/10.1038/s41467-019-13036-1

Jung P., Azua-Bustos A., Gonzalez-Silva C., Mikhailyuk T., Zabicki D., Holzinger A., Lakatos M. & Büdel B. 2021. — Emendation of the coccoid cyanobacterial genus *Gloeocapsopsis* and description of the new species *Gloeocapsopsis diffluens* sp. nov. and *Gloeocapsopsis dulcis* sp. nov. isolated from the coastal range of the Atacama Desert (Chile). *Frontiers in Microbiology* 12: 1628.

Junier P., Witzel K.-P. & Hadas O. 2007. — Genetic diversity of cyanobacterial communities in Lake Kinneret (Israel) using 16S rRNA gene, *psb*A and *ntc*A sequence analyses. *Aquatic Microbial Ecology* 49 (3): 233-241. https://doi.org/10.3354/ame01161

Kabirnataj S., Nematzadeh G. A., Talebi A. F., Tabatabaei M. & Singh P. 2018. — *Neowestiellopsis* gen. nov, a new genus of true branched cyanobacteria with the description of *Neowestiellopsis persica* sp. nov. and *Neowestiellopsis bilateralis* sp. nov., isolated from Iran. *Plant Systematics and Evolution* 304 (4): 501-510. https://doi.org/10.1007/s00606-017-1488-6

Kallas T., Rebiere M., Rippka R. & de Marsac N. T. 1983. — The structural *nif* genes of the cyanobacteria *Gloeothece* sp. and *Calothrix* sp. share homology with those of *Anabaena* sp., but the Gloeothece genes have a different arrangement. *Journal of Bacteriology* 155 (1): 427-431. https://doi.org/10.1128/jb.155.1.427-431.1983

Kaneko T., Sato S., Kotani H., Tanaka A., Asamizu E., Nakamura Y., Miyajima N., Hirosawa M., Sugiura M. & Sasamoto S. 1996. — Sequence analysis of the genome of the unicellular cyanobacterium *Synechocystis* sp. strain PCC6803. II. Sequence determination of the entire genome and assignment of potential protein-coding regions. *DNA Research* 3 (3): 109-136. https://doi.org/10.1093/dnares/3.3.109

Kang Y., Gu C., Yuan L., Wang Y., Zhu Y., Li X., Luo Q., Xiao J., Jiang D. & Qian M. 2014. — Flexibility and symmetry of prokaryotic genome rearrangement reveal lineage-associated core-gene-defined genome organizational frameworks. *mBio* 5 (6): e01867-01814. https://doi.org/10.1128/mBio.01867-14

Katoh H., Shiga Y., Nakahira Y. & Ohmori M. 2003. — Isolation and characterization of a drought-tolerant cyanobacterium, *Nostoc* sp. HK-01. *Microbes and Environments* 18 (2): 82-88. https://doi.org/10.1264/jsme2.18.82

Katrianna H., Fewer D. P., Fewer L. M., Lyra C., Eronen E. & Sivonen K. 2008. — Genetic diversity in strains of the genus *Anabaena* isolated from planktonic and benthic habitats of the Gulf of Finland (Baltic Sea). *FEMS Microbiology Ecology* 64 (2): 199-208. https://doi.org/10.1111/j.1574-6941.2008.00461.x

Kim Y.-J., Park H.-K. & Kim I.-S. 2020. — Invasion and toxin production by exotic nostocalean cyanobacteria (*Cuspidothrix*, *Cylindrospermopsis*, and *Sphaerospermopsis*) in the Nakdong River, Korea. *Harmful Algae* 100: 101954.

Kim Y., Joachimiak G., Ye Z., Binkowski T. A., Zhang R., Gornicki P., Callahan S. M., Hess W. R., Haselkorn R. & Joachimiak A. 2011. — Structure of transcription factor *het*R required for heterocyst differentiation in cyanobacteria. *Proceedings of the National Academy of Sciences* 108 (25): 10109-10114. https://doi.org/10.1073/pnas.1106840108

Kloub L., Gosselin S., Fullmer M., Graf J., Gogarten J. P. & Bansal M. S. 2021. — Systematic detection of large-scale multigene horizontal transfer in prokaryotes. *Molecular Biology and Evolution* 38 (6): 2639-2659. https://doi.org/10.1093/molbev/msab043

Komárek J. 2020. — Quo vadis, taxonomy of cyanobacteria (2019). *Fottea* 20 (1): 104-110. https://doi.org/10.5507/fot.2019.020

Komárek J., Kaštovský J., Mareš J. & Johansen J. R. 2014. — Taxonomic classification of cyanoprokaryotes (cyanobacterial genera) 2014, using a polyphasic approach. *Preslia* 86 (4): 295-335.

Konstantinou D., Voultsiadou E., Panteris E., Zervou S. K., Hiskia A. & Gkelis S. 2019. — *Leptothoe*, a new genus of marine cyanobacteria (Synechococcales) and three new species associated with sponges from the Aegean Sea. *Journal of Phycology* 55 (4): 882-897. https://doi.org/10.1111/jpy.12866

Koonin E. V., Makarova K. S. & Aravind L. 2001. — Horizontal gene transfer in prokaryotes: quantification and classification. *Annual Reviews in Microbiology* 55 (1): 709-742. https://doi.org/10.1146/annurev.micro.55.1.709

Korelusová J. 2008. — *Phylogeny of heterocystous cyanobacteria (Nostocales and Stigonematales)*. MSc Thesis, University of South Bohemia, 33 p.

Krugman T., Satish N., Vinogradova O., Beharav A., Kashi Y. & Nevo E. 2001. — Genome diversity in the cyanobacterium *Nostoc linckia* at 'Evolution Canyon', Israel, revealed by inter-HIP1 size polymorphisms. *Evolutionary Ecology Research* 3 (8): 899-915.

Kumar D., Dhar D. W., Nehra P. & Kumar N. 2017. — Similarity analysis of *Spirulina*/*Arthrospira* strains on the basis of phycocyanin operon locus (*cpc*B-IGS-*cpc*A) and 16S rRNA gene sequences. *Indian Journal of Biotechnology* 16 (1): 84-90.

KUMAR K., MELLA-HERRERA R. A. & GOLDEN J. W. 2010. — Cyanobacterial heterocysts. *Cold Spring Harbor Perspectives in Biology* 2 (4): a000315. https://doi.org/10.1101/cshperspect.a000315

LAAMANEN M. J., GUGGER M. F., LEHTIMÄKI J. M., HAUKKA K. & SIVONEN K. 2001. — Diversity of toxic and nontoxic *Nodularia* isolates (Cyanobacteria) and filaments from the Baltic Sea. *Applied and Environmental Microbiology* 67 (10): 4638-4647. https://doi.org/10.1128/AEM.67.10.4638-4647.2001

LATYSHEVA N., JUNKER V. L., PALMER W. J., CODD G. A. & BARKER D. 2012. — The evolution of nitrogen fixation in cyanobacteria. *Bioinformatics* 28 (5): 603-606. https://doi.org/10.1093/bioinformatics/bts008

LEE N.-J., SEO Y., KI J.-S. & LEE O.-M. 2020. — A study of newly recorded species for freshwater cyanobacteria *Microcystis protocystis* (Chroococcales, Cyanobacteria) in Korea. *The Microbiological Society of Korea* 56 (1): 36-43.

