THESES OF DOCTORAL (PhD) DISSERTATION

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MOSONMAGYARÓVÁR
2020

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MOLECULAR TAXONOMIC CHARACTERIZATION OF PREVIOUSLY MORPHOLOGICALLY IDENTIFIED *ANABAENA* STRAINS FROM THE MOSONMAGYARÓVÁR ALGAL CULTURE COLLECTION (MACC)

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1. INTRODUCTION

Cyanobacteria are a vast and morphologically diverse group of photo-oxygenic bacteria with wide ecological tolerances and found in most habitats on Earth. Their taxa were traditionally identified based on morphological characters; however, molecular techniques are increasingly incorporated into their study. The combination of molecular (e.g. 16S rRNA, ITS, rbclx, rpoC1) markers and morphological and ecological characteristics (the "polyphasic approach") has become the golden standard in cyanobacterial taxonomy.

Heterocytous cyanobacteria may be difficult to characterize as their morphology are similar and numerous morphologically well-defined genera appear polyphyletic. One such example is the genus *Anabaena*, which was found polyphyletic by several researchers and currently represents multiple genera. Several new genera have been described and erected from the original genus and many taxa have been transferred to *Dolichospermum*, *Trichormus*, *Chrysosporum* and *Sphaerospermopsis*. The original genus *Anabaena*, according to the type species, is closer to a large clade containing *Trichormus*, *Nostoc*, *Cylindrospermum* and *Wollea*.

Scrutinizing genera, especially *Anabaena*, is essential with the increasing interest in their toxicology and prevalence through blooms. *Anabaena* is an important genus due to the innumerous biologically active compounds they can produce. Certain *Anabaena* species produce harmful toxins with detrimental effects, and projections indicate that these will increase with environmental changes. Several *Anabeana* strains found in the MACC (Mosonmagyaróvár Algal Culture Collection), such as *Anabaena sphaerica* (Bornet & Flahault), *Anabaena constricta* (Szafer

Geitler) and *Anabaena miniata* (Skuja), have demonstrated ecotoxicological effects against the cabbage root fly as well as fungicidal properties. With the tentative goals of further exploring the ecotoxicology of the MACC isolates and the prevalence of cyanobacterial blooms warranting proper species identification, it is imperative to legitimately identify isolates and provide a molecular framework for future work.

There are currently 280 cyanobacterial strains in the MACC collection. This research focuses on the phylogenetic relationships of 82 MACC strains previously morphologically identified as *Anabaena*. Since this part of the MACC collection lacks molecular scrutiny, the author evaluated its phylogeny and carried out reclassification of the strains using partial 16S rRNA housekeeping gene.

Objectives:

- Phylogenetic grouping and positioning of MACC *Anabaena* strains after their identification by using 16S rRNA. This demonstrates the current location of the MACC *Anabaena* strains on a section of the cyanobacterial tree of life.
- Promoting akinete formation, which paves the way for further successful taxonomic studies.
- Selecting strains that are systematically close to MACC *Anabaena* strains previously classified antimicrobial. These may be recommended for further testing.

2. MATERIALS AND METHODS

2.1. Strain propagation

The stock cultures are maintained in the liquid medium used for isolation or mostly in agar-solidified medium at the Department of Plant Sciences of the Széchenyi István University (Figure 1.).

Figure 1. Maintenance of stock cultures on agar-solidified medium at the Mosonmagyaróvár Algae Collection.

Eighty-two strains were selected from the MACC collection, Széchenyi István University, Mosonmagyaróvár, Hungary. Sixty strains originated from Serbia (University of Novi Sad), 12 strains from Hungary, 3 strains from Russia (IPPAS), 2 strains from England, 2 strains from the Czech Republic (CCALA – Trebon), 2 strains from Ukraine and one strain is from Brazil. Strains from stock cultures were inoculated into 500 mL Erlenmeyer flasks containing 250 mL modified Z8 medium at 24-26 °C under a light intensity of 130 μM m^{-2} s^{-1} provided by Lumoflor and cool white fluorescent tubes (14 h/10 h light/dark cycle). Cultures were aerated

with 20 L h^{-1} (=1.33 L air L^{-1} nutrient medium per minute) sterile humidified air enriched with 1.5 % CO_2 during the light period (Figure 2.). The air was introduced into the cultures via a special, sterile cotton pad. To prevent sedimentation, the cultures were manually agitated twice each day.

