MICROALGAL FUNCTIONAL TRAITS

**Review Paper** 



# Welcome to the jungle!: An overview of modern taxonomy of cyanobacteria

Jan Kaštovský D

Received: 24 January 2023 / Revised: 13 June 2023 / Accepted: 20 August 2023 / Published online: 12 September 2023 © The Author(s) 2023

Abstract The application of modern molecular methods and phylogenetic approaches saw an explosion in cyanobacterial taxonomy in the first two decades of the twenty-first century. The relative ease of description of new taxa and the pressure to publish a high number of scientific papers has created apparent confusion. The situation is particularly complicated for ecologically oriented limnological research and practical hydrobiologists especially have numerous criticisms of this trend. On closer observation, however, the situation is not as tragic as it first appears. More than a thousand new species have been discovered or renamed and only 18 percent are freshwater planktonic species, which garner the most interest in routine analyses. Most new taxa are described from terrestrial habitats. Despite the increase in studies from tropical areas, most of the new species are from the temperate zone, which probably does not account for the reality. Significant advances in modern taxonomy are visible mainly for the trichal types, but other groups such as the pleurocapsal species are considerably less studied. In this article I try to show that, despite all the difficulties and limitations, it is not

Guest editors: Viktória B-Béres, Luigi Naselli-Flores, Judit Padisák & Gábor Borics / Trait-Based Approaches in Micro-Algal Ecology

J. Kaštovský (⊠) Faculty of Science, University of South Bohemia, 37005 Ceske Budejovice, Czech Republic e-mail: hanys@prf.jcu.cz necessary to consider these rapid changes as a complication in common cyanobacteriological research.

**Keywords** Blue-green algae · New species · Phylogeny

# Introduction

Blue-green algae or Myxophyceae Wallroth 1833; Phycochromaceae Rabenhorst 1865; Schizophyceae Cohn 1879; Cyanophyta Steinecke 1931; Cyanobacteria Stanier 1974 or Stanier ex Cavalier-Smith, 2002 respectively; Oxyphotobacteria Gibbons & Murray 1978; Cyanoprokaryota Komárek & Anagnostidis 1998 or Cyanobacteriota Oren, Mareš & Rippka 2022 are an extremely interesting group of organisms. From an anthropocentric point of view, we mainly consider their role in the toxic aquatic blooms of eutrophic fresh and salt waters (Huismann et al., 2018), but their real importance is much deeper. In the past, they played a crucial role in the process of increasing the oxygen content of the Earth's atmosphere (Great Oxidation Event-2.4-2.0 billion years ago, Lyons et al., 2014), and today they play an important role in global oxygen, carbon, and nitrogen cycles. Thanks to a wide range of original adaptations such as photosynthesis, akinetes, heterocytes, or aerotopes, they can adapt to almost any condition on the planet, and thus inhabit almost all of freshwater, marine and terrestrial biomes, as well as a variety of extreme habitat types (Whiton, 2012).

Given this importance, the effort to describe their diversity is understandable (Komárek et al., 2014). Taxonomy is the most comprehensive way to grasp the diversity of all groups of organisms. Although this discipline is considered to be a somewhat oldfashioned field of scientific inquiry, it has adopted the results and methods of modern approaches very rapidly. This development has greatly benefited taxonomy as a scientific discipline, allowing us to take our knowledge of the organisms we study to a new level. However, there's always a quid pro quo. The conservatism of the results of the "pre-molecular" taxonomic research had a certain advantage of stability in the application of the results. After all, it took almost 70 years from the monographic systematic treatment of cyanobacteria by Geitler (1932) to publish the at least somewhat differently constructed monographs by Komárek & Anagnostidis (1998, 2005) and Komárek (2013). (The works of Elenkin (1936), Desikachary (1959) or Starmach (1966), with all due respect, represent only minor additions to Geitler, 1932.)

Maintaining a basic overview of the current situation today requires considerable effort. The segment of the scientific community that works in fields other than taxonomy (e.g., practicing hydrobiologists) views the situation as chaotic. Like a real jungle, the taxonomic cyanobacterial "jungle" is an ambiguous space, orientation is very difficult. Where only yesterday there were clear paths, today there are no routes, even seemingly easy trails are obstructed by hard-to-pass barriers. You will appreciate an experienced guide. The main objective of the following basic overview of trends in cyanobacterial taxonomy should reduce this negative impression. Because if you follow its rules, you can get along even in the jungle quite well (Kipling, 1894).