LEHTIMÄKI J., LYRA C., SUOMALAINEN S., SUNDMAN P., ROUHIAINEN L., PAULIN L., SALKINOJA-SALONEN M. & SIVONEN K. 2000. — Characterization of *Nodularia* strains, cyanobacteria from brackish waters, by genotypic and phenotypic methods. *International Journal of Systematic and Evolutionary Microbiology* 50 (3): 1043-1053. https://doi.org/10.1099/00207713-50-3-1043

LEÓN-TEJERA H. P., GONZALEZ-RESENDIZ L., JOHANSEN J. R., SEGAL-KISCHINEVSKY C., ESCOBAR V. & LOIS L. A. 2016. — Phylogenetic position reevaluation of *Kyrtuthrix* and description of a new species *K. huatulcensis* from Mexico's Pacific coast. *Phytotaxa* 278 (1): 1-18. https://doi.org/10.11646/phytotaxa.278.1.1

LEPÈRE C., WILMOTTE A. & MEYER B. 2000. — Molecular diversity of *Microcystis* strains (Cyanophyceae, Chroococcales) based on 16S rDNA sequences. *Systematics and Geography of Plants* 70 (2): 275-283. https://doi.org/10.2307/3668646

LIAIMER A., JENSEN J. B. & DITTMANN E. 2016. — A Genetic and Chemical Perspective on Symbiotic Recruitment of Cyanobacteria of the Genus *Nostoc* into the Host Plant *Blasia pusilla* L. *Frontiers in Microbiology* 7: 1693. https://doi.org/10.3389/fmicb.2016.01693

LIN S., WU Z., YU G., ZHU M., YU B. & LI R. 2010. — Genetic diversity and molecular phylogeny of *Planktothrix* (Oscillatoriales, cyanobacteria) strains from China. *Harmful Algae* 9 (1): 87-97. https://doi.org/10.1016/j.hal.2009.08.004

LUDWIG W., SCHLEIFER K. & WHITMAN W. 2009. — Revised road map to the phylum Firmicutes, *in* DE VOS, GARRITY, JONES, KRIEG, LUDWIG, RAINEY, SCHLEIFER & WHITMAN (eds), *Bergey's Manual of Systematic Bacteriology*. Vol. 3: *The Firmicutes*. Springer, New York: 1-14.

LUNDGREN P., JANSON S., JONASSON S., SINGER A. & BERGMAN B. 2005. — Unveiling of novel radiations within *Trichodesmium* cluster by *het*R gene sequence analysis. *Applied and Environmental Microbiology* 71 (1): 190-196. https://doi.org/10.1128/AEM.71.1.190-196.2005

LUQUE I., RIERA-ALBEROLA M. L., ANDUJAR A. & OCHOA DE ALDA J. A. 2008. — Intraphylum diversity and complex evolution of cyanobacterial aminoacyl-tRNA synthetases. *Molecular Biology and Evolution* 25 (11): 2369-2389. https://doi.org/10.1093/molbev/msn197

LYRA C., LAAMANEN M., LEHTIMÄKI J. M., SURAKKA A. & SIVONEN K. 2005. — Benthic cyanobacteria of the genus *Nodularia* are nontoxic, without gas vacuoles, able to glide and genetically more diverse than planktonic *Nodularia*. *International Journal of Systematic and Evolutionary Microbiology* 55 (2): 555-568. https://doi.org/10.1099/ijs.0.63288-0

LYRA C., SUOMALAINEN S., GUGGER M., VEZIE C., SUNDMAN P., PAULIN L. & SIVONEN K. 2001. — Molecular characterization of planktic cyanobacteria of *Anabaena*, *Aphanizomenon*, *Microcystis* and *Planktothrix* genera. *International Journal of Systematic and Evolutionary Microbiology* 51 (2): 513-526. https://doi.org/10.1099/00207713-51-2-513

MACGREGOR B. J., VAN MOOY B., BAKER B. J., MELLON M., MOISANDER P. H., PAERL H. W., ZEHR J., HOLLANDER D. & STAHL D. A. 2001. — Microbiological, molecular biological and stable isotopic evidence for nitrogen fixation in the open waters of Lake Michigan. *Environmental Microbiology* 3 (3): 205-219. https://doi.org/10.1046/j.1462-2920.2001.00180.x

MAHANSARIA A. P., JAISANKAR P. & MUKHERJEE J. 2018. — *Oxynema aestuarii* sp. nov.(Microcoleaceae) isolated from an Indian mangrove forest. *Phytotaxa* 374 (1): 24-40. https://doi.org/10.11646/phytotaxa.374.1.2

MAI T., JOHANSEN J. R., PIETRASIAK N., BOHUNICKÁ M. & MARTIN M. P. 2018. — Revision of the Synechococcales (cyanobacteria) through recognition of four families including Oculatellaceae fam. nov. and Trichocoleaceae fam nov. and seven new genera containing 14 species. *Phytotaxa* 365 (1): 1-59. https://doi.org/10.11646/phytotaxa.365.1.1

MANEN J.-F. & FALQUET J. 2002. — The *cpc*B-*cpc*A locus as a tool for the genetic characterization of the genus *Arthrospira* (Cyanobacteria): evidence for horizontal transfer. *International Journal of Systematic and Evolutionary Microbiology* 52 (3): 861-867.

MAREŠ J. 2018. — Multilocus and SSU rRNA gene phylogenetic analyses of available cyanobacterial genomes, and their relation to the current taxonomic system. *Hydrobiologia* 811 (1): 19-34. https://doi.org/10.1007/s10750-017-3373-2

MAREŠ J., HROUZEK P., KAŇA R., VENTURA S., STRUNECKÝ O. & KOMÁREK J. 2013. — The primitive thylakoid-less cyanobacterium *Gloeobacter* is a common rock-dwelling organism. *PLoS ONE* (6): e66323. https://doi.org/10.1371/journal.pone.0066323

MARQUARDT J. & PALINSKA K. A. 2007. — Genotypic and phenotypic diversity of cyanobacteria assigned to the genus *Phormidium* (Oscillatoriales) from different habitats and geographical sites. *Archives of Microbiology* 187 (5): 397-413. https://doi.org/10.1007/s00203-006-0204-7

MARTINS M. D., MACHADO DE LIMA N. M. & BRANCO L. H. Z. 2019. — Polyphasic approach using multilocus analyses supports the establishment of the new aerophytic cyanobacterial genus *Pycnacronema* (Coleofasciculaceae, Oscillatoriales). *Journal of Phycology* 55 (1): 146-159. https://doi.org/10.1111/jpy.12805

MARTINS M. D., RIGONATO J., TABOGA S. R. & BRANCO L. H. Z. 2016. — Proposal of *Ancylothrix* gen. nov., a new genus of Phormidiaceae (Cyanobacteria, Oscillatoriales) based on a polyphasic approach. *International Journal of Systematic and Evolutionary Microbiology* 66 (6): 2396-2405. https://doi.org/10.1099/ijsem.0.001044

MASEPOHL B., GÖRLITZ K. & BÖHME H. 1996. — Long tandemly repeated repetitive (LTRR) sequences in the filamentous cyanobacterium *Anabaena* sp. PCC 7120. *Biochimica et Biophysica Acta (BBA)-Gene Structure and Expression* 1307 (1): 26-30. https://doi.org/10.1016/0167-4781(96)00040-1

MAZEL D., HOUMARD J., CASTETS A. & DE MARSAC N. T. 1990. — Highly repetitive DNA sequences in cyanobacterial genomes. *Journal of Bacteriology* 172 (5): 2755-2761. https://doi.org/10.1128/jb.172.5.2755-2761.1990

MAZEL D., BERNARD C., SCHWARZ R., CASTETS A., HOUMARD J. & DE MARSAC N. T. 1991. — Characterization of two insertion sequences, IS701 and IS702, from the cyanobacterium *Calothrix* species PCC 7601. *Molecular Microbiology* 5 (9): 2165-2170. https://doi.org/10.1111/j.1365-2958.1991.tb02146.x