Figure 2. Laboratory for cultivation of MACC microalgae strains.

2.2. Morphometry

Strain morphology was observed using an Olympus BX60 microscope. For taxonomical classification of the MACC strains, the author used the AlgaeBase (www.algaebase.org) database, which is constantly updated and available on the Internet. At least 30 trichomes per strain were photographed with a digital camera (Olympus DP 70, magnification 400x). Dimensions of vegetative cells and heterocytes were measured using image analysis software (Olympus DP Soft 3.2). The contrast of the photos was enhanced by Adobe Lightroom software.

The morphological delineation of 63 strains were carried out using 7 parameters: 1. vegetative cell width, 2. vegetative cell length, 3.

heterocyte width, 4. heterocyte length, 5. vegetative cell shape, 6. heterocyte shape, 7. location of heterocyte within the filament. Although, these cannot replace the presence of akinets and their pattern, location within the thread, since it is classified as a diacritical characteristic in the cyanobacterial taxonomy. However, it can be a starting point for delimiting the strains.

2.3. DNA extraction, PCR, sequence analyses

For DNA analysis, the partial 16S rRNA gene of 82 MACC strains was sequenced. Sequencing and evaluation of their data was performed by Dr. Gergely Maróti et al. (Seqomics Kft., Mórahalom). Total genomic DNA was extracted using the GeneJET Genomic DNA Purification Kit (Thermo Fisher Scientific).

The 16S rRNA gene was amplified using primers 8F (AGAGTTTGATCCTGGCTCAG) and S8 (TCTACGCATTTCACCGCTAC). The PCR mix contained 10 μL Phusion Flash High-Fidelity PCR Master Mix (Thermo Fisher Scientific), 7 μL dH2O, 1 μL of each primer and 1 μL purified DNA (50–100 ng). PCR device data: Initial denaturation was performed at 98 °C for 30 sec, followed by denaturation at 98 °C for 10 sec, annealing at 58 °C for 20 sec, extension at 72 °C for 30 sec, and the final extension at 72 °C for 1 min over 40 cycles. The final volume of the PCR reaction solution was 20 μL, which contained a final concentration of 0.5 μmol per primer. The length of the PCR product ranged from 510 to 660 bp. After DNA amplification, products were visualized on a 1.5% agarose gel. The PCR products were purified using the GeneJET Gel Extraction Kit (Thermo Fisher Scientific). Purity of the PCR product was tested at 260/280 nm by

Nanodrop™. For sequencing, a LifeTech 3500 Genetic Analyzer (Thermo Fisher Scientific) capillary sequencer was used.

The binding position of the forward primer 8F is 8-27, while the binding position of the reverse primer S8 is 649-630. Determination of the binding position of the primers based on the 16S rRNA sequence of Anabaena sp. PCC 7120 strain. Only a minimal, qualitatively inadequate beginning (few base pairs) of the sequences were deleted as part of quality trimming. Because of their size, the MACC sequences did not extend beyond the longer reference sequences, therefore, from this reason, there was no need to trim them. Trimmed sequences have been uploaded for use in the NCBI database. Sequences were compared with other sequences from the NCBI GenBank database to find out which known taxa show the greatest similarity with the author's samples. The search was performed in the Nucleotide Collection Database (nr/nt) using the Standard Nucleotide BLAST program, with megablast (highly similar sequences) algorithm with default setting.

Reference sequences of Nostocaceae strains (*Anabaena*, *Cylindrospermopsis*, *Desmonostoc*, *Nostoc*, *Roholtiella*, *Trichormus* and *Wollea*) were downloaded from GenBank and *Chroococcidiopsis thermalis* PCC 7203 was added as a non-heterocytous outgroup taxa. The complete matrix contained 147 sequences. Sequences were aligned using MUSCLE through MEGA 7. jModelTest 2 was run to determine substitution models for nucleotide evolution with the TIM2+G+Imodel as best fit (1000 bootstrap iterations). Phylogenetic relationships among the sequences were calculated with Geneious 10.2.3. Maximum Likelihood (ML) analysis was run using RAxML. For the Bayesian analysis, two runs of four Markov chains were executed using MrBayes v. 3.1.2 for 2.5 × 107

generations with default parameters, sampling every 100 generations (the final mean standard deviation of split frequencies was lower than 0.01). The first 25% of sampled trees were discarded as burn-in, the rest were used to calculate posterior probabilities of branches.