# Materials and methods

Literature describing new taxa of cyanobacteria has been continuously collected as part of long-term projects (Hoffmann et al., 2005; Kaštovský et al., 2010 and Komárek et al., 2014) by checking the Web of Science database (https://www.webofscience.com) and Google Scholar (https://scholar.google.com) using a combination of the keywords "Cyanobacteria, Cyanophyta, Cyanoprokaryota, Myxophyceae" or "blue green algae," respectively, and "new species, new genus, new taxa, new taxon, spec nov, taxonomy, phylogeny" or "species." Researchgate (https://www. researchgate.net), CyanoDB2 (https://www.cyanodb. cz, Hauer & Komárek, 2022) and AlgaeBase (https:// www.algaebase.org, Guiry & Guiry, 2022) were used as supporting and cross-checking sources. I selected January 1, 2000, as the starting point for data collection. Species described before this date will continue to be referred to as "old," whereas species described after this date will be referred to as "new." Data collection was terminated on July 1, 2022.

For the analysis, the descriptions of new species that fully or at least mostly fulfilled the basic taxonomic criteria of the International Code of Nomenclature for Algae, Fungi and Plants (Turland et al., 2018) were used. Fossil species were not included in the review, mainly because subsequent analysis of ecology and classification would be highly speculative.

For all species, the following data were indexed: (1) year of description, (2) if species are only renamed or newly discovered, (3) if only morphospecies (no molecular data), (4) if cryptospecies, (5) continent of known occurrence (more than 2 continents as "worldwide"), (6) biome of known occurrence (polar and subpolar, boreal-temperate, Mediterranean/dry suband tropical, humid sub- and tropical, according Beck et al., 2018), (7) habitat of occurrence: (in categories freshwater plankton, freshwater nonplankton (primarily periphyton and benthic species), high salinity plankton (marine, brackish, and inland saline waters), high salinity nonplankton (primarily periphyton and benthic species from marine, brackish, and inland saline waters), and species from special biotopes (caves, hot springs, etc.)). Even in these categories there are species with two records (e.g., occurring in both planktonic and periphytic or species from polar and boreal temperate areas).

For better orientation of the results, they were visualized in graphs using MS Excel (Microsoft Corporation).

# Results

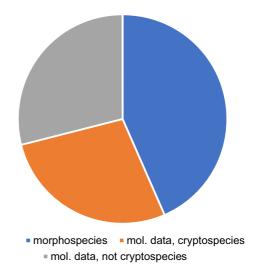
In total, 274 papers describing a new cyanobacterial taxon were published in the monitored period, 86 of

these are younger than January 1, 2020. In addition to the 3733 existing "old" nonfossil species of cyanobacteria, 1073 new taxa have been described. Of this number are 626 are new for science and 447 have been renamed as of January 1, 2000. The trend in the number of new species over the last 22 years is shown in Fig. 1. The number of new species for year 2022 is an estimate, created as a double of the number of new species by 1 July 2022, when literature excerption was stopped.

Somewhat surprising is still the proportion of new species described or renamed in the old-fashioned way, only on the basis of morphological data—it is about 43%. Of the species described using molecular data, about half are cryptic and the other half also show morphological features that allow them to be distinguished by light microscopy (Fig. 2).

The proportions of new species between continents or biomes are shown in Figs. 3, 4, 5. 322 new species are known from Europe, 275 from North America, 146 from South America, 224 from Asia, 56 from Australia-Pacific, 54 from Africa, and 27 from Antarctica. 83 are found worldwide (Fig. 3). The discrepancy between the consideration given by cyanobacteriologists to different continents is particularly noticeable when the numbers of new species are related to the size of these continents (Fig. 4).