MEEKS J. C., JOSEPH C. M. & HASELKORN R. 1988. — Organization of the *nif* genes in cyanobacteria in symbiotic association with *Azolla* and *Anthoceros*. *Archives of Microbiology* 150 (1): 61-71. https://doi.org/10.1007/BF00409719

MEYER K. A., DAVIS T. W., WATSON S. B., DENEF V. J., BERRY M. A. & DICK G. J. 2017. — Genome sequences of lower Great Lakes *Microcystis* sp. reveal strain-specific genes that are present and expressed in western Lake Erie blooms. *PLoS ONE* 12 (10): e0183859. https://doi.org/10.1371/journal.pone.0183859

Miklaszewska M., Waleron M., Morin N., Calusinska M., Wilmotte A., de Marsac N. T., Rippka R. & Waleron K. 2012. — Elucidation of the gas vesicle gene clusters in cyanobacteria of the genus *Arthrospira* (Oscillatoriales, Cyanophyta) and correlation with ITS phylogeny. *European Journal of Phycology* 47 (3): 233-244. https://doi.org/10.1080/09670262.2012.692817

Miller S. R., Augustine S., Olson T. L., Blankenship R. E., Selker J. & Wood A. M. 2005. — Discovery of a free-living chlorophyll d-producing cyanobacterium with a hybrid proteobacterial/cyanobacterial small-subunit rRNA gene. *Proceedings of the National Academy of Sciences* 102 (3): 850-855. https://doi.org/10.1073/pnas.0405667102

Miller T. R. & Mcmahon K. D. 2011. — Genetic diversity of cyanobacteria in four eutrophic lakes. *FEMS Microbiology Ecology* 78 (2): 336-348. https://doi.org/10.1111/j.1574-6941.2011.01162.x

Min X., Xu X., Hong G. & Kong R. 2007. — High variability of the *gvp*A-*gvp*C region in *Microcystis*. *Progress in Natural Science* 17 (11): 1290-1295.

Misztak A. E., Waleron M., Furmaniak M., Waleron M. M., Bazhenova O., Daroch M. & Waleron K. F. 2021. — Comparative Genomics and Physiological Investigation of a New *Arthrospira*/*Limnospira* Strain O9. 13F Isolated from an Alkaline, Winter Freezing, Siberian Lake. *Cells* 10 (12): 3411. https://doi.org/10.3390/cells10123411

Mlouka A., Comte K., Castets A.-M., Bouchier C. & de Marsac N. T. 2004. — The gas vesicle gene cluster from *Microcystis aeruginosa* and DNA rearrangements that lead to loss of cell buoyancy. *Journal of Bacteriology* 186 (8): 2355-2365. https://doi.org/10.1128/JB.186.8.2355-2365.2004

Morales M. C., Villalobos K., Rodríguez A. R., Simón N. M. & Umaña-Castro R. 2017. — Identificación y caracterización molecular de cianobacterias tropicales de los géneros *Nostoc*, *Calothrix*, *Tolypothrix* y *Scytonema* (Nostocales: Nostocaceae), con posible potencial biotecnológico. *Cuadernos de Investigación UNED* 9 (2): 280-288.

Morandi A., Zhaxybayeva O., Gogarten J. P. & Graf J. 2005. — Evolutionary and diagnostic implications of intragenomic heterogeneity in the 16S rRNA gene in *Aeromonas* strains. *Journal of Bacteriology* 187 (18): 6561-6564. https://doi.org/10.1128/JB.187.18.6561-6564.2005

Moro I., Rascio N., La Rocca N., Sciuto K., Albertano P., Bruno L. & Andreoli C. 2010. — Polyphasic characterization of a thermo-tolerant filamentous cyanobacterium isolated from the Euganean thermal muds (Padua, Italy). *European Journal of Phycology* 45 (2): 143-154. https://doi.org/10.1080/09670260903564391

Morozova T., Seo W. & Zimmerly S. 2002. — Non-cognate template usage and alternative priming by a group II intron-encoded reverse transcriptase. *Journal of Molecular Biology* 315 (5): 951-963. https://doi.org/10.1006/jmbi.2001.5320

Muhlsteinova R., Johansen J. R., Pietrasiak N., Martin M. P., Osorio-Santos K. & Warren S. D. 2014. — Polyphasic characterization of *Trichocoleus desertorum* sp. nov.(Pseudanabaenales, Cyanobacteria) from desert soils and phylogenetic placement of the genus *Trichocoleus*. *Phytotaxa* 163 (5): 241-261. https://doi.org/10.11646/phytotaxa.163.5.1

Mulligan M. & Haselkorn R. 1989. — Nitrogen fixation (*nif*) genes of the cyanobacterium *Anabaena* species strain PCC 7120: the *nif*B-*fdx*N-*nif*S-*nif*U operon. *Journal of Biological Chemistry* 264 (32): 19200-19207.

Mulo P., Sicora C. & Aro E.-M. 2009. — Cyanobacterial *psb*A gene family: optimization of oxygenic photosynthesis. *Cellular and Molecular Life Sciences* 66 (23): 3697. https://doi.org/10.1007/s00018-009-0103-6

Muralitharan G. & Thajuddin N. 2011. — Rapid differentiation of phenotypically and genotypically similar *Synechococcus elongatus* strains by PCR fingerprinting. *Biologia* 66 (2): 238-243. https://doi.org/10.2478/s11756-011-0003-8

Mus F., Colman D. R., Peters J. W. & Boyd E. S. 2019. — Geobiological feedbacks, oxygen, and the evolution of nitrogenase. *Free Radical Biology and Medicine* 140: 250-259.

Nakamura Y., Itoh T., Matsuda H. & Gojobori T. 2004. — Biased biological functions of horizontally transferred genes in prokaryotic genomes. *Nature Genetics* 36 (7): 760-766. https://doi.org/10.1038/ng1381

Negi Y., Sharma S., Sutradhar N. & Adhikari S. 2019. — A study on the differentiation of filamentous cyanobacterial isolates using DNA fingerprinting approach. *IJBT* 18 (4): 337-345.

Neilan B., Saker M., Fastner J., Törökné A. & Burns B. 2003. — Phylogeography of the invasive cyanobacterium *Cylindrospermopsis raciborskii*. *Molecular Ecology* 12 (1): 133-140. https://doi.org/10.1046/j.1365-294X.2003.01709.x

Neilan B. A., Jacobs D. & Goodman A. E. 1995. — Genetic diversity and phylogeny of toxic cyanobacteria determined by DNA polymorphisms within the phycocyanin locus. *Applied and Environmental Microbiology* 61 (11): 3875-3883. https://doi.org/10.1128/aem.61.11.3875-3883.1995

Neilan B. A., Stuart J. L., Goodman A. E., Cox P. T. & Hawkins P. R. 1997. — Specific amplification and restriction polymorphisms of the cyanobacterial rRNA operon spacer region. *Systematic and Applied Microbiology* 20 (4): 612-621. https://doi.org/10.1016/S0723-2020(97)80033-1

Nilsson M., Bhattacharya J., Rai A. & Bergman B. 2002. — Colonization of roots of rice (*Oryza sativa*) by symbiotic *Nostoc* strains. *New Phytologist* 156 (3): 517-525.