The final phylogenetic tree was constructed from a concatenated alignment employing Bayesian inference in MrBayes 3.1.2 and maximum likelihood analysis in RAxML 7.3.2. Phylogenetic trees were drawn and edited using Adobe Illustrator CC version 2014.01. Similarity matrix (percentages) for MACC strains comparing partial sequences of the 16S rRNA gene was calculated in Geneious 10.2.3, while p-distances were calculated with MEGA 7.

2.4. Triggering akinete formation

Phosphorus and iron deficiency: Strains from stock cultures were inoculated into 500 mL Erlenmeyer flasks containing 250 mL modified Z8 medium, in which the 9.3 g of K_2HPO_4 component was replaced by KNO_3. Instead of 1.3515 g $FeCl_3 * 6H_2O$, the same amount of Milli-Q® water was added to the medium. Strains were propagated the same way as mentioned before.

Lower Temperature: The above-mentioned deficient medium was solidified with agar (1.5%) and filled into Petri dishes. From the enrichment culture, the microalgae suspension was diluted on level 10^5–10^7 with liquid medium. The diluted suspension was spread on the surface of solidified medium in a Petri dish. The samples were stored in a refrigerator at 10 °C. The formed akinetes were examined with an Olympus BX60 microscope, and the cell number was determined in a

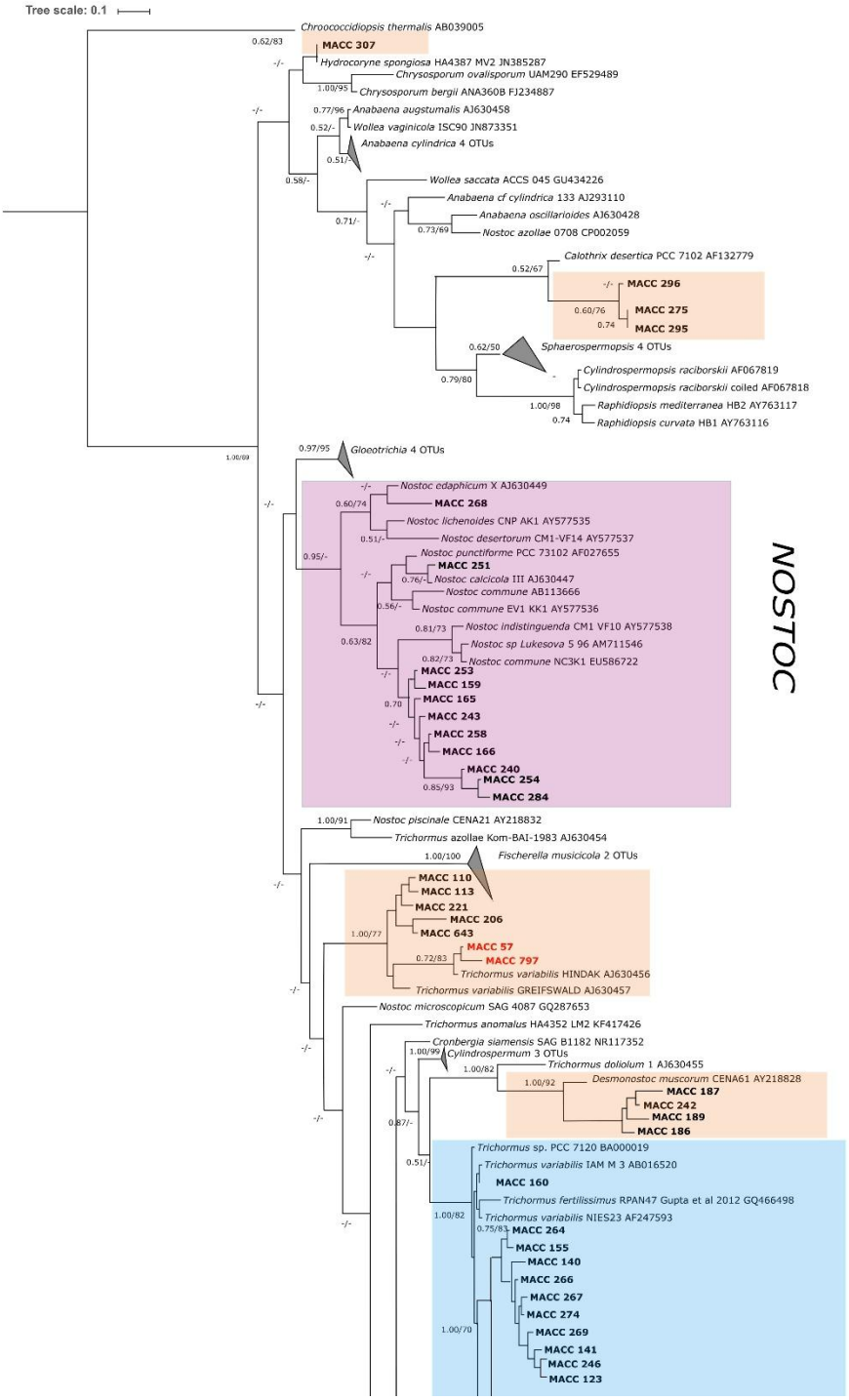
Bürker chamber on the 10th, 20th and 30th day of culturing. The experiment was performed in triplicate for each strain.

