Türler ve Habitatlar

(2025) 6(1): 20–29
e-ISSN: 2717-770X
https://dergipark.org.tr/tr/pub/turvehab

Research Article

https://doi.org/10.53803/turvehab.1679198

A new species of *Phormidium* (Cyanobacteria, Oscillatoriales), Lake Tuz (Türkiye)

Tahir Atıcı

Department of Mathematics and Science Education, Gazi Faculty of Education, Gazi University, TR-06560, Ankara, Türkiye

[2] Department of Biology, Faculty of Science, Ankara University, TR-06100, Ankara, Türkiye

Correspondence: Tahir Atıcı, *tahir@gazi.edu.tr*

Received: 18.04.2025 Accepted: 07.05.2025 Published Online: 20.05.2025

Abstract

Some interesting Cyanobacteria (Oscillatoriales) samples adapted to the high salt environment were collected from shore of Lake Tuz (Central Anatolia, Türkiye). After detailed examination, it was determined that the samples belonged to the *Phormidium* genus, but had some differences in trichome structure and cell size. As a result of comparison with similar species of the genus, it was determined that these differences were of species-level importance. Based on morphological and ecological data, the Lake Tuz samples, which were decided to be a new species for the scientific world, were named *Phormidium obaliae*. The samples of the new species grow in regions with high saltwater, where seasonal streams flow into Lake Tuz. *Phormidium obaliae* is closely related to *P. coricum* and *P. retzi*. However, in *P. obaliae*, the apical cells are dome-shaped (not truncated), and the sheaths are thin and colorless (not thick and dark green to brown). The description of the new species, its comparison with similar taxa, informative photographs, and some of its ecological preferences are given in this study.

Keywords: Central Anatolia, Lake Tuz, Oscillatoriales, *Phormidium*, new species

Yeni Bir *Phormidium* Türü (Cyanobacteria, Oscillatoriales), Tuz Gölü (Türkiye)

Özet

Tuz Gölü'nden (Orta Anadolu, Türkiye), yoğun tuz ortamına uyum sağlamış bazı ilginç Cyanobacteria (Oscillatoriales) örnekleri toplandı. Detaylı inceleme sonucunda örneklerin *Phormidium* cinsine ait olduğu, ancak trikom yapısı ve hücre boyutları bakımından bazı farklara sahip olduğu belirlendi. Cinse ait benzer türlerle yapılan karşılaştırılma sonucunda, bu farkların tür düzeyinde öneme sahip olduğu tespit edildi. Morfolojik ve ekolojik verilere dayanarak bilim dünyası için yeni bir tür olduğuna karar verilen Tuz Gölü örnekleri *Phormidium obaliae* olarak adlandırıldı. Yeni türün örnekleri, mevsimsel akarsuların Tuz Gölüne karıştığı yoğun tuzlu su bulunan bölgelerde yetişir. *Phormidium obaliae*, *P. coricum* ve *P. retzi* ile yakından ilişkilir. Ancak farklı olarak *P. obaliae*'de apical hücreler kümbet-şekillidir (trunkat değil), kılıflar ise ince ve renksizdir (kalın ve koyu yeşilden kahveye doğru değil). Burada yeni türün tanımı, benzer taksonlarla karşılaştırılması, bilgilendirici fotoğrafları ve bazı ekolojik tercihlerine yer verilmiştir.

Anahtar kelimeler: Orta Anadolu, Tuz Gölü, Oscillatoriales, *Phormidium*, yeni tür

INTRODUCTION

Cyanobacteria are among the most abundant organisms on Earth. They are exciting due to their phylogeny, ecological diversity, and evolutionary importance (Whitton & Potts, 2000; Shi &

Suggested Citation:
Atıcı, T. (2025). A new species of *Phormidium* (Cyanobacteria, Oscillatoriales), Lake Tuz (Türkiye). *Türler ve Habitatlar* 6(1): 20–29.