Nowruzi B. & Blanco S. 2019. — In silico identification and evolutionary analysis of candidate genes involved in the biosynthesis methylproline genes in cyanobacteria strains of Iran. *Phytochemistry Letters* 29: 199-211. https://doi.org/10.1016/j.phytol.2018.12.011

Nowruzi B. & Soares F. 2021. — *Alborzia kermanshahica* gen. nov., sp. nov.(Chroococcales, Cyanobacteria), isolated from paddy fields in Iran. *International Journal of Systematic and Evolutionary Microbiology* 71 (6): 004828. https://doi.org/10.1099/ijsem.0.004828

Nowruzi B. & Lorenzi A. S. 2021. — Characterization of a potentially microcystin-producing *Fischerella* sp. isolated from Ajigol wetland of Iran. *South African Journal of Botany* 137: 423-433. https://doi.org/10.1016/j.sajb.2020.11.013

Nowruzi B. & Shalygin S. 2021. — Multiple phylogenies reveal a true taxonomic position of *Dulcicalothrix alborzica* sp. nov. (Nostocales, Cyanobacteria). *Fottea* 21 (2): 235-246. https://doi.org/10.5507/fot.2021.008

Nowruzi B., Khavari-Nejad R.-A., Nejadsattari T., Sivonen K. & Fewer D. 2016. — A proposal for the unification of two cyanobacterial strains of *Nostoc* as the same species. *Rostaniha* 17 (2): 161-172.

Nowruzi B., Khavari-Nejad R.-A., Sivonen K., Kazemi B., Najafi F. & Nejadsattari T. 2012. — Identification and toxigenic potential of a *Nostoc* sp. *Algae* 27 (4): 303-313. https://doi.org/10.4490/algae.2012.27.4.303

Nowruzi B., Khavari-Nejad R. A., Sivonen K., Kazemi B., Najafi F. & Nejadsattari T. 2013. — Identification and toxigenic potential of a cyanobacterial strain (*Stigomena* sp.). *Progress in Biological Sciences* 3 (1): 79-85.

Ogier J.-C., Galan M., Barret M. & Gaudriault S. 2019. — *rpo*B, a promising marker for analyzing the diversity of bacterial communities by amplicon sequencing. *BMC Microbiology* 19 (1): 1-16.

Orcutt K., Rasmussen U., Webb E. A., Waterbury J. B., Gundersen K. & Bergman B. 2002. — Characterization of *Trichodesmium* spp. by genetic techniques. *Applied and Environmental Microbiology* 68 (5): 2236-2245. https://doi.org/10.1128/AEM.68.5.2236-2245.2002

Oren A. 2011. — Naming Cyanophyta/Cyanobacteria – a bacteriologist's view. *Fottea* 11 (1): 9-16. https://doi.org/10.5507/fot.2011.002

Oren A. 2020. — Three alternative proposals to emend the Rules of the International Code of Nomenclature of Prokaryotes to resolve the status of the Cyanobacteria in the prokaryotic nomenclature. *International Journal of Systematic and Evolutionary Microbiology* 70 (7): 4406-4408. https://doi.org/10.1099/ijsem.0.004268

Oren A. & Garrity G. M. 2014. — Proposal to change General Consideration 5 and Principle 2 of the International Code of Nomenclature of Prokaryotes. *International Journal of Systematic and Evolutionary Microbiology* 64 (1): 309-310. https://doi.org/10.1099/ijs.0.059568-0

Osorio-Santos K., Pietrasiak N., Bohunická M., Miscoe L. H., Kováčik L., Martin M. P. & Johansen J. R. 2014. — Seven new species of *Oculatella* (Pseudanabaenales, Cyanobacteria): taxonomically recognizing cryptic diversification. *European Journal of Phycology* 49 (4): 450-470. https://doi.org/10.1080/09670262.2014.976843

Otsuka S., Suda S., Li R., Matsumoto S. & Watanabe M. M. 2000. — Morphological variability of colonies of *Microcystis* morphospecies in culture. *The Journal of General and Applied Microbiology* 46 (1): 39-50. https://doi.org/10.2323/jgam.46.39

Otten T. G. & Paerl H. W. 2011. — Phylogenetic inference of colony isolates comprising seasonal *Microcystis* blooms in Lake Taihu, China. *Microbial Ecology* 62 (4): 907-918. https://doi.org/10.1007/s00248-011-9884-x

Pace N. R. 2009. — Mapping the tree of life: progress and prospects. *Microbiology and Molecular Biology Reviews* 73 (4): 565-576. https://doi.org/10.1128/MMBR.00033-09

Palenik B. & Swift H. 1996. — Cyanobacterial evolution and Prochlorophyte diversity as seen in DNA-dependent RNA polymerase gene sequences 1. *Journal of Phycology* 32 (4): 638-646. https://doi.org/10.1111/j.0022-3646.1996.00638.x

Pancrace C., Barny M.-A., Ueoka R., Calteau A., Scalvenzi T., Pédron J., Barbe V., Piel J., Humbert J.-F. & Gugger M. 2017. — Insights into the *Planktothrix* genus: Genomic and metabolic comparison of benthic and planktic strains. *Scientific Reports* 7 (1): 1-10.

Perkerson III R. B., Johansen J. R., Kovacik L., Brand J., Kaštovský J. & Casamatta D. A. 2011. — A unique Pseudanabaenalean (Cyanobacteria) genus *Nodosilinea* gen. nov. based on morphological and molecular data 1. *Journal of Phycology* 47 (6): 1397-1412. https://doi.org/10.1111/j.1529-8817.2011.01077.x

Peters J. W., Boyd E. S., D'adamo S., Mulder D. W., Therien J. & Posewitz M. C. 2013. — Hydrogenases, nitrogenases, anoxia, and H2 production in water-oxidizing phototrophs, *in* Borowitzka M. A. & Moheimani N. R. (eds), *Algae for biofuels and energy*. Springer, New York: 37-75.

Piccin-Santos V., Brandão M. M. & Bittencourt-Oliveira M. D. C. 2014. — Phylogenetic study of *Geitlerinema* and *Microcystis* (Cyanobacteria) using PC-IGS and 16S-23S ITS as markers: investigation of horizontal gene transfer. *Journal of Phycology* 50 (4): 736-743. https://doi.org/10.1111/jpy.12204

Pietrasiak N., Osorio-Santos K., Shalygin S., Martin M. P. & Johansen J. R. 2019. — When is a lineage a species? A case study in *Myxacorys* gen. nov.(Synechococcales: Cyanobacteria) with the description of two new species from the Americas. J*ournal of Phycology* 55 (5): 976-996. https://doi.org/10.1111/jpy.12897

Pinevich A. V. 2015. — Proposal to consistently apply the International Code of Nomenclature of Prokaryotes (ICNP) to names of the oxygenic photosynthetic bacteria (cyanobacteria), including those validly published under the International Code of Botanical Nomenclature (ICBN)/International Code of Nomenclature for algae, fungi and plants (ICN), and proposal to change Principle 2 of the ICNP. *International Journal of Systematic and Evolutionary Microbiology* 65 (3): 1070-1074. https://doi.org/10.1099/ijs.0.000034

Powell R., Walsby A., Hayes P. & Porter R. 1991. — Antibodies to the N-terminal sequence of GVPa bind to the ends of gas vesicles. *Microbiology* 137 (10): 2395-2400.

Prabha R. & Singh D. P. 2019. — Cyanobacterial phylogenetic analysis based on phylogenomics approaches render evolutionary diversification and adaptation: an overview of representative orders. *3 Biotech* 9 (3): 87.