3. RESULTS AND CONCLUSION

3.1. Molecular biological analysis of eighty-two MACC strains

The author placed the 82 MACC strains on the cyanobacterial tree using 147 strains previously studied in the literature (Figure 3). MACC strains have been highlighted in bold. MACC strains also marked in red means they have already been studied by the Department of Plant Sciences and proved to be valuable strains. In this dissertation, the word ‘valuable’ means that they produced secondary metabolic product and proved to be fungicidal against plant fungal diseases or insect repellent cyanobacterial strains.

The author formed three well supported groups within the Nostocales order, two of which were monophyletic. The author's researches revealed that the relationships between the MACC strains within the genus *Anabaena* do not match the earlier morphological classification, and consequently the strains belong to at least three different genera. According to this, there are 44 strains of the genus *Trichormus*, 11 strains of the genus *Nostoc* and 8 strains of the genus *Desmonostoc*. Nineteen of the 82 MACC strains were distinguished by pastel peach color on the tree because they are not well supported in comparison with the three large groups and require further genetic analysis to be accurately identified.


Tree scale: 0.1
Chroococcidiopsis thermalis AB039005
MACC 307
Hydrocoryne spongiosa HA4387 MV2 JN385287
Chrysosporum ovalisporum UAM290 EF529489
Chrysosporum bergii ANA360B FJ234887
Anabaena augstumalis AJ630458
Wollea vaginicola ISC90 JN873351
Anabaena cylindrica 4 OTUs
Wollea saccata ACCS 045 GU434226
Anabaena cf cylindrica 133 AJ293110
Anabaena oscillarioides AJ630428
Nostoc azollae 0708 CP002059
Calothrix desertica PCC 7102 AF132779
MACC 296
MACC 275
MACC 295
Sphaerospermopsis 4 OTUs
Cylindrospermopsis raciborskii AF067819
Cylindrospermopsis raciborskii coiled AF067818
Raphidiopsis mediterranea HB2 AY763117
Raphidiopsis curvata HB1 AY763116
Gloeotrichia 4 OTUs
Nostoc edaphicum X AJ630449
MACC 268
Nostoc lichenoides CNP AK1 AY577535
Nostoc desertorum CM1-VF14 AY577537
Nostoc punctiforme PCC 73102 AF027655
MACC 251
Nostoc calcicola III AJ630447
Nostoc commune AB113666
Nostoc commune EV1 KK1 AY577536
Nostoc indistinguenda CM1 VF10 AY577538
Nostoc sp Lukesova 5 96 AM711546
Nostoc commune NC3K1 EU586722
MACC 253
MACC 159
MACC 165
MACC 243
MACC 258
MACC 166
MACC 240
MACC 254
MACC 284
NOSTOC
Nostoc piscinale CENA21 AY218832
Trichormus azollae Kom-BAI-1983 AJ630454
Fischerella musicicola 2 OTUs
MACC 110
MACC 113
MACC 221
MACC 206
MACC 643
MACC 57
MACC 797
Trichormus variabilis HINDAK AJ630456
Trichormus variabilis GREIFSWALD AJ630457
Nostoc microscopicum SAG 4087 GQ287653
Trichormus anomalus HA4352 LM2 KF417426
Cronbergia siamensis SAG B1182 NR117352
Cylindrospermum 3 OTUs
Trichormus doliolum 1 AJ630455
Desmonostoc muscorum CENA61 AY218828
MACC 187
MACC 242
MACC 189
MACC 186
Trichormus sp. PCC 7120 BA000019
Trichormus variabilis IAM M 3 AB016520
MACC 160
Trichormus fertilissimus RPAN47 Gupta et al 2012 GQ466498
Trichormus variabilis NIES23 AF247593
MACC 264
MACC 155
MACC 140
MACC 266
MACC 267
MACC 274
MACC 269
MACC 141
MACC 246
MACC 123

