

cryptogamie

Algologie

2024 • 45 • 6

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art. 45 (6) — Published on 12 July 2024
www.cryptogamie.com/algologie

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Cryptogamie, Algologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
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diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

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

A journey through Cyanobacteria in Brazil: a review of novel genera and 16S rRNA sequences

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Submitted on 21 August 2023 | Accepted on 14 February 2024 | Published on 12 July 2024

Hentschke G. S., Santos K. R. de S., Mattos L. de, Oliveira F. & Vasconcelos V. M. 2024. — A journey through Cyanobacteria in Brazil: a review of novel genera and 16S rRNA sequences. *Cryptogamie, Algologie* 45 (6): 63-75. <https://doi.org/10.5252/cryptogamie-algologie2024v45a6>. <http://cryptogamie.com/algologie/45/6>

ABSTRACT

In this paper we present a bibliographical review of the newly described Brazilian cyanobacterial genera, based on 16S rDNA analysis. Moreover, we discuss their position according to the current classification system of Cyanobacteria. Additionally, in order to comprehend the diversity of Brazilian 16S rDNA sequences deposited in GenBank (NCBI), we constructed a phylogeny based on an alignment of these sequences with cyanobacterial reference strains. The bibliographical review resulted in 26 papers. We identified 30 cyanobacterial genera described from Brazil, distributed across eight orders. The order Nostocales is the most well-represented with 11 genera. The genera described based on Brazilian strains are from terrestrial, aquatic (marine and freshwater), and extreme habitats (alkaline saline lakes). The terrestrial habitat hosts the largest number of genera, with 17 in total. The studies are primarily concentrated in the Atlantic Rainforest, Amazon, Caatinga, and Pantanal Biomes, while the Pampa Biome remains unstudied. Most of the Brazilian genera are monophyletic, with the exception of *Brasilonema* Fiore, Sant'Anna, de Paiva Azevedo, Komarek, Kaštovský, Sulek & Lorenzi, which is intermixed with *Iphinoe* Lamprinou & Pantazidou and *Symphyonemopsis* Tiwari & Mitra; and *Capilliphycus* Caires, Sant'Anna & Nunes, which is polyphyletic. Genera like *Marmoreocelis* Machado-de-Lima & Branco, *Monilinema* Malone, Genuário, Vaz, Fiore & Sant'Anna, *Insularia* Araújo, Schnadelbach, Nunes &

KEY WORDS

South America,
Brazil,
Tropical environments,
Subtropical environments,
cyanobacteria,
phylogeny.

Caires, and *Microlinema* Araújo, Schnadelbach, Nunes & Caires require revision in their taxonomical classifications. Our findings reveal that numerous Brazilian 16S rDNA sequences in GenBank are unidentified or misidentified, indicating a need for at least 15 genera to be described based on these strains. Here we also elucidate that the Brazilian cyanobacterial diversity is significantly underestimated.