Prabha R., Singh D. P., Somvanshi P. & Rai A. 2016. — Functional profiling of cyanobacterial genomes and its role in ecological adaptations. *Genomics Data* 9: 89-94. https://doi.org/10.1016/j.gdata.2016.06.005

Prasanna R., Kumar R., Sood A., Prasanna B. & Singh P. 2006. — Morphological, physiochemical and molecular characterization of *Anabaena* strains. *Microbiological Research* 161 (3): 187-202. https://doi.org/10.1016/j.micres.2005.08.001

Premanandh J., Priya B., Teneva I., Dzhambazov B., Prabaharan D. & Uma L. 2006. — Molecular characterization of marine cyanobacteria from the Indian subcontinent deduced from sequence analysis of the phycocyanin operon (*cpc*B-IGS-*cpc*A) and 16S-23S ITS region. *The Journal of Microbiology* 44 (6): 607-616.

Raabova L., Kovacik L., Elster J. & Strunecký O. 2019. — Review of the genus *Phormidesmis* (Cyanobacteria) based on environmental, morphological, and molecular data with description of a new genus *Leptodesmis*. *Phytotaxa* 395 (1): 1-16. https://doi.org/10.11646/phytotaxa.395.1.1

Rajaniemi P., Hrouzek P., Kaštovska K., Willame R., Rantala A., Hoffmann L., Komárek J. & Sivonen K. 2005. — Phylogenetic and morphological evaluation of the genera *Anabaena*, *Aphanizomenon*, *Trichormus* and *Nostoc* (Nostocales, Cyanobacteria). *International Journal of Systematic and Evolutionary Microbiology* 55 (1): 11-26. https://doi.org/10.1099/ijs.0.63276-0

Rantala A., Fewer D. P., Hisbergues M., Rouhiainen L., Vaitomaa J., Börner T. & Sivonen K. 2004. — Phylogenetic evidence for the early evolution of microcystin synthesis. *Proceedings of the National Academy of Sciences* 101 (2): 568-573. https://doi.org/10.1073/pnas.0304489101

Rasmussen U. & Svenning M. M. 1998. — Fingerprinting of cyanobacteria based on PCR with primers derived from short and long tandemly repeated repetitive sequences. *Applied and Environmental Microbiology* 64 (1): 265-272. https://doi.org/10.1128/AEM.64.1.265-272.1998

Řeháková K., Johansen J. R., Casamatta D. A., Xuesong L. & Vincent J. 2007. — Morphological and molecular characterization of selected desert soil cyanobacteria: three species new to science including *Mojavia pulchra* gen. et sp. nov. *Phycologia* 46 (5): 481-502. https://doi.org/10.2216/06-92.1

Robertson B. R., Tezuka N. & Watanabe M. M. 2001. — Phylogenetic analyses of *Synechococcus* strains (cyanobacteria) using sequences of 16S rDNA and part of the phycocyanin operon reveal multiple evolutionary lines and reflect phycobilin content. *International Journal of Systematic and Evolutionary Microbiology* 51 (3): 861-871. https://doi.org/10.1099/00207713-51-3-861

Rocap G., Distel D. L., Waterbury J. B. & Chisholm S. W. 2002. — Resolution of *Prochlorococcus* and *Synechococcus* ecotypes by using 16S-23S ribosomal DNA internal transcribed spacer sequences. *Applied and Environmental Microbiology* 68 (3): 1180-1191. https://doi.org/10.1128/AEM.68.3.1180-1191.2002

Roeselers G., Stal L. J., Van Loosdrecht M. C. & Muyzer G. 2007. — Development of a PCR for the detection and identification of cyanobacterial *nif*D genes. *Journal of Microbiological Methods* 70 (3): 550-556. https://doi.org/10.1016/j.mimet.2007.06.011

Rouhiainen L., Sivonen K., Buikema W. J. & Haselkorn R. 1995. — Characterization of toxin-producing cyanobacteria by using an oligonucleotide probe containing a tandemly repeated heptamer. *Journal of Bacteriology* 177 (20): 6021-6026. https://doi.org/10.1128/jb.177.20.6021-6026.1995

Rudi K., Skulberg O. M. & Jakobsen K. S. 1998. — Evolution of cyanobacteria by exchange of genetic material among phyletically related strains. *Journal of Bacteriology* 180 (13): 3453-3461. https://doi.org/10.1128/JB.180.13.3453-3461.1998

Sabehi G., Shaulov L., Silver D. H., Yanai I., Harel A. & Lindell D. 2012. — A novel lineage of myoviruses infecting cyanobacteria is widespread in the oceans. *Proceedings of the National Academy of Sciences* 109 (6): 2037-2042. https://doi.org/10.1073/pnas.1115467109

Sanangelantoni A. M., Barbarini D., Di Pasquale G., Cammarano P. & Tiboni O. 1990. — Cloning and nucleotide sequence of an archaebacterial glutamine synthetase gene: phylogenetic implications. *Molecular and General Genetics* 221 (2): 187-194. https://doi.org/10.1007/BF00261719

Sánchez-Baracaldo P. 2015. — Origin of marine planktonic cyanobacteria. *Scientific Reports* 5 (1): 1-10.

Sánchez-Baracaldo P., Ridgwell A. & Raven J. A. 2014. — A neoproterozoic transition in the marine nitrogen cycle. *Current Biology* 24 (6): 652-657. https://doi.org/10.1016/j.cub.2014.01.041

Sanchez-Baracaldo P., Hayes P. & Blank C. E. 2005. — Morphological and habitat evolution in the Cyanobacteria using a compartmentalization approach. *Geobiology* 3 (3): 145-165. https://doi.org/10.1111/j.1472-4669.2005.00050.x

Sánchez-Baracaldo P. & Cardona T. 2020. — On the origin of oxygenic photosynthesis and Cyanobacteria. *New Phytologist* 225 (4): 1440-1446. https://doi.org/10.1111/nph.16249

Saraf A. G., Dawda H. G. & Singh P. 2019. — *Desikacharya* gen. nov., a phylogenetically distinct genus of Cyanobacteria along with the description of two new species, *Desikacharya nostocoides* sp. nov. and *Desikacharya soli* sp. nov., and reclassification of *Nostoc thermotolerans* to *Desikacharya thermotolerans* comb. nov. *International Journal of Systematic and Evolutionary Microbiology* 69 (2): 307-315. https://doi.org/10.1099/ijsem.0.003093

Schatz D., Keren Y., Hadas O., Carmeli S., Sukenik A. & Kaplan A. 2005. — Ecological implications of the emergence of non-toxic subcultures from toxic Microcystis strains. *Environmental Microbiology* 7 (6): 798-805. https://doi.org/10.1111/j.1462-2920.2005.00752.x

Schirrmeister B. E., Gugger M. & Donoghue P. C. 2015. — Cyanobacteria and the Great Oxidation Event: evidence from genes and fossils. *Palaeontology* 58 (5): 769-785. https://doi.org/10.1111/pala.12178

Schirrmeister B. E., de Vos J. M., Antonelli A. & Bagheri H. C. 2013. — Evolution of multicellularity coincided with increased diversification of cyanobacteria and the Great Oxidation Event. *Proceedings of the National Academy of Sciences* 110 (5): 1791-1796. https://doi.org/10.1073/pnas.1209927110

Schloss P. D. & Handelsman J. 2005. — Introducing DOTUR, a computer program for defining operational taxonomic units and estimating species richness. *Applied and Environmental Microbiology* 71 (3): 1501-1506. https://doi.org/10.1128/AEM.71.3.1501-1506.2005

Schopf J., Tripathi A. & Kudryavtsev A. 2006. — Three-dimensional optical confocal imagery of Precambrian microscopic organisms. *Astrobiology* 1: 1-16. https://doi.org/10.1089/ast.2006.6.1

Schoch C. L., Ciufo S., Domrachev M., Hotton C. L., Kannan S., Khovanskaya R., Leipe D., Mcveigh R., O'Neill K., Robbertse B., Sharma S., Soussov V., Sullivan J. P., Sun L., Turner S., Karsch-Mizrachi I. 2020 — *NCBI Taxonomy: a comprehensive update on curation, resources and tools*. Database, Oxford.