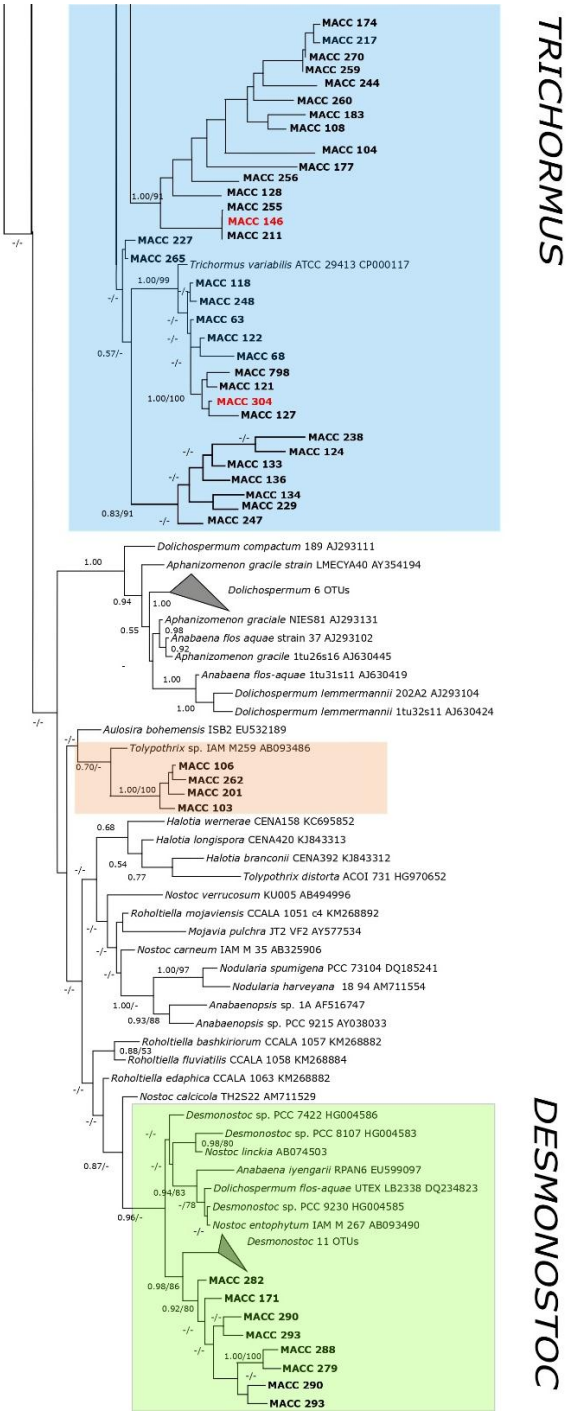


Figure 3. Phylogenetic tree based on 16S rRNA gene

Bioactive strains

The MACC 146 strain (Figure 3.) has been studied previously at the Department of Plant Sciences of the Széchenyi István University and proved to be a moderately insect repellant cyanobacterial strain. Since MACC 211 and 255 strains are close to MACC 146 on the phylogenetic tree, the author suggests further investigation on these strains to prove their repellant effect.