Falkowski, 2008). Their classification has traditionally been based on morphological characters in both ecological and bacteriological systems (Walsby, 1987; Anagnostidis & Komárek, 1988; Javor, 1989; Komárek & Anagnostidis, 1998; Castenholz, 2001; Walsby et al., 2003; Whitton, 2012; Komárek et al., 2014).

They are small and usually unicellular or filamentous and multicellular prokaryotes. They often form large colonies and are systematically called Cyanophyceae (Cyanobacteria, Blue-Green Algae). They are autotrophic (have chlorophyll a) and perform oxygenic photosynthesis associated with photosystem I and photosystem II (Pisciotta et al., 2010). They also form symbiotic relationships with some members of Animalia, Fungi, Bryophyta, Pteridophyta, Gymnospermae, and Angiospermae (Douglas, 1994). Although they are found in various habitats, they especially prefer aquatic habitats (marine, fresh, and salty inland waters). Salt waters are suitable for cultivating cyanobacteria (Dadheech et al., 2014; Des Marais, 2023).

Having chromatophores that carry out photochemical reactions is one of the most important features distinguishing cyanobacteria from other algae. Their phycocyanin is often dense enough to cover the chlorophyll pigment (Asadi et al., 2011). In addition, some species may appear reddish or purple because they contain red pigment. Their cells contain glycogen as a storage polysaccharide, as in animals. Another important feature of cyanobacteria is that they are the only prokaryotic phototrophic organisms that carry out photosynthesis, which results in oxygen production.

Cyanobacteria are diverse in morphology, ranging from unicellular and filamentous to colonial forms. Filamentous forms exhibit functional cell differentiation into heterocysts (for nitrogen fixation), akinetes (resting cells), and hormogonia (motile filaments for reproduction). Each cell (individual cyanobacteria) typically has a thick, gelatinous cell wall. They lack flagella, but the hormogonia of some species can move by gliding along surfaces. Most multicellular filamentous forms in the genus *Oscillatoria* are capable of undulatory locomotion, with the filaments swinging back and forth. In the water column, some cyanobacteria can swim by forming gas vesicles, as do members of the archaea. Morphologically, they can form variations such as unicellular (*Synechocystis, Synechococcus*), non-heterocystous (*Arthrospira maxima*, *Trichodesmium*, *Phormidium*, pseudo- or non-branching heterocyst (*Nostoc*, *Brasilonema*), and true branching heterocyst (*Stigonema*).

Oscillatoriales are simple, unbranched filamentous cyanobacteria composed of cells of the same type. Members of the order generally appear in vegetative masses with cells in sticky and scattered sheaths, like mucous sheets or pencil tufts. Their trichomes are cylindrical, parallel, or interdigitated, except for a slight and short taper in the apical region. Their apical cells are conical, blunt-tipped, capitate, and sometimes have calyptra. Individual sheaths are often indistinct and difficult to observe, but the diffusion sheaths of the vegetative mass are visible. The cells are shorter than they are wide or square-shaped, with narrowed cross walls in some species (Wilde & Mullineaux, 2015; Schuergers et al., 2017).

Oscillatoriaceae is the most important family reflecting all the characters of the order. *Phormidium* and *Oscillatoria*, which are evaluated within this family, are two morphologically very similar genera. Under certain conservation conditions, the sheath structure of species in the *Phormidium* genus can be so complex to observe that it is possible to confuse them with some Oscillatoria forms (Khayatan et al., 2015). The sheath is what separates the two genera. Phormidium species are generally distinguished by the tight, felt-like layer they form in the field and their macroscopic appearance. While the masses of some *Oscillatoria* species form partially

similar mats, the trichomes are easily separated when collected. In *Phormidium* members, the mats formed are tight and do not separate. According to current sources, there are more than 207 *Phormidium* species today (Guiry & Guiry, 2022).