The largest proportion of new species is from the boreal/temperate zone (413 species), followed by species from the humid sub- and tropical zone (390 taxa). The Mediterranean/dry subtropical has 323

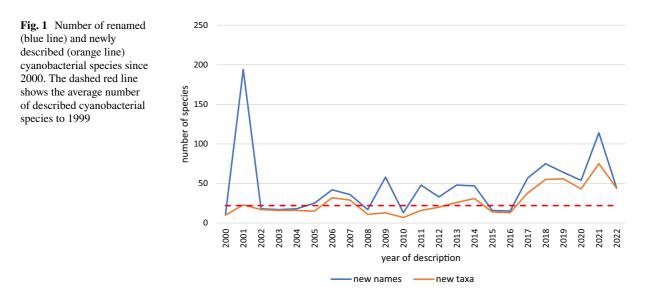


**Fig. 2** The 466 new species are described solely on the basis of morphological data, 607 also on the basis of molecular data. Of these 607, 296 are cryptic, indistinguishable except by DNA sequences. The figure shows the relative proportions of these categories

species and polar or subpolar region is a habitat for 71 new cyanobacteria taxa (Fig. 5).

Regarding the main habitats of cyanobacteria, 36 of the new species are saline plankton, 157 saline nonplankton, 200 freshwater plankton, 290 freshwater nonplankton, 331 terrestrial and 132 from special biotopes (Fig. 6).

The distribution of new species among cyanobacterial lineages (orders) is also irregular: 3 new



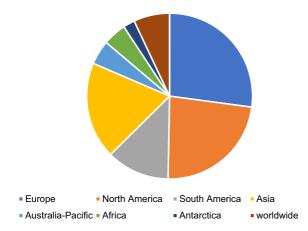


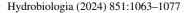
Fig. 3 Geographical distribution of new cyanobacterial species on continents

species are from the order Gloeobacterales, 323 from Synechococcales, 63 Pseudoanabaenales, 10 Thermostichales, 92 Chroococcales, 13 Chroococcidiopsidales, 239 Oscillatoriales, 12 Pleurocapsales, 4 Spirulinales, and 314 Nostocales (Fig. 7).

# Discussion

# General comments

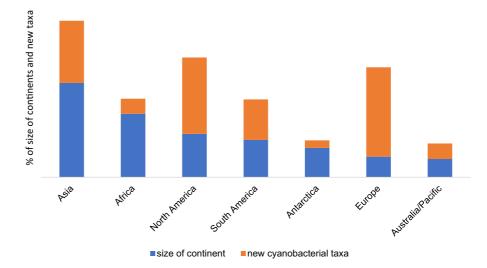
"Taxonomic decisions are to be considered opinions, not facts" (Malavasi & Škaloud, 2022). Thus, the total numbers of species reported in this review



differ somewhat in detail from the total numbers reported by other authors (e.g., Nabout et al., 2013; Guiry & Guiry, 2022). How strict the criteria chosen by which author plays a major role. Many realworld taxa do not have completely valid names for some reason, usually the absence of a physiologically inactive herbarium. There are numerous examples of less-than-ideal taxonomic status, e.g., several coccal species, otherwise very well documented by Joosten (2006) or Chroogloeocystis siderophila Brown, Mummey & Cooksey (Brown et al., 2005). According to the published data Ch. siderophila is clearly a good taxon, having available morphology, ecology, 16S rRNA nucleotide sequences, TEM, SEM, interesting physiological data etc. However, it is not described validly (Guiry & Guiry, 2022) and it is a matter of opinion if it should be included in the reviews or not. I have included such species in this review.

If we consider the oldest reliably described cyanobacteria to be *Phormidium subsalsum* Gomont, 1829 (Nabout et al., 2013), the average number of described cyanobacteria up to 1999 is almost than 22 species per year. This number has been exceeded 11 times since 2000. Since 2017, this has happened every year and numbers are more than double the average. Even though the variability in values precludes any plausible predictions of future trends (Fig. 1), the rate of new species descriptions is increasing significantly and is likely to accelerate further.