MACC 304 (Figure 3.) was also studied previously in the department and proved to be fungicidal against plant fungal diseases such as *Alternaria, Fusarium, Rhizoctonia, Pythium, Phaeoramularia, Botrytis* and *Sclerotinia*. The author proposes to investigate the fungicidal effect of the MACC 127 because it is close to MACC 304 on the phylogenetic tree.

The author also suggests MACC 110, 113, 206, 221, and 643 strains (Figure 3.) for testing their effect on the egg laying habits of cabbage root flies. These strains are close to MACC 57 and 797 which have been proven to inhibit egg laying of the above mentioned insect.

3.2. Morphological examination of sixty-three MACC strains

***Trichormus* group**

The members of the group appear in the catalog as *Anabaena azollae, A. constricta, A. flos-aquae, A. hassalii, A. miniata, A. tenericualis, A. sp., A. sphaerica* and *A. variabilis*. As a result of genetic analysis, they have been found to be members of the *Trichormus* genus (Figure 4.), so the author suggests changing the designation based on earlier morphological studies and applying the new designation based on

phylogenetic studies. Due to the increasing use of genetic analysis in recent years, a significant number of *Anabaena* species have been transferred to the *Trichormus* genus. The cells have specific barrel and spherical shape, and the trichomes contain spherical and oval heterocytes (Figure 4.). The species level identification is not possible by morphological examination because the dormant cells (akinetes) - required for species-level identification - are not present in culture.

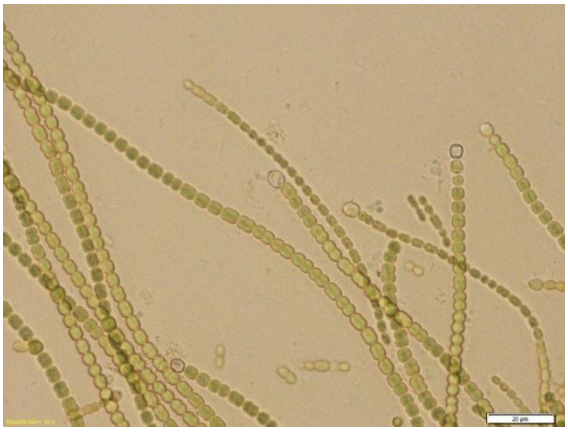


Figure 4. Microscopic image at 400x magnification of the MACC 269 *Trichormus sp.*, a typical strain of the *Trichormus* group.

Nostoc **group**

The author proposes that strains of the group should be renamed to *Nostoc sp.* in the MACC collection. This was confirmed by the results of phylogenetic analysis. Current designation: *Anabaena constricta*, *A. sp.* and *A. variabilis*. These strains are good examples that the *Nostoc* and *Anabaena* (*Trichormus*) genera do not differ significantly morphologically in laboratory cultures and, therefore, difficult to distinguish (Figure 5). Again, in this case only the fragmentation of the trichomes indicates that

it is a *Nostoc* species. Further molecular studies are needed to identify the strains to species level.

Figure 5. Microscopic image at 400x magnification of the MACC 286 *Nostoc sp.*, a typical strain of the *Nostoc* group.

***Desmonostoc* group**

Author identified the strains of this group as *Desmonostoc sp.* The members originally designated as *Anabaena affinis*, *A. constricta* and *A. variabilis* in the MACC collection. Genetic analysis made it possible to reclassify them at the genus level. Recently, some of the *Nostoc* species have been transferred to the *Desmonostoc* genus. In this case, as well, the author proposes the use of new designations based on phylogenetic studies instead of the earlier, morphological designation. Members of the group have typical barrel-shaped and oval cells, and the trichomes have spherical and oval heterocytes, sometimes at the end of the filament (Figure 6).