MATERIAL AND METHOD

Samples taken from the southwest shore of Lake Tuz (Figure 1) using special methods were kept under appropriate storage conditions and brought to Gazi University Gazi-MACC laboratory on the same day without being fixed to be cultured to detect the presence of cyanobacteria. After their identification, their photographs were taken under an Olympus brand microscope. Physical and chemical analyses were performed on the samples taken simultaneously in an accredited laboratory using the ICP-MS 17294 annex 1 and 2 methods.

Identification and classification of cyanobacteria were made according to Round (1984) and Anagnostidis & Komárek (1988), and relevant sources were used (Stanier et al., 1976; Stainer & Cohen-Bazire, 1977; Gerrath & Denny, 1980; Humm & Wick, 1980; Komárek, 2010; Lamprinou et al., 2013; Nies et al., 2017; Guiry & Guiry, 2022).

BG-11 (Atıcı, 2020; Koch et al., 2022) culture medium was prepared for the growth of cyanobacteria. To prepare this medium; component stock solution for 1 liter ($g.l^{-1}$ dH_2O), Ammonium ferric citrate (6) 1 ml, $NaNO_3$ 1.5 g, $K_2HPO_4.3H_3O$ 1 ml, $MgSO_4.7H_2O$ 1 ml, $CaCl_2.2H_2O$ 1 ml, Na_2CO_3 1 ml, Na-EDTA 1 ml and basic elements H_3BO_3, $MnCl_2.4H_2O$, $ZnSO_4.7H_2O$, $CuSO_4.5H_2O$, $Na_2MoO_4.2H_2O$, $Co(NO_3)_2.6H_2O$ were used.

Figure 1. Sample collection stations in Lake Tuz.

RESULTS AND DISCUSSION

Phylum: Cyanobacteria
Class: Cyanophyceae
Order: Oscillatoriales
Family: Oscillatoriaceae

Phormidium obaliae Atıcı, **sp. nov.** (Figure 2).

Holotype. TÜRKİYE. Konya: Cihanbeyli, NE of Gölyazı, Lake Tuz, 38˚36.41.00'N-33˚18.53.10'E, 24 May 2023, planktonic sample Gazi MACC, permanent samples deposited in the Gazi MACC (Gazi University, Gazi Faculty of Education, Ankara, Türkiye) are materials collected as phytoplankton (known only from type locality).

Diagnosis. *Phormidium obaliae* is related to *P. coricum* and *P. retzi*. It differs from *P. coricum*, mainly by cell width 2.3-3 μ (not 3-4.5 μ); cell length 3-4 μ (not 3.4-8 μ); cell shape isodiametric (not non-isodiametric); apical cells dome-shaped or elongated (not truncate); sheaths thin, colorless, and occasionally becoming wide and diffluent (not thick, dark green to brown, solid). Also, it differs from *P. retzi*, mainly by cell width 2.3-3 μ (not 4.5-12 μ); cell length 3-4 μ (not 4-9 μ); cell shape isodiametric and longer than wide (not non-isodiametric and shorter than wide); sheaths thin, colorless, and occasionally becoming wide and diffluent (not thick, dark green to brown, solid).

Description and growth features. *Phormidium obaliae* trichomes are long, unbranched, blue-green, mucous-sheeting trichomes that grow as straight or gracefully curved filaments and do not produce any specialized cells such as heterocysts under the growth conditions tested. Individual cells are usually 3–4 μm long and 2.5–3 μm wide, with filaments extending to 55–85 μm. Frequently, individual sheaths are observed with several parallel filaments, often distinct and lamellar, directly adjacent to each other, forming a sheet-like structure that may contribute to biofilm formation (Figure 2).