**Fig. 4** Comparison of the geographical size of the continents and the number of new cyanobacterial species on them (percentage). The figure does not reflect the 83 new species known from more than two continents (category "worldwide" from Fig. 3)



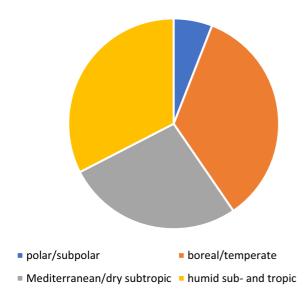


Fig. 5 Comparison of the number of new cyanobacterial species with respect to the main biomes

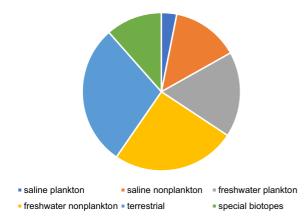


Fig.6 Distribution of new species among the major cyanobacterial habitat types

### Cryptic diversity

One of the least "treasured" phenomena that the application of molecular methods to taxonomy entails is the discovery of strong cryptic diversity. This phenomenon has been widely commented in various papers (Casamatta et al., 2003; Osorio-Santos et al., 2014; Shalygin et al., 2017; Stanojkovic et al., 2022). In the case of the new cyanobacterial species, almost a quarter are cryptic. However, approximately the same number of modern described species (i.e.,

using molecular data) are well recognizable morphologically. The situation is therefore not so critical that optical microscope observations lose their usefulness for the determination of new cyanobacterial species (Fig. 2). In this context, it is important to note a problem already discussed by Hentschke & Sant'Anna (2014). In a polyphasic approach to the description of new taxa, we apply almost only morphological observations of cyanobacteria in cultures, not in natural populations. These features, however, can be significantly different (e.g., Berrendero et al., 2016). This problem could be solved by careful study of living material in nature, but due to time and technical complications this is usually completely ignored. If the material has been studied only in culture, this should at least be explicitly mentioned in the taxon descriptions. I consider this one of the great weaknesses of modern taxonomy.

# Biogeographical point of view

Most of the diversity of almost all organisms is found in the tropics (Brown, 2014). However, it appears in the case of cyanobacteria, as if this does not apply. Despite the fact that more and more research is being done in tropical areas (colleagues from Brazil, Mexico, India, and Australia and many others are particularly active), the boreal temperate zone in general and Europe in particular are still the most common source of new taxa (Figs. 3, 4, 5). However, this is highly unlikely. A clear underestimation of the existing biodiversity in the tropics has already been pointed out by some other authors (Sant'Anna et al., 2010; Dvořák et al., 2021). In particular, we know little about the diversity of African cyanobacteria due to firstly, the absence of a major center for cyanobacterial studies and, secondly, the security instability. This discrepancy becomes even more evident if we compare the percentage size of each continent and the percentage of new cyanobacterial species on it (Fig. 4). The situation is special in the Antarctic. This continent is overall unsuitable for life, and indeed there are likely to be relatively few species of cyanobacteria in general. Metagenomic studies (e.g., Pearce et al., 2012) indicate a relatively common level of genetic variation in communities that is quite similar to temperate data. However, this is maritime Antarctica, which is not such an extreme habitat and which occupies only

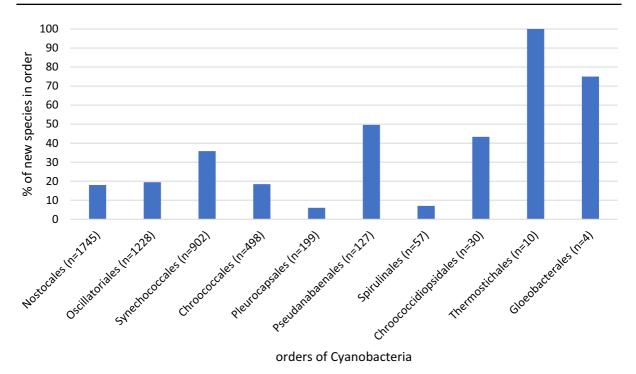


Fig.7 Percentages of new species in each order, sorted by total order size (n=total number of species in order)

a small portion of the land area; the rest of the continent is likely to be truly species-poor.