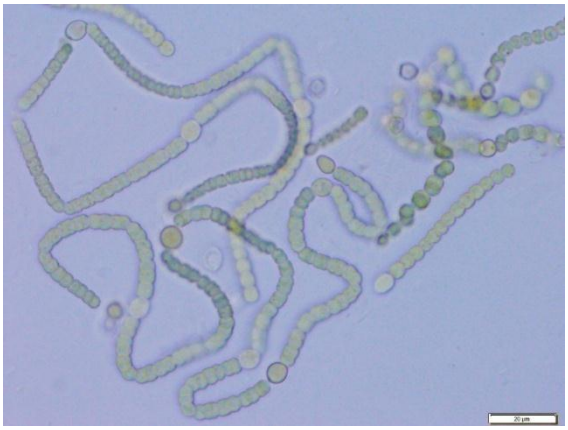


Figure 6. Microscopic image at 400x magnification of the MACC 109 *Desmonostoc sp.*, a typical strain of the Desmonostoc group.

Akinete formation

Phosphorus and iron deficient media at low temperatures resulted akinete formation only in case of one strain, MACC 110. According to the author, it cannot be excluded that other strains of MACC may be able to form akinetes by modifying other environmental conditions or by removing additional minerals. This is the basic condition of species level identification.

4. NEW SCIENTIFIC RESULTS

1. For first time in the history of the Mosonmagyaróvár Algae Culture Collection (MACC), the author isolated, amplified by PCR, then sequenced and systematically analyzed the genomic DNA of 82 MACC cyanobacteria strains previously identified as members of the *Anabaena* genus. This based on the partial 16S rRNA ribosomal gene. This was amplified using primers 8F (5'-AGA GTT TGA TCC TGG CTC AG-3 ') and S8 (5'-CTT CGA GCC CCC AAC TTT C-3'). The length of the PCR product ranged from 510 to 660 bp.
2. The author pointed out that most of the strains, due to the significant changes in cyanobacterial taxonomy in recent years, should be classified into new genera. Contributing to this, there was a new opportunity for their phylogenetic determination using the 16S rRNA marker gene. In addition, it was found that the majority of strains can be classified into 3 phylogenetic groups on the cyanobacterial phylogenetic tree. According to molecular data, eight of the 63 strains are *Desmonostoc*, eleven are members of the genus *Nostoc*, and forty-four strains show genetic similarity to the genus *Trichormus*. Additional genes need to be examined to accurately identify nineteen strains.
3. The author showed that strains close to those on the tree, which were previously studied at the Department of Plant Sciences, may also have inhibitory activity against cabbage root fly egg laying habits or fungicidal effect against plant fungicides, but further studies are necessary to prove this. The following strains were classified as

bioactive in phylogenetic analysis: MACC 110, MACC 113, MACC 127, MACC 206, MACC 211, MACC 221, MACC 255, MACC 643.

4. The author performed microscopic analysis on eighty-two strains. It was pointed out that the morphological definition should be strengthened with molecular biological results, since in the age of rapid, large-scale phylogenetic data, even the genus-level identification cannot be assured at the morphological level. In the absence of akinetes, the morphological comparison of the strains was based on seven parameters: 1. vegetative cell width, 2. vegetative cell length, 3. heterocyte width, 4. heterocyte length, 5. vegetative cell shape, 6. heterocyte shape, 7. location of heterocyte within the filament.
5. The author was the first to investigate the presence of akinetes in the Mosonmagyaróvár Algae Culture Collection (MACC). Combined with the induction of phosphorus and iron deficiency, low temperatures and flushing with ultra-clear (Mili-Q®) water, the MACC 110 strain has been observed to produce akinete. Besides the 14-16 μm long and 9-10 μm wide akinetes, in some cases so-called proakinets (young akinets) could also be discovered.

5. PUBLICATIONS RELATED TO THE SUBJECT OF THE PRESENT DISSERTATION

Publications in an international scientific journal with impact factor:

1. **N. Horváth**, S. Katona, D.E. Berthold, Z. Molnár, P. Bálint, V. Ördög, B. Pap, G. Maróti, F. Bánáti, K. Szenthe, L. Vörös, C. Kilgore, H.D. Laughinghouse 2019: The reclassification of 37 strains from The Mosonmagyaróvár Algal Culture Collection, Hungary, which were previously identified as *Anabaena* (Cyanobacteria, Nostocaceae). South African Journal of Botany. 123, 333-340. Q2, **IF: 1.792**.
2. S. Katona, **N. Horváth**, D.E. Berthold, Z. Molnár, P. Bálint, V. Ördög, B. Pap, G. Maróti, F. Bánáti, K. Szenthe, L. Vörös, C. Kilgore, H.D. Laughinghouse 2019: Phylogenetic re-evaluation of previously identified *Chlamydomonas* (Chlorophyta, Chlamydomonadaceae) strains from The Mosonmagyaróvár Algal Culture Collection, Hungary, using molecular data. South African Journal of Botany. 125, 16-23. Q2, **IF: 1.792**.