Apical cells are round, not capitate, but slightly domed. Filaments are very tangled and can swim freely among other algae and tychoplankton, and may be straight or curved and flexible; sheaths are initially apparent, later spreading. *P. obaliae* cells exhibit red autofluorescence during vegetative growth, indicating the presence of photopigments. They are capable of rotatory movement. Detailed examination has not revealed significant gaps between cells. Two additional outer layers of extracellular polysaccharide structure are seen. This membranous structure's extracellular polymeric (EPS) forms mucilage, protecting the cell from desiccation. These filament layers probably play an important role in tolerance to high salinity and alkalinity conditions. *P. obaliae* can produce significantly more bubbles on the surface of the culture with a doubling time of approximately 48 h. When examined under the microscope, the filaments showed significant gliding motility.

Etymology. This new species is named in honor of the Turkish Hydrobiologist Prof. Dr. Emine Olcay OBALI (Biology Department, Ankara University, Ankara) and describes its ecological habitat.

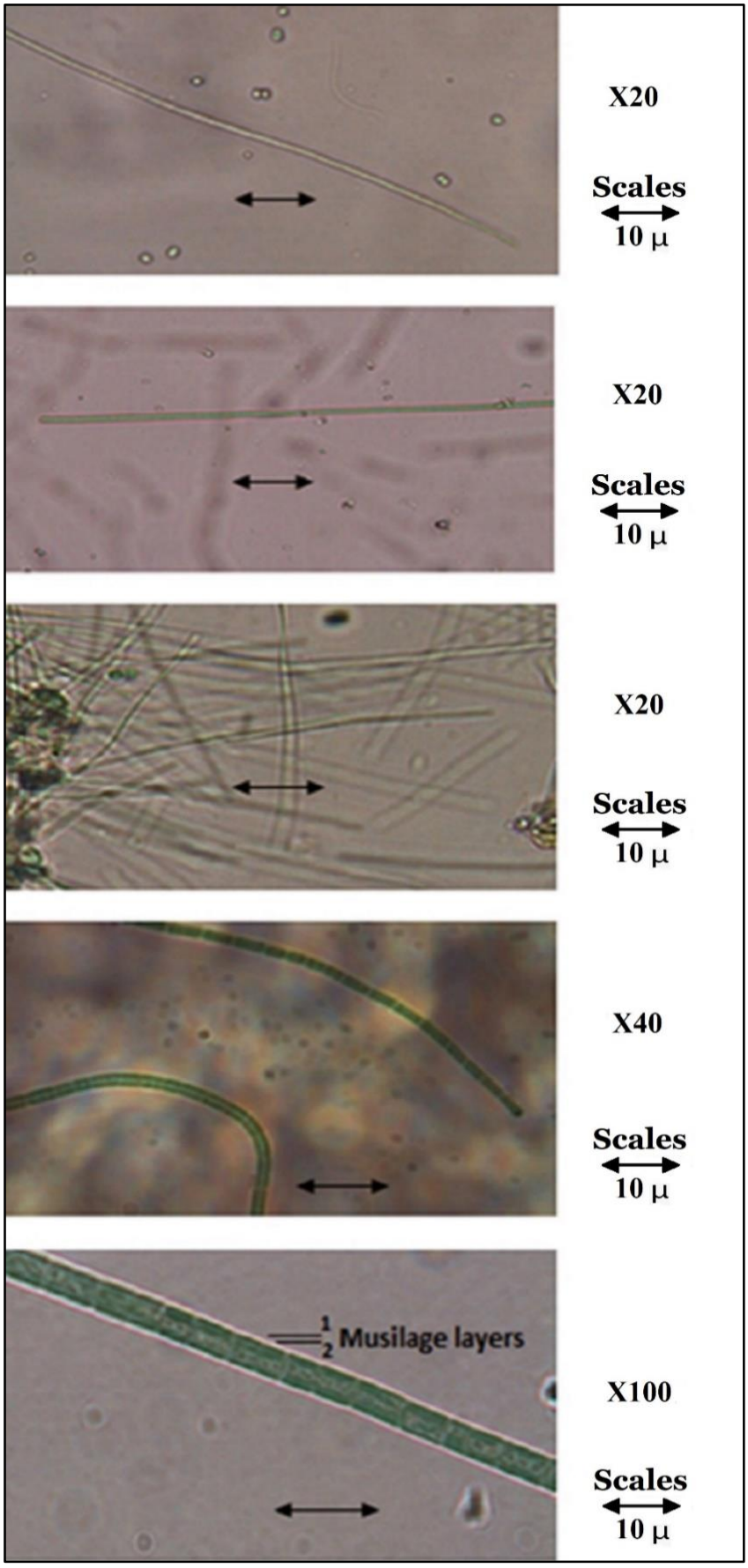

Figure 2. Microscopic images of *Phormidium obaliae*.

Habitat and ecology

Lake Tuz is ideal for Cyanobacteria that love salty habitats. Like many other lakes in the Konya Closed Basin, it started to dry out over time in the early Holocene period (the end of the last ice age) and was part of a vast lake that broke into small pieces (Atıcı et al., 2001; Atıcı, 2022). Water samples were taken from the station points determined in Lake Tuz for chemical analysis (Figure 1, Table 1). Chemical analysis is important in defining the habitat and determining the ecological requirements of the species.

Table 1. Chemical analysis of water samples taken from Lake Tuz (Figure 1).

Parameter / Unit	**TSI drinking water standards**	**Lake Tuz Station**
	Parameter value	**Parameter value**
Cadmium	0.005 mg/L	< 0,001 mg/L
Chromium	0.050 mg/L	< 0,002 mg/L