Sciuto K., Andreoli C., Rascio N., La Rocca N. & Moro I. 2012. — Polyphasic approach and typification of selected *Phormidium* strains (Cyanobacteria). *Cladistics* 28 (4): 357-374. https://doi.org/10.1111/j.1096-0031.2011.00386.x

Selvakumar G. & Gopalaswamy G. 2008. — PCR based fingerprinting of *Westiellopsis* cultures with short tandemly repeated repetitive (STRR) and highly iterated palindrome (HIP) sequences. *Biologia* 63 (3): 283-288. https://doi.org/10.2478/s11756-008-0065-4

Shalygin S., Pietrasiak N., Gomez F., Mlewski C., Gerard E. & Johansen J. R. 2018. — *Rivularia halophila* sp. nov.(Nostocales, Cyanobacteria): the first species of *Rivularia* described with the modern polyphasic approach. *European Journal of Phycology* 53 (4): 537-548. https://doi.org/10.1080/09670262.2018.1479887

Sheridan K. J., Duncan E. J., Eaton-Rye J. J. & Summerfield T. C. 2020. — The diversity and distribution of D1 proteins in cyanobacteria. *Photosynthesis Research* 145 (2): 111-128. https://doi.org/10.1007/s11120-020-00762-7

Shestakov S. & Karbysheva E. 2015. — The role of viruses in the evolution of cyanobacteria. *Biology Bulletin Reviews* 5 (6): 527-537. https://doi.org/10.1134/S2079086415060079

Shi T. & Falkowski P. G. 2008. — Genome evolution in cyanobacteria: the stable core and the variable shell. *Proceedings of the National Academy of Sciences* 105 (7): 2510-2515. https://doi.org/10.1073/pnas.0711165105

Shokraeia R., Fahimia H., Blancob S. & Nowruzic B. 2019. — Genomic fingerprinting using highly repetitive sequences to differentiate close cyanobacterial strains. *Microbial Bioactives* 2 (1): 68-75.

Shukla E., Singh S. & Mishr A. 2013. — Fingerprinting and phylogeny of some heterocystous cyanobacteria using short tandemly repeated repetitive and highly iterated palindrome sequences. *Microbiology* 82 (6): 801-808. https://doi.org/10.1134/S0026261714010123

Shukla E., Singh P., Singh V. K., Singh S. S. & Mishra A. K. 2021. — Homology modeling in combination of phylogenetic assortment, a new approach to resolve the phylogeny of selected heterocystous cyanobacteria based on phycocyanin encoding *cpc*BA-IGS locus. *Vegetos* 34 (2): 339-354. https://doi.org/10.1007/s42535-021-00207-z

Sicora C. I., Ho F. M., Salminen T., Styring S. & Aro E.-M. 2009. — Transcription of a "silent" cyanobacterial *psb*A gene is induced by microaerobic conditions. *Biochimica et Biophysica Acta (BBA)-Bioenergetics* 1787 (2): 105-112. https://doi.org/10.1016/j.bbabio.2008.12.002

Siegesmund M. A., Johansen J. R., Karsten U. & Friedl T. 2008. — *Coleofasciculus* gen. nov.(Cyanobacteria): Morphological and Molecular Criteria for Revision of the Genus *Microcoleus* Gomont 1. *Journal of Phycology* 44 (6): 1572-1585. https://doi.org/10.1111/j.1529-8817.2008.00604.x

Sihvonen L. M., Lyra C., Fewer D. P., Rajaniemi-Wacklin P., Lehtimäki J. M., Wahlsten M. & Sivonen K. 2007. — Strains of the cyanobacterial genera *Calothrix* and *Rivularia* isolated from the Baltic Sea display cryptic diversity and are distantly related to *Gloeotrichia* and *Tolypothrix*. *FEMS Microbiology Ecology* 61 (1): 74-84. https://doi.org/10.1111/j.1574-6941.2007.00321.x

Singh P., Fatma A. & Mishra A. K. 2015. — Molecular phylogeny and evogenomics of heterocystous cyanobacteria using *rbc*L gene sequence data. *Annals of Microbiology* 65 (2): 799-807. https://doi.org/10.1007/s13213-014-0920-1

Singh T. & Bhadury P. 2019. — Description of a new marine planktonic cyanobacterial species *Synechococcus moorigangaii* (Order Chroococcales) from Sundarbans mangrove ecosystem. *Phytotaxa* 393 (3): 263-277. https://doi.org/10.11646/phytotaxa.393.3.3

Smith J., Parry J., Day J. & Smith R. 1998. — A PCR technique based on the Hipl interspersed repetitive sequence distinguishes cyanobacterial species and strains. *Microbiology* 144 (10): 2791-2801. https://doi.org/10.1099/00221287-144-10-2791

Soo R. M., Hemp J., Parks D. H., Fischer W. W. & Hugenholtz P. 2017. — On the origins of oxygenic photosynthesis and aerobic respiration in Cyanobacteria. *Science* 355 (6332): 1436-1440. https://doi.org/10.1126/science.aal3794

Stackebrandt E. & Goebel B. M. 1994. — Taxonomic note: a place for DNA-DNA reassociation and 16S rRNA sequence analysis in the present species definition in bacteriology. *International Journal of Systematic and Evolutionary Microbiology* 44 (4): 846-849. https://doi.org/10.1099/00207713-44-4-846

Strunecký O., Bohunicka M., Johansen J., Capkova K., Raabova L., Dvorak P. & Komarek J. 2016. — A revision of the genus *Geitlerinema* and a description of the genus *Anagnostidinema* gen. nov (Oscillatoriophycidae, Cyanobacteria). *Fottea* 17: 114-126. https://doi.org/10.5507/fot.2016.025

Strunecký O., Ivanova A. P. & Mareš J. 2022. — An updated classification of cyanobacterial orders and families based on phylogenomic and polyphasic analysis 1. *Journal of Phycology* 59 (1): 12-51. https://doi.org/10.1111/jpy.13304

Stucken K., Koch R. & Dagan T. 2013. — Cyanobacterial defense mechanisms against foreign DNA transfer and their impact on genetic engineering. *Biological Research* 46 (4): 373-382. https://doi.org/10.4067/S0716-97602013000400009

Suda S., Watanabe M. M., Otsuka S., Mahakahant A., Yongmanitchai W., Nopartnaraporn N., Liu Y. & Day J. G. 2002. — Taxonomic revision of water-bloom-forming species of oscillatorioid cyanobacteria. *International Journal of Systematic and Evolutionary Microbiology* 52 (5): 1577-1595.

Sullivan M. B., Lindell D., Lee J. A., Thompson L. R., Bielawski J. P. & Chisholm S. W. 2006. — Prevalence and evolution of core photosystem II genes in marine cyanobacterial viruses and their hosts. *PLoS Biology* 4 (8): e234. https://doi.org/10.1371/journal.pbio.0040234

Sun D.-L., Jiang X., Wu Q. L. & Zhou N.-Y. 2013. — Intragenomic heterogeneity of 16S rRNA genes causes overestimation of prokaryotic diversity. *Applied and Environmental Microbiology* 79 (19): 5962-5969. https://doi.org/10.1128/AEM.01282-13

Svenning M. M., Eriksson T. & Rasmussen U. 2005. — Phylogeny of symbiotic cyanobacteria within the genus *Nostoc* based on 16S rDNA sequence analyses. *Archives of Microbiology* 183 (1): 19-26. https://doi.org/10.1007/s00203-004-0740-y

Szöllősi G. J., Davín A. A., Tannier E., Daubin V. & Boussau B. 2015. — Genome-scale phylogenetic analysis finds extensive gene transfer among fungi. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370 (1678): 20140335. https://doi.org/10.1098/rstb.2014.0335

Tamas I., Svircev Z. & Andersson S. G. 2000. — Determinative value of a portion of the *nif*H sequence for the genera *Nostoc* and *Anabaena* (Cyanobacteria). *Current Microbiology* 41 (3): 197-200.