Various hotspots in cyanobacterial diversity are showing up around the world-for example, the widely studied Atlantic Forest in Brazil (Fiore et al., 2007; Sant'Anna et al., 2010, 2011; Ferreira et al., 2013; Komárek et al., 2013; Sant'Anna et al., 2013; Gama et. al., 2014; Silva et al., 2014; Hentschke et al., 2016; Rigonato et al., 2016; Alvarenga et al., 2017; Gama et. al., 2019; Alvarenga et al., 2021). Many of these hotspots are somewhat surprising, such as the newly discovered genera of branching cyanobacteria in Greek and Spanish caves-Iphinoe Lamprinou & Pantazidou and Loriellopsis Hernandéz-Mariné & Canals (Lamprinou et al 2011), Toxopsis Lamprinou, Skaraki, Kotoulas, Economou-Amilli & Pantazidou (Lamprinou et al., 2012), Spelaeonaias Lamprinou, Christodoulou, Hernández-Mariné & Economou-Amilli (Lamprinou et al., 2016). However, much of this is likely to be an undersampling effect-there would probably be many more similar rich localities if surveyed in detail. For example, very recent studies have found this to be the case in the Azores archipelago (Luz et al., 2023a, b). Further changes and new

species from tropical and subtropical countries are therefore to be expected.

## **Ecological point of view**

# Poor plankton

Oceans cover most of the Earth's surface. Despite this fact, the number of new cyanobacterial species in the marine plankton is very small-less than one fifth compared to new freshwater planktonic species (Fig. 6). Given the number of studies devoted to oceanic waters, e.g., environmental sequencing of seawater during the Tara Oceaens project (Pierella Karlusich et al, 2020), this will not be mainly due to the unexplored character of the area, but rather to the considerable uniformity of the open ocean as a habitat and the lack of microhabitats that are distinct from each other. However, some studies point to a certain spatial heterogeneity of marine picocyanobacteria populations (Kashtan et al., 2014). It is possible that here, unlike in the terrestrial environment, there may be a smaller number of genera, but with a larger number of species. However, taxonomic conclusions have not yet been established.

Freshwater plankton is not a group that has been significantly "affected" by modern methods either, with only 18% of new species coming from this environment. The main reason is probably that it is the most important group from our point of view and therefore already extensively studied in the past. However, the relatively small taxonomic shifts are certainly good news for practicing hydrobiologists.

#### Rich terrestrial

The highest number of new taxa is described from terrestrial localities (Fig. 6). This is probably due to two effects: firstly, terrestrial habitats were not so intensively studied before and now this is being repaired. An equally important reason is that these types are well cultivated and thus easier to explore than, for example, planktonic species. This hypothesis is supported by the increase of new species in groups with aggressive growth on agar plates, such as Leptolyngbya-like species. The former genus Nostoc is also a good example. Now we recognize 15 other genera: Aliinostoc Bagchi, Dubey & Singh (Bagchi et al., 2017); Amazonocrinis Alvarenga, Andreote, Branco, Delbaje, Cruz, De Mello Varani & Fiore (Alvarenga et al., 2021); Atlanticotrix Alvarenga, Andreote, Branco, Delbaje, Cruz, De Mello Varani & Fiore (Alvarenga et al., 2021); Compactonostoc Cai & Li (Cai et al., 2019a); Dendronalium Alvarenga, Andreote, Branco, Delbaje, Cruz, De Mello Varani & Fiore (Alvarenga et al., 2021); Desikacharya Saraf & Singh (Saraf et al., 2019); Desmonostoc Hrouzek & Ventura (Hrouzek et al., 2013); Komarekiella Hentschke, Johansen & Sant'Anna (Hentschke et al., 2017); Halotia Genuário, Viera Vaz, Hentschke, Sant'Anna & (Genuário et al., 2015); Mojavia Řeháková & Johansen (Řeháková et al., 2007); *Minunostoc* Cai & Li, (Cai et al., 2019b); Parakomarekiella Soares, Ramos & Portugal (Soares et al., 2021); Pseudoaliinostoc Lee, Bang, Kim, Ki & Lee (Lee et al., 2021), Purpureonostoc Cai & Li (Cai et al., 2020a) and Violetonostoc Cai & Li (Cai et al., 2020b). In addition, there are other taxa that never belonged to Nostoc, but their morphological similarity is considerable (e.g., Cyanocohniella Kaštovský, Berrendero Gómez, Hladil & Johansen (Kaštovský et al., 2014).