Copper	0.002 mg/L	0,2 mg/L
Lead	0.010 mg/L	< 0,005 mg/L
Mercury	0.010 mg/L	< 0,0005 mg/L
Zinc	-	< 0,001 mg/L
Ammonium	0.050 mg/L	3,5 mg/L
Chloride	250 mg/L	5000 mg/L
Color	Acceptable to consumers and no abnormal changes	Dark Green- Brown
PH	≥6,5 and ≥9,5	8
Iron	0.200 mg/L	< 0,01 mg/L
Odor	Acceptable to consumers and no abnormal changes	There is a smell
Sulfate	0.250 mg/L	0,347 mg/L
Sodium	0.200 mg/L	3256 mg/L
Calcium	-	158,6 mg/L
Magnesium	-	451,3 mg/L
Total phosphorus	0.005 mg/L	5,18 mg/L
Blur	Acceptable to consumers and no abnormal changes	Blurry

When water samples taken from the station are examined, the first thing that stands out is the dark brown and green color. In addition, the intense odor in the region is another prominent element. The most striking fact is that the N and total P values, which cause algae proliferation, especially cyanobacteria species in Lake Tuz, are incredibly high. The fact that the total phosphorus values are much higher than normal values causes excessive algae proliferation in the water entering Lake Tuz (Table 1). The high total phosphorus density indicates that excessive algae proliferation can always occur in the water when suitable conditions occur (Shelknanloymilan et al., 2012).

Copper is an element that is particularly involved in cyanobacteria's pigment (phycocyanin) structure and causes them to appear blue-green. Sodium values are high, but this is normal for Lake Tuz. Lake Tuz contains approximately 9-10 times more sodium than seawater. Lake Tuz, one of the few salty lakes in the world, reaches its high salinity rates thanks to Ca and Mg. Due to the high temperatures in the region, Ca and Mg values have increased to extreme levels. The diversity of cyanobacteria and algae in Lake Tuz was examined, and these species were encountered in almost every environment. These species generally have halophytic characteristics (Atıcı et al., 2001). Cyanobacteria species, in particular, have adapted to the physical and chemical values of the environment and are widely seen as dominant in the environment.