Tan W., Liu Y., Wu Z., Lin S., Yu G., Yu B. & Li R. 2010. — *cpc*BA-IGS as an effective marker to characterize *Microcystis wesenbergii* (Komárek) Komárek in Kondrateva (cyanobacteria). *Harmful Algae* 9 (6): 607-612. https://doi.org/10.1016/j.hal.2010.04.011

Tanabe Y., Kasai F. & Watanabe M. M. 2007. — Multilocus sequence typing (MLST) reveals high genetic diversity and clonal population structure of the toxic cyanobacterium *Microcystis aeruginosa*. *Microbiology* 153 (11): 3695-3703. https://doi.org/10.1099/mic.0.2007/010645-0

Tanabe Y., Hodoki Y., Sano T., Tada K. & Watanabe M. M. 2018. — Adaptation of the freshwater bloom-forming cyanobacterium *Microcystis aeruginosa* to brackish water is driven by recent horizontal transfer of sucrose genes. *Frontiers in Microbiology* 9: 1150. https://doi.org/10.3389/fmicb.2018.01150

Teikari J. E., Popin R. V., Hou S., Wahlsten M., Hess W. R. & Sivonen K. 2019. — Insight into the genome and brackish water adaptation strategies of toxic and bloom-forming Baltic Sea *Dolichospermum* sp. UHCC 0315. *Scientific Reports* 9 (1): 1-13. https://doi.org/10.1038/s41598-019-40883-1

Teneva I., Belkinova D., Moten D. & Dzhambazov B. 2019. — In search of new molecular markers for taxonomic classification of cyanobacteria. *International Multidisciplinary Scientific GeoConference: SGEM* 19 (5.2): 461-468.

Thajuddin N., Muralitharan G., Sundaramoorthy M., Ramamoorthy R., Ramachandran S., Akbarsha M. A. & Gunasekaran M. 2010. — Morphological and genetic diversity of symbiotic cyanobacteria from cycads. *Journal of Basic Microbiology* 50 (3): 254-265. https://doi.org/10.1002/jobm.200900343

Thiel T. 2019. — Organization and regulation of cyanobacterial *nif* gene clusters: implications for nitrogenase expression in plant cells. *FEMS Microbiology Letters* 366 (7): fnz077. https://doi.org/10.1093/femsle/fnz077

Thomazeau S., Houdan-Fourmont A., Coute A., Duval C., Couloux A., Rousseau F. & Bernard C. 2010. — The Contribution of Sub-Saharan African Strains to the Phylogeny of Cyanobacteria: Focusing on the Nostocaceae (Nostocales, Cyanobacteria) 1. *Journal of Phycology* 46 (3): 564-579. https://doi.org/10.1111/j.1529-8817.2010.00836.x

Thompson C. C., Vicente A. C. P., Souza R. C., Vasconcelos A. T. R., Vesth T., Alves N., Ussery D. W., Iida T. & Thompson F. L. 2009. — Genomic taxonomy of vibrios. *BMC Evolutionary Biology* 9 (1): 1-16. https://doi.org/10.1186/1471-2148-9-258

Tiboni O., di Pasquale G. & Ciferri O. 1984. — Two *tuf* genes in the cyanobacterium *Spirulina platensis*. *Journal of Bacteriology* 159 (1): 407-409. https://doi.org/10.1128/jb.159.1.407-409.1984

Toledo G. & Palenik B. 1997. — *Synechococcus* diversity in the California current as seen by RNA polymerase (*rpo*C1) gene sequences of isolated strains. *Applied and Environmental Microbiology* 63 (11): 4298-4303. https://doi.org/10.1128/aem.63.11.4298-4303.1997

Tomitani A., Knoll A. H., Cavanaugh C. M. & Ohno T. 2006. — The evolutionary diversification of cyanobacteria: molecular-phylogenetic and paleontological perspectives. *Proceedings of the National Academy of Sciences* 103 (14): 5442-5447. https://doi.org/10.1073/pnas.0600999103

Tompa M. 1999. — An exact method for finding short motifs in sequences, with application to the ribosome binding site problem. *Proceedings of International Conference on Intelligent Systems for Molecular Biology* 99: 262-271.

Turner S. 1997. — Molecular systematics of oxygenic photosynthetic bacteria, *in* Bhattacharya D. (ed.), *Origins of Algae and their Plastids*. Springer, Vienna: 13-52.

Urbach E., Robertson D. L. & Chisholm S. W. 1992. — Multiple evolutionary origins of prochlorophytes within the cyanobacterial radiation. *Nature* 355 (6357): 267-270. https://doi.org/10.1038/355267a0

Urrejola C., Alcorta J., Salas L., Vásquez M., Polz M. F., Vicuña R. & Díez B. 2019. — Genomic features for desiccation tolerance and sugar biosynthesis in the extremophile *Gloeocapsopsis* sp. UTEX B3054. *Frontiers in Microbiology* 10: 950. https://doi.org/10.3389/fmicb.2019.00950

Valério E., Pereira P., Saker M., Franca S. & Tenreiro R. 2005. — Molecular characterization of *Cylindrospermopsis raciborskii* strains isolated from Portuguese freshwaters. *Harmful Algae* 4 (6): 1044-1052. https://doi.org/10.1016/j.hal.2005.03.002

Valerio E., Chambel L., Paulino S., Faria N., Pereira P. & Tenreiro R. 2009. — Molecular identification, typing and traceability of cyanobacteria from freshwater reservoirs. *Microbiology* 155 (2): 642-656. https://doi.org/10.1099/mic.0.022848-0

Vaz M. G. M. V., Genuário D. B., Andreote A. P. D., Malone C. F. S., Sant'anna C. L., Barbiero L. & Fiore M. F. 2015. — *Pantanalinema* gen. nov. and *Alkalinema* gen. nov.: novel pseudanabaenacean genera (Cyanobacteria) isolated from saline-alkaline lakes. *International Journal of Systematic and Evolutionary Microbiology* 65 (1): 298-308. https://doi.org/10.1099/ijs.0.070110-0

Villanueva C. D., Garvey A. D., Hašler P., Dvořák P., Poulíčková A., Norwich A. R. & Casamatta D. A. 2019. — Descriptions of *Brasilonema geniculatum* and *Calothrix dumus* (Nostocales, Cyanobacteria): two new taxa isolated from cemetery tombstones. *Phytotaxa* 387 (1): 1-20. https://doi.org/10.11646/phytotaxa.387.1.1

Vuong M. 2014. — *Investigation in HIP1-Related Sequence in Cyanobacteria A and B*.