#### Phylogenetical point of view

It is quite understandable that taxonomic changes do not occur in many enigmatic genera or higher taxa. These are sometimes species that have not been found in nature since their description (Dzensia Woronichin, Lithococcus Ercegovic, Lithoderma Areschoug, Paracapsa Naumann, Rhodostichus Geitler & Pascher, Sokolovia Elenkin, Thalpophilla Borzi, Tubiella Hollerbach, etc.) or entire families of rare and especially difficult to cultivate cyanobacteria (Xenococcaceae, Enthophysalidaceae). However, even in some quite common taxa modern taxonomy is not yet sorted. For example, members of the family Coleosphaeriaceae are very abundant in nature, and there are only 4 new Woronichinia Elenkin among the "new" taxa, 3 described and one renamed by Joosten (2006) based on morphological characters only, but no modern studies have led to taxonomic conclusions. Similarly, we have no such data from large common genera such as Planktolyngyba Anagnostidis & Komárek (where there are no taxonomic changes at all) or Schizothrix Kützing ex Gomont-here are 113 old species and 7 new combinations plus 5 new species, but again all these changes were made only based on morphological studies without molecular data (Anagnostidis, 2001; Xiao et al., 2005; Turicchia et al., 2009; Komárek & Kováčik, 2013; Kaštovský et al., 2016). Thick sheaths make DNA isolation difficult, and these species are also not very easy to cultivate. Similarly, many coccoid groups and especially pleuropcapsalean types are "unpopular" (6% of new species of Pleurocapsales). For reasons that are not entirely clear, very few new species are also described in the Spirulinales (7%, Fig. 7).

Apart from the non-numerous orders Thermostichales, Gloeobacterales and Chroococcidiopsidales, there is a remarkably high percentage of new taxa in Pseudanabaenales and Synechococcales (49 respect. 35%, Fig. 7). Especially the filamentous types are extremely frequent targets of taxonomic change. For example, in the family Leptolyngbyaceae there are 122 new taxa (62 renamed and 60 new for science), 28 new genera—and only 3 old ones (*Leptolyngbya* Anagnostidis & Komárek, *Planktolyngbya*, and *Leibleinia* (Gomont) Hoffmann). Similarly, the Prochlothrichaceae have increased intensively, 5 new genera of 20 species have been added to the old *Prochlorothrix* Burger-Wiesma, Stal & Mur. Then the large families Oculatellaceae and Coleofasciculaceae are completely new. The first *Coleofasciculus* (*C. chtonoplastes* Siegesmund, Johansen & Friedel) was described in 2008 (Siegesmund et al., 2008) and today there are 17 genera with 39 species in the family. Similarly, the first *Oculatella* was described in 2012 (*O. subterranean* Zammit, Billi & Albertano, Zammit et al., 2012); today the family contains 13 genera and 40 species.

Similar irregular taxonomic movements occur in the Nostocales, with the Aphanizomenonaceae, Nostocaceae, Rivulariaceae, or Scytonemataceae showing considerable taxonomic change, while the less easily cultivated and considerably rarer Stigonemataceae, or Capsosiraceae show almost none.

#### Problems with names

The lack of clarity in the current state of cyanobacterial taxonomy and systematics stems, among other things, arises from frequent changes in nomenclature, with taxa appearing, disappearing and changing names. This does not only apply to individual species, but also to larger taxonomic units. For example, the Prochlorophyta as a putative evolutionarily significant group containing chlorophyll b originated in 1976 (Lewin, 1976), were renamed Chloroxybacteria in 1982 (Margulis & Schwartz, 1982), and disappeared as a class in 1992 due to the discovery of their polyphyletic character (Palenik & Haselkorn, 1992). Some species are also in a similar situation. For example, Sphaerocavum Azevedo & Sant'Anna originated in 2003 (Azevedo & Sant'Anna, 2003) and disappeared after 14 years as a separate genus (Rigonato et al., 2017).