Phormidium obaliae is described in Figure 2. It is shown to have some differences from the other *Phormidium* members (Guiry & Guiry, 2022). The key to the genus *Phormidium* is consolidated in this new species (Table 2). Filamentous; filaments unbranched, microscopic and later macroscopic to several mm in diameter. Usually covering substrates of different types, rarely solitary, usually in fine, smooth, layered to leathery strata (mats), and with cells 3-4µ long; asexual and sexual reproduction unknown; trichomes isopolar, more or less straight, usually 55-85 µm long, in addition, the cell wall is covered with two or more mucilage layers.

Table 2. Comparison of diagnostic characters of *Phormidium obaliae* and related species.

Characters	***P. obaliae***	***P. coricum***	***P. retzi***
Cell width (µ)	2,5-3	3-4.5	4.5-12
Cell length (µ)	3-4	3.4-8	4-9
Cell shape	isodiametric, longer than wide	non-isodiametric, longer than wide	non-isodiametric, shorter than wide
Cross-wall	slightly constricted	slightly constricted to strongly constricted	slightly constricted to strongly constricted
Apical cells	dome-shaped or elongated	truncate	truncate or elongated
Sheaths	thin, colorless, occasionally becoming broad and diffuse	thick, dark green to brown, solid	thick, dark green to brown, solid
Habitat	intense salty water	not salt water	not salt water

Diagnostic Key to *Phormidium obaliae* and related species

1. Trichomes are short, Cyanophyta species (e.g., Microcystis) live in the mucus layer …. ***mucicola***
1. Trichomes are long and do not live in the mucus layer of other algae ……..……...…. 2
2. There is narrowing of the cross walls of the trichomes ……...……...…… 3
2. No constriction of the cross walls of the trichomes ……. 6
3. The tip of the trichomes is capitate ……..…..…… ***lucidum***
3. The tip of the trichomes is not capitate ..……...…..... 4
4. Apical cells distinctly elongated and pointed ……..…….....……...…….…….. ***tenue***
4. Apical cells short, not pointed or slightly pointed ……..……...……. 5
5. Cells are 2.5µ in diameter and 2-4µ long ……..……...……...…… ***minnesotense***
5. Cells are 4-6µ in diameter and 1.2-2.7 µ long ……..…….. ***ambiquum***

6. The tips of the trichomes are noticeably bent or hooked ……..…..…….. ***uncinatum***
6. The tips of the trichomes are not bent, they are straight or slightly curved ……...…… 7
7. Apical cells are capitate ……...……..……. 8
7. Apical cells are not capitate ……....……. 11
8. Trichomes are conical and pointed with calyptra …….……....…… ***setchellianum***
8. Trichomes broadly rounded or convex calyptra …….…… 9
9. Trichomes are curved, flexible …..……..…….……. ***autumnale***
9. Trichomes are flat ……..……..……. 10
10. Cells are longer than wide ……...……. ***favosum***
10. Cells are shorter than wide ……..……..……..…… ***subfuscum***
11. Plant mass covered with lime ……..…….. ***incrustatum***
11. Plant mass is not covered with lime ….……...……... 12
12. Cross walls granulated ……..……..…....……..……. ***inundatum***
12. Cross walls not granulated ……...…….. 13
13. Apical cells dome-shaped; sheaths thin and colorless ……..…….. ***obaliae***
13. Apical cells are truncate; sheaths are thick and dark green to brown …….....…….. 14
14. Trichomes curved, flexible; cells 3-4.5µ wide, 3.4-8µ long ……....…… ***coricum***
14. Trichomes are flat; cells are 4.5-12µ wide and 4-9µ long …….…….…… ***retzi***

AUTHOR CONTRIBUTION STATEMENT

In this study, the study idea and design, data collection, analysis, interpretation of the results, and drafting of the article were made by Tahir Atıcı.

REFERENCES

Anagnostidis, K. & Komárek, J. (1988). Modern approach to the classification system of the Cyanophytes 3: Oscillatoriales. *Algological Studies* 50: 327-472.