Publications in a Hungarian scientific journal:

3. S. Katona, **N. Horváth**, Z. Molnár, V. Ördög 2018: Extracellular polysaccharides in twenty *Chlamydomonas* strains of the Mosonmagyaróvár Algal Culture Collection. Acta Agronomica Óváriensis. 59, 62-81.

4. **N. Horváth**, Z. Molnár, V. Ördög 2016: Az *Anabaena* cianobakterium nemzetség biotechnológiai felhasználása és taxonómiai áttekintése. Botanikai közlemények. 103, 135-152.

Foreign language presentation at an international conference:

5. **N. Horváth**, S. Katona, Z. Molnár, V. Ördög 2019: Extracellular polysaccharides in twenty *Chlamydomonas* strains of the Mosonmagyaróvár Algal Culture Collection. 9th Symposium on Microalgae and Seaweed Products. Mosonmagyaróvár, 25-26 June, 2019

Posters presented at an international conference:

6. S. Katona, **N. Horváth**, D.E. Berthold, Z. Molnár, P. Bálint, V. Ördög, B. Pap, G. Maróti, F. Bánáti, K. Szenthe, L. Vörös, C. Kilgore, IV H.D. Laughinghouse 2019: The reclassification of 37 strains from The Mosonmagyaróvár Algal Culture Collection, Hungary, which were previously identified as *Anabaena* (Cyanobacteria, Nostocaceae). 9th Symposium on Microalgae and Seaweed Products. Mosonmagyaróvár, 25-26 June, 2019.
7. **N. Horváth**, S. Katona, Z. Molnár, V. Ördög 2015: Review of the possible ways to enhance the akinete germination of the genus *Anabaena*. 7th Symposium on Microalgae and Seaweed Products. Mosonmagyaróvár, 29-30 June, 2015.
8. S. Katona, **N. Horváth**, Z. Molnár, V. Ördög 2015: Review of the biotechnological research results of the genus *Chlamydomonas*. 7th Symposium on Microalgae and Seaweed Products. Mosonmagyaróvár, 29-30 June, 2015.

9. **N. Horváth**, S. Katona, Z. Molnár, V. Ördög 2014: Taxonomic and phylogenetic analysis of *Anabaena* cyanobacterium strains. XXXV. Óvári Tudományos Nap. Mosonmagyaróvár, 13 November, 2014.
10. S. Katona, **N. Horváth**, Z. Molnár, V. Ördög 2014: Taxonomic and phylogenetic analysis of *Chlamydomonas* green alga strains. XXXV. Óvári Tudományos Nap. Mosonmagyaróvár, 13 November, 2014.
11. **N. Horváth**, S. Katona, Z. Molnár, V. Ördög 2014: Phylogenetic and taxonomic review of the *Anabaena* (Nostocales, Cyanobacteria) cyanobacteria strains. 11th Congress of the Hungarian Society of Plant Biology. Szeged, 27-29 August, 2014.
12. S. Katona, **N. Horváth**, Z. Molnár, V. Ördög 2014: Phylogenetic and taxonomic review of the *Chlamydomonas* (Volvocales, Chlorophyta) green algae strains. 11th Congress of the Hungarian Society of Plant Biology. Szeged, 27-29 August, 2014.
13. **N. Horváth**, S. Katona, N. Makra, Z. Molnár, V. Ördög 2013: Application of PCR methods on the algae strains of Mosonmagyaróvár Algae Culture Collection (MACC). 6th Symposium on "Microalgae and seaweed products in plant/soil-systems". Mosonmagyaróvár, 24-25 June, 2013.
14. S. Katona, **N. Horváth**, Z. Molnár, V. Ördög 2012: Gibberellinsav és mikroalga kezelés hatása néhány fűszernövény magjának csírázására. XXXIV. Óvári Tudományos Nap. Mosonmagyaróvár, 2012. október 5.