This situation is compounded by the difficulty of using inappropriate names that do not conform to the rules of the International Code of Nomenclature for Algae, Fungi, and Plants (Turland et al., 2018) and which then need to be changed. For example, the name *Purpurea* Cai & Li (2020) was changed to *Purpureonostoc* (Cai et al., 2020a) 6 months after description (because the name of a genus may not coincide with a Latin technical term in use in morphology). Similarly, *Moorea* (Engene et al., 2012) was renamed *Moorena* (because the name *Moorea* has been used in botanical code before, Tronholm & Engene, 2019).

Actually, the most commonly used name of all "blue-green algae" today—Cyanobacteria—is not the only legally used one, according to the International Code of Nomenclature of Prokaryotes the name Cyanobacteriota is also valid(Oren et al., 2022). Of all the names listed in the introduction, Schizophyceae is no longer actually used. However, Myxophyceae has been used 27 times according to Web of Science and the latest record is from this year (Dutta, 2022), Cyanoprokaryota 180 times, Cyanophyta 999 times and Cyanobacteria 41,447 times (the very recent term Cyanobacteriota four times so far).

#### Constant disintegration

It is true that the majority of modern taxonomic studies split a cluster of morphologically identical forms into multiple genera-see earlier for examples. But many of the taxonomic changes made are only expressions of long-suspected changes and present almost no difficulties, e.g., the division of the genus Anabaena Bory ex Bornet & Flahault into the "true" Anabaena (benthic and without aerotopes), and Dolichospermum (Ralfs ex Bornet & Flahault) Wacklin, Hoffmann & Komárek (planktonic with aerotopes, Wacklin et al., 2009), or Anathece (Komárek & Anagnostidis) Komárek, Kaštovský & Jezberová (with small cells) and Aphanothece Nägeli (with large cells) which have long been regarded as separate subgenera (Komárek et al., 2011), etc. However, a somewhat dangerous phenomenon must be pointed out with such clear changes: many of these examples are made on the basis of molecular data, and the rest are completed on the basis of morphology alone. For example, most representatives of the genus Dolichospermum are still waiting for their molecular data, and almost all representatives of the genus Tapinothrix Sauvageau are similarly affected (Bohunická et al., 2011). Therefore, it is possible that recent changes in these were not the last.

Taxa are not only split into smaller ones, but some are also merged, simplifying the situation—e.g., the merging of the genera *Cylindrospermopsis Seenayya et Subba Raju* and *Raphidiopsis* Fritsch & Rich (Aquillera et al., 2018). However, "splitting" prevails over "merging."

The problem is that tiny and essentially very simple organisms, such as cyanobacteria, do not have many features visible under an optical microscope. However, such features are often revealed by electron microscopy methods. For example, the radial position of thylakoids in the case of the genus *Annamia* Nguyen reliably distinguishes it from the genus *Pseudanabaena* Lauterborn (Nguyen et al., 2013), or the existence of pores on true *Oscillatoria* Vaucher ex Gomont compared to "false" *Oscillatoria* (Mühlsteinová et al., 2018). It is true, however, that such characters are as useless for routine determination as molecular characters. Interestingly, we indeed have no problem admitting convergent evolution in the case of ichthyosaurus, dolphin or fish, but if the same process generates a cryptic diversity of microorganisms, it causes a controversy.

#### Moral appeals and cheap publications

Describing a new of cyanobacteria based on a single sequence and very rough (or non-existent) morphological and ecological data is not a complicated matter. In particular, if the new species is listed as cryptic (i.e., no further consideration of the morphological or ecological features of the organism is needed) and if only a mechanistic view of the arbitrary boundary between taxa is used. The threshold criterion used here is 95% or 94,5% similarity of 16S rRNA for genus (Wayne et al., 1987 or Yarza et al., 2014, respectively) and 97.5-99% for species (Stackebrand & Gobel, 1994; Stackebrand & Ebers, 2006; Kim et al., 2014; Yarza et al., 2014). Many previous authors suggested that it cannot be used as an absolute criterium (Casamatta et al., 2006; Johansen et al., 2014; Oren & Garitty, 2014, Hentschke et al., 2017), yet it's still being applied en masse. In fact, such studies are essentially very "cheap" publications-both financially and mentally; they are a completely routine application of procedures that have been tested hundreds of times. Moreover, the statement of cryptic diversity will limit the need to engage in a truly thorough analysis of older taxonomic papers. I consider far more valuable, intellectually more provocative, and also more useful, those publications that bring new data to existing species-by studying older literature, type localities, ideally type items, and so on. They require more work but bring more utility (e.g., Mühlsteinová et al., 2018; Fukuoka et al., 2022; Lv et al., 2022). It would be great if the number of such studies would increase.