Asadi, A., Khavari-Nejad, R., Soltani, N., Najafi, F. & Molaie-Rad, A. (2011). Physiological and antimicrobial characterizations of some cyanobacteria isolated from the rice fields in Iran. *Journal of Agricultural Technology* 7(3): 649-663.

Atıcı, T. (2020). Production and collection of microalgae isolated from freshwater reserves in Central Anatolia, Turkey. *Türler ve Habitatlar* 1(1): 37-44.

Atıcı, T. (2022). Tuz Gölü Özel Çevre Koruma Bölgesi Göllerinde Alg Çeşitliliği ve Potansiyel Siyanobakteri Toksisitesi. *Türler ve Habitatlar* 3(2): 94-109.

Atıcı, T., Obalı, O., Akköz, C. & Elmacı, A. (2001). Isolation and Identification of Halophytic Algae from Salty Soil around Salt Lake of Turkey. *Pakistan Journal of Biological Sciences* 4(3): 298-300.

Castenholz, R.W. (2001). [General Characteristics of the Cyanobacteria] In: Boone, R.D., Castenholz, R.W. & Garrity, G.M. (Eds.). *Bergey's Manual of Systematic Bacteriology. Volume One: The Archaea and the Deeply Branching and Phototrophic Bacteria*. Springer, pp. 474-487.

Dadheech, P.K., Mahmoud, H., Kotut, K. & Krienitz, L. (2014). *Desertifilum fontinale* sp. nov. (Oscillatoriales, Cyanobacteria) from a warm spring in East Africa, based on conventional and molecular studies. *Fottea* 14: 129-140.

Des Marais, D.J. (2023). Biogeochemistry of Hypersaline Microbial Mats Illustrates the Dynamics of Modern Microbial Ecosystems and the Early Evolution of the Biosphere. *Biological Bulletin* 204(2):160-167. DOI: https://doi.org/10.2307/1543552.

Douglas, S.E. (1994). [Chloroplast origins and evolution]. In: Bryant, D.A. (Ed.). *The Molecular Biology of Cyanobacteria. Advances in Photosynthesis.* Vol 1, Springer, Dordrecht, pp. 91-118.

Gerrath, J.F. & Denny, P. (1980). *Freshwater algae of Sierra Leone III. Cyanophyta, Chrysophyta, Xantophyta, Chloromonadophyta, Cryptophyta, Dinophyta*. Nova Hedwigia 33: 445-463.

Guiry, M. & Guiry, G.M. (2022). AlgaeBase. World-wide electronic publication. National University of Ireland, Galway. https://www.algaebase.org [22.03.2025]

Humm, H.J. & Wick, S.R. (1980). *Introduction and guide to the Marine Bluegreen Algae*. John Wiley and Sons, Brisbane.

Javor, B. (1989). *Hypersaline Environments*. Springer-Verlag, Berlin.

Khayatan, B., Meeks, J.C. & Risser, D.D. (2015). Evidence that a modified type IV pilus-like system powers gliding motility and polysaccharide secretion in filamentous cyanobacteria. *Molecular Microbiology* 98(6): 1021-1036. DOI: https://doi.org/10.1111/mmi.13205.

Koch, M., Noonan, A.J.C., Qiu, Y., Dofher, K., Kieft, B., Mottahedeh, S., Shastri, M. & Hallam, S.J. (2022). The survivor strain: isolation and characterization of *Phormidium yuhuli* AB48, a filamentous phototactic cyanobacterium with biotechnological potential. *Front Bioeng Biotechnol* 10: 932695. DOI: https://doi.org/10.3389/fbioe.2022.932695.

Komárek, J. (2010). Recent changes (2008) in cyanobacteria taxonomy based on a combination of molecular background with phenotype and ecological consequences (genus and species concept). *Hydrobiologia* 639: 245-259. DOI: https://doi.org/10.1007/s10750-009-0031-3.