Walter J. M., Coutinho F. H., Dutilh B. E., Swings J., Thompson F. L. & Thompson C. C. 2017. — Ecogenomics and taxonomy of Cyanobacteria phylum. *Frontiers in Microbiology* 8: 2132. https://doi.org/10.3389/fmicb.2017.02132

WANG Y., JIA N., GENG R., YU G. & LI R. 2021. — Phylogenetic insights into *Chroococcus*-like taxa (Chroococcales, Cyanobacteria), describing *Cryptochroococcus tibeticus* gen. nov. sp. nov. and *Limnococcus fonticola* sp. nov. from Qinghai-Tibet plateau. *Journal of Phycology* 57 (6): 1739-1748. https://doi.org/10.1111/jpy.13205

WANIGATUNGE R., MAGANA-ARACHCHI D., CHANDRASEKHARAN N. & KULASOORIYA S. 2014. — Genetic diversity and molecular phylogeny of cyanobacteria from Sri Lanka based on 16S rRNA gene. *Environmental Engineering Research* 19 (4): 317-329. https://doi.org/10.4491/eer.2014.035

WARSHAN D., ESPINOZA J. L., STUART R. K., RICHTER R. A., KIM S.-Y., SHAPIRO N., WOYKE T., CKYRPIDES N., BARRY K. & SINGAN V. 2017. — Feathermoss and epiphytic *Nostoc* cooperate differently: expanding the spectrum of plant-cyanobacteria symbiosis. *The ISME Journal* 11 (12): 2821-2833. https://doi.org/10.1038/ismej.2017.134

WATANABE T. & HORIIKE T. 2021. — The Evolution of Molybdenum Dependent Nitrogenase in Cyanobacteria. *Biology* 10 (4): 329. https://doi.org/10.3390/biology10040329

WILLIS A. & WOODHOUSE J. N. 2020. — Defining cyanobacterial species: diversity and description through genomics. *Critical Reviews in Plant Sciences* 39 (2): 101-124. https://doi.org/10.1080/07352689.2020.1763541

WILMOTTE A. 1994. — Molecular evolution and taxonomy of the cyanobacteria, *in* BRYANT D. A. (ed.), *The Molecular Biology of Cyanobacteria*. Springer, Dordrecht: 1-25.

WILMOTTE A. & HERDMAN M. 2001. — Phylogenetic relationships among the cyanobacteria based on 16S rRNA sequences, *in* GARRITY G. M. & CASTENHOLZ R. W., *Bergey's Manual of Systematic Bacteriology*. Vol. 1: *The Archaea and the Deeply Branching and Phototrophic Bacteria*. Williams & Wilkins, Philadelphia: 487-493.

WILMOTTE A., LAUGHINGHOUSE I. H. D., CAPELLI C., RIPPKA R. & SALMASO N. 2017. — Taxonomic identification of cyanobacteria by a polyphasic approach, *in* KURMAYER R., SIVONEN K., WILMOTTE A. & SALMASO N. (eds), *Molecular Tools for the Detection and Quantification of Toxigenic Cyanobacteria*. John Wiley & Sons, Hoboken: 79-119.

WILSON K. M., SCHEMBRI M. A., BAKER P. D. & SAINT C. P. 2000. — Molecular characterization of the toxic cyanobacterium *Cylindrospermopsis raciborskii* and design of a species-specific PCR. *Applied and Environmental Microbiology* 66 (1): 332-338. https://doi.org/10.1128/AEM.66.1.332-338.2000

WOESE C. R. 2004. — A new biology for a new century. *Microbiology and Molecular Biology Reviews* 68 (2): 173-186. https://doi.org/10.1128/MMBR.68.2.173-186.2004

WU Z., SHI J., XIAO P., LIU Y. & LI R. 2011. — Phylogenetic analysis of two cyanobacterial genera *Cylindrospermopsis* and *Raphidiopsis* based on multi-gene sequences. *Harmful Algae* 10 (5): 419-425. https://doi.org/10.1016/j.hal.2010.05.001

XIE W.-Q., JÄGER K. & POTTS M. 1989. — Cyanobacterial RNA polymerase genes *rpo*C1 and *rpo*C2 correspond to *rpo*C of *Escherichia coli*. *Journal of Bacteriology* 171 (4): 1967-1973. https://doi.org/10.1128/jb.171.4.1967-1973.1989

XU M., LAWRENCE J. G. & DURAND D. 2018. — Selection, periodicity and potential function for Highly Iterative Palindrome-1 (HIP1) in cyanobacterial genomes. *Nucleic Acids Research* 46 (5): 2265-2278. https://doi.org/10.1093/nar/gky075

YAP W. H., ZHANG Z. & WANG Y. 1999. — Distinct types of rRNA operons exist in the genome of the actinomycete *Thermomonospora chromogena* and evidence for horizontal transfer of an entire rRNA operon. *Journal of Bacteriology* 181 (17): 5201-5209. https://doi.org/10.1128/JB.181.17.5201-5209.1999

ZANI S., MELLON M. T., COLLIER J. L. & ZEHR J. P. 2000. — Expression of *nif*H genes in natural microbial assemblages in Lake George, New York, detected by reverse transcriptase PCR. *Applied and Environmental Microbiology* 66 (7): 3119-3124. https://doi.org/10.1128/AEM.66.7.3119-3124.2000

ZEHR J. P., MELLON M. T. & HIORNS W. D. 1997. — Phylogeny of cyanobacterial *nif*H genes: evolutionary implications and potential applications to natural assemblages. *Microbiology* 143 (4): 1443-1450. https://doi.org/10.1099/00221287-143-4-1443

ZEHR J. P., WATERBURY J. B., TURNER P. J., MONTOYA J. P., OMOREGIE E., STEWARD G. F., HANSEN A. & KARL D. M. 2001. — Unicellular cyanobacteria fix N2 in the subtropical North Pacific Ocean. *Nature* 412 (6847): 635-638. https://doi.org/10.1038/35088063

ZEHR J. P., BENCH S. R., CARTER B. J., HEWSON I., NIAZI F., SHI T., TRIPP H. J. & AFFOURTIT J. P. 2008. — Globally distributed uncultivated oceanic N2-fixing cyanobacteria lack oxygenic photosystem II. *Science* 322 (5904): 1110-1112. https://doi.org/10.1126/science.1165340

ZEIDNER G., PRESTON C. M., DELONG E. F., MASSANA R., POST A. F., SCANLAN D. J. & BÉJÀ O. 2003. — Molecular diversity among marine picophytoplankton as revealed by *psb*A analyses. *Environmental Microbiology* 5 (3): 212-216. https://doi.org/10.1046/j.1462-2920.2003.00403.x

ZHANG H. & YANG C. 2019. — Arginine and nitrogen mobilization in cyanobacteria. *Molecular Microbiology* 111 (4): 863-867. https://doi.org/10.1111/mmi.14204

ZHAXYBAYEVA O., GOGARTEN J. P., CHARLEBOIS R. L., DOOLITTLE W. F. & PAPKE R. T. 2006. — Phylogenetic analyses of cyanobacterial genomes: quantification of horizontal gene transfer events. *Genome Research* 16 (9): 1099-1108. https://doi.org/10.1101/gr.5322306

ZHENG W., NILSSON M., BERGMAN B. & RASMUSSEN U. 1999. — Genetic diversity and classification of cyanobacteria in different *Azolla* species by the use of PCR fingerprinting. *Theoretical and Applied Genetics* 99 (7-8): 1187-1193.

ZIMBA P. V., SHALYGIN S., HUANG I.-S., MOMČILOVIĆ M. & ABDULLA H. 2021. — A new boring toxin producer *Perforafilum tunnelli* gen. & sp. nov. (Oscillatoriales, Cyanobacteria) isolated from Laguna Madre, Texas, USA. *Phycologia* 60 (1): 10-24. https://doi.org/10.1080/00318884.2020.1808389

Submitted on 4 May 2022;
accepted on 22 February 2023;
published on 28 June 2023.