Related to this is the necessity to respect taxonomic rules. Not only physics (according to Isaac Newton) but also biology stands "on the shoulders of giants" and to discard the work of previous authors is irrational. Inventing new paths without continuity with existing work will not bring clarity. The use of modern methods does not necessarily improve the situation, e.g., the papers by Walter et al. (2017) or Salazar et al. (2020) use a new view to taxonomical work, and it is certainly beneficial to know their results, but ignoring previous results and rules complicates rather than enriches taxonomic research (see, e.g., Komárek, 2020 for a more detailed discussion).

# Many new species are cool

Lots of new species don't elicit too much emotion. Another new cryptic genus of a Leptolyngbya-like or Nostoc-like organism isn't very exciting. But some of the new taxa are amazingly interesting. I've already mentioned the discovery of whole evolutionary lineages unknown until recently, such as the numerous families Oculatellaceae or Coleofasciculaceae. Also, the first Geminocystis Korelusová, Kaštovský & Komárek is known since 2009 (Korelusová et al., 2009), and today this new family is very nicely characterized by the very unique parallel position of the thylakoids (Mareš et al., 2019; Pokorný et al., 2023). Other new species are extraordinarily important in terms of their chemical content and biotechnological applications (Moorena, Engene et al., 2012). The study of the toxic, American eagle-killing species Aetoktohonos hydrilicola Wilde & Johansen has provided an amazing story about the consequences of invasive species on native biota. Indeed, its toxin is only poisonous after binding to bromine, which is extensively taken up from the water by the invasive plant Hydrilla verticillata Linneaeus on which it often grows (Breinlinger et al., 2021). Another important discovery is the closest relative of plant chloroplasts, which is the inconspicuous cyanobacterium Gloeomargarita lithophora Moreira, Tavera, Benzerara, Skouri-Panet, Couradeau, Gérard, Loussert Fonta, Novelo, Zivanovic & López-García (Moreira et al., 2017). These are the discoveries that justify all the effort.

# **Concluding remarks**

Understanding the real biodiversity of Cyanobacteriota (as well as other organisms) is the first step toward understanding their role in nature. The discovery of new taxa describes the real situation in the living world and, especially in lesser-known areas (either geographically or habitat-wise), will continue to bring new findings and changes in experienced paradigms.

This situation may be confusing and not userfriendly at first glance, but it is necessary not to panic. It should be pointed out that, especially for temperate aquatic taxa (plankton and periphyton), the classic species still exist in monographs such as the books by Komárek and Anagnostidis (or even Geitler, 1932), only they have been sorted into different genera. Other changes are very rare. Thus, anyone involved in the analysis of cyanobacterial community composition in normal aquatic systems can use these classic works as determination literature. Only then, to finalize their work, can they seek the help of experienced "jungle guides." These are primarily databases such as Algaebase.org (Guiry & Guiry, 2022) or CyanoDB (Hauer & Komárek, 2022), and here it is easy to find new classifications of these species into modern genera. I think the editorial teams of these databases deserve our great thanks. Modern taxonomy has brought us not only complications, but also a whole range of amazing stories and new knowledge. I have therefore attempted to show that this is not a hostile discipline and that it has plenty to offer scientist. Being in the jungle has its problems, but it is a beautiful biotope and has not yet given up all its secrets. Therefore, in the end, perhaps taxonomists and limnologist can say with Kipling, "We be of one blood, you and I." (Kipling, 1894).

Acknowledgements This study was supported by Ministry of Education of the Czech Republic by project Inter-Excellence LTAUSA 18008. Thank of Ryan Scott for language correction.

**Funding** Open access publishing supported by the National Technical Library in Prague. Funding was provided by Ministry of Education of the Czech Republic (Grant No. LTAUSA18008).

**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

#### Declarations

**Conflict of interest** The author declares no conflict of interest.

Ethical approval Not applicable/not required.

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