Komárek, J. & Anagnostidis, K. (1998). [Cyanoprokaryota 1. Chroococcales]. In: Ettl, H., Gärtner, G., Heynig, H. & Mollenhauer, D. (Eds). *Süsswasserflora von Mitteleuropa 19/1*. Gustav Fischer, Jena-Stuttgart-Lübeck-Ulm.

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

Lamprinou, V., Skaraki, K., Kotoulas, G., Anagnostidis, K., Economou-Amilli, A. & Pantazidou, A. (2013). A new species of *Phormidium* (Cyanobacteria, Oscillatoriales) from three Greek Caves: morphological and molecular analysis. *Fundam Appl Limnol* 182(2): 109-116. DOI: https://doi.org/10.1127/1863-9135/2013/0323.

Nies, F., Wörner, S., Wunsch, N., Armant, O., Sharma, V., Hesselschwerdt, A., Falk, F., Weber, N., Weiß, J., Trautmann, A., Posten, C., Prakash, T. & Lamparter, T. (2017). Characterization of *Phormidium lacuna* strains from the North Sea and the Mediterranean Sea for biotechnological applications. *Process Biochemistry* 59(B): 194-206. DOI: https://doi.org/10.1016/j.procbio.2017.05.015.

Pisciotta, J.M., Zou, Y. & Baskakov, I.V. (2010). Light-dependent electrogenic activity of cyanobacteria. *PloS One* 5(5): e10821. DOI: https://doi.org/10.1371/journal.pone.0010821.

Round, F.E. (1984). *The Ecology of Algae*. Cambridge University Press, Cambridge.

Schuergers, N., Mullineaux, C. W., & Wilde, A. (2017). Cyanobacteria in motion. *Curr Opin Plant Biol* 37: 109-115. DOI: https://doi.org/10.1016/j.pbi.2017.03.018.

Shelknanloymilan, L., Atıcı, T. & Obalı, O. (2012). Removal of nitrogen and phosphate by using *Chlorella vulgaris* on synthetic and organic materials wastewater. *Biological Diversity and Conservation* 5(2): 89-94.

Shi, T. & Falkowski, P.G. (2008). Genome evolution in cyanobacteria: the stable core and the variable shell. *Proc Natl Acad Sci* 105: 2510-2515. DOI: https://doi.org/10.1073/pnas.0711165105

Stanier, R.Y., Adelberg, E.A. & Ingraham, J. (1976). *The Microbial World*. *The Blue-Green Bacteria*. 13th Ed., Prentice-Hall, Englewood Cliffs, New Jersey.

Stainer, R.Y. & Cohen-Bazire, C.G. (1977). Phototrophic Prokaryotes: The Cyanobacteria. *Ann Rev Microbiol* 31: 225-274.

Walsby, A.E. (1987). [Mechanisms of buoyancy regulation by planktonic cyanobacteria with gas vesicles]. In: Fay, P. & Van Baalen, C. (Eds.). *The Cyanobacteria: A Comprehensive Review*. Elsevier, Amsterdam, pp. 376-392.

Walsby, A.E., Yacobi, Y. & Zohary, T. (2003). Annual changes in the mixed depth and critical depth for photosynthesis by *Aphanizomenon ovalisporum* that allow growth of the cyanobacterium in Lake Kinneret. *Israel Journal of Plankton* 25 (6): 608-613.

Whitton, B.A. (2012). *The Ecology of Cyanobacteria II: Their Diversity in Time and Space*. Springer, Dordrecht.

Whitton, B.A. & Potts, M. (2000). *Introduction to Cyanobacteria, The Ecology of Cyanobacteria, Their Diversity in Time and Space*. Kluwer Academic, Hingham.

Wilde, A. & Mullineaux, C.W. (2015). Motility in cyanobacteria: polysaccharide tracks and Type IV pilus motors. *Molecular Microbiology* 98(6): 998-1001. DOI: https://doi.org/10.1111/mmi.13242.