RÉSUMÉ

Un voyage à travers les cyanobactéries au Brésil: une revue des genres nouveaux et des séquences de l'ARNr 16S. Dans cet article, nous présentons une revue bibliographique des genres de cyanobactéries brésiliennes nouvellement décrits, basée sur l'analyse de l'ADN ribosomique 16S et, nous discutons de leur position selon le système de classification actuel des cyanobactéries. Afin de comprendre la diversité des séquences 16S rDNA brésiliennes déposées dans GenBank (NCBI), nous avons construit une phylogénie basée sur un alignement de ces séquences avec des souches de référence de cyanobactéries. La revue bibliographique a été réalisée sur la base de 26 articles. Nous avons identifié 30 genres de cyanobactéries décrits au Brésil, répartis dans huit ordres. L'ordre des Nostocales est le plus représenté avec 11 genres. Les genres décrits à partir de souches brésiliennes proviennent de milieux terrestres, aquatiques (marins et d'eau douce), ainsi que d'habitats extrêmes (lacs salins alcalins). L'habitat terrestre héberge le plus grand nombre de genres, avec un total de 17. Les études sont principalement concentrées dans les biomes de la forêt atlantique, de l'Amazonie, de la Caatinga et du Pantanal, tandis que le biome des Pampas reste non étudié. La plupart des genres brésiliens sont monophylétiques, à l'exception de *Brasilonema* Fiore, Sant'Anna, de Paiva Azevedo, Komárek, Kaštovský, Sulek & Lorenzi, qui est entremêlé avec *Iphinoe* Lamprinou & Pantazidou et *Symphyonemopsis* Tiwari & Mitra; et de *Capilliphyucus* Caires, Sant'Anna & Nunes, qui est polyphylétique. Des genres comme *Marmoreocelis* Machado-de-Lima & Branco, *Monilinema* Malone, Genuário, Vaz, Fiore & Sant'Anna, *Insularia* Araújo, Schnadelbach, Nunes & Caires, et *Microlinema* Araújo, Schnadelbach, Nunes & Caires nécessitent une révision de leurs classifications taxonomiques. Nos résultats révèlent que de nombreuses séquences brésiliennes de 16S rDNA dans GenBank ne sont pas identifiées ou mal identifiées, ce qui indique la nécessité de décrire au moins 15 genres basés sur ces souches. Cet article met également en évidence que la diversité des cyanobactéries brésiliennes est nettement sous-estimée.

MOTS CLÉS
Amérique du Sud,
Brésil,
environnements tropicaux,
environnements
subtropicaux,
cyanobactéries,
phylogénie.

INTRODUCTION

Cyanobacteria are Gram-negative bacteria (Prokaryotes) that perform oxygenic photosynthesis and participate in the major biogeochemical cycles of carbon, nitrogen, and oxygen on Earth for billions of years (Couradeau *et al.* 2011). Whilst these microorganisms play an essential role, they can also inflict environmental harm. For instance, cyanobacterial blooms can trigger severe ecological and economic consequences, raising concerns for public and environmental health due to the production of cyanotoxins. These toxins adversely affect various organisms, including invertebrates, fish, birds, mammals, and even humans (Carmichael *et al.* 2001). Moreover, these blooms can block sunlight, leading to a depletion of oxygen levels in the water column (Whitton & Potts 2012). Taking an alternative perspective, cyanobacteria offer immense biotechnological potential, synthesizing a plethora of organic compounds with properties such as antioxidants, anticancer agents, and antiviral agents. Also, cyanobacteria serve as fertilizers, generate secondary metabolites like exopolysaccharides, vitamins, enzymes, toxins, and pharmaceuticals that have applications in aquaculture, wastewater treatment, and food production (Lopes *et al.* 2022).

Cyanobacteria (commonly known as blue-green algae), were initially classified by botanists as algae. This systematic categorization adhered to the *International Code of Botanical*

Nomenclature, now referred to as the *International Code of Nomenclature for algae, fungi, and plants*. This botanical classification was revised by Komárek (2013) and Komárek & Anagnostidis (1999, 2005), where revisions that were primarily based on morphological attributes such as thallus structure, cell division mechanisms, and differentiated cell production, resulted in the division of the group into four orders: Chroococcales, Oscillatoriales, Nostocales, and Stigonematales, with a total of approximately 2800 species.

Following the employment of the 16S rRNA gene phylogenetic analysis for the classification of Cyanobacteria (Hoffmann *et al.* 2005; Komárek *et al.* 2014) and the official recognition of Cyanobacteria by the *International Code of Nomenclature of Prokaryotes* (ICNP), many changes occurred. These changes resulted in the current classification system proposed by Strunecký *et al.* (2023), in which a phylogeny with 120 protein sequences was constructed. The molecular era in Cyanobacteria allowed the unraveling of many cyanobacterial new taxa, the description of many cryptic taxa, and the review of traditional genera, such as *Anabaena* Bory de Saint-Vincent ex Bornet & Flahault, from which *Dolichospermum* (Ralfs ex Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek was separated (Wacklin *et al.* 2009).

Cyanobacterial diversity in Brazil is remarkably large and documented historically in papers, which used classical (morphological) taxonomy (Sant'Anna 1997; Werner & Sant'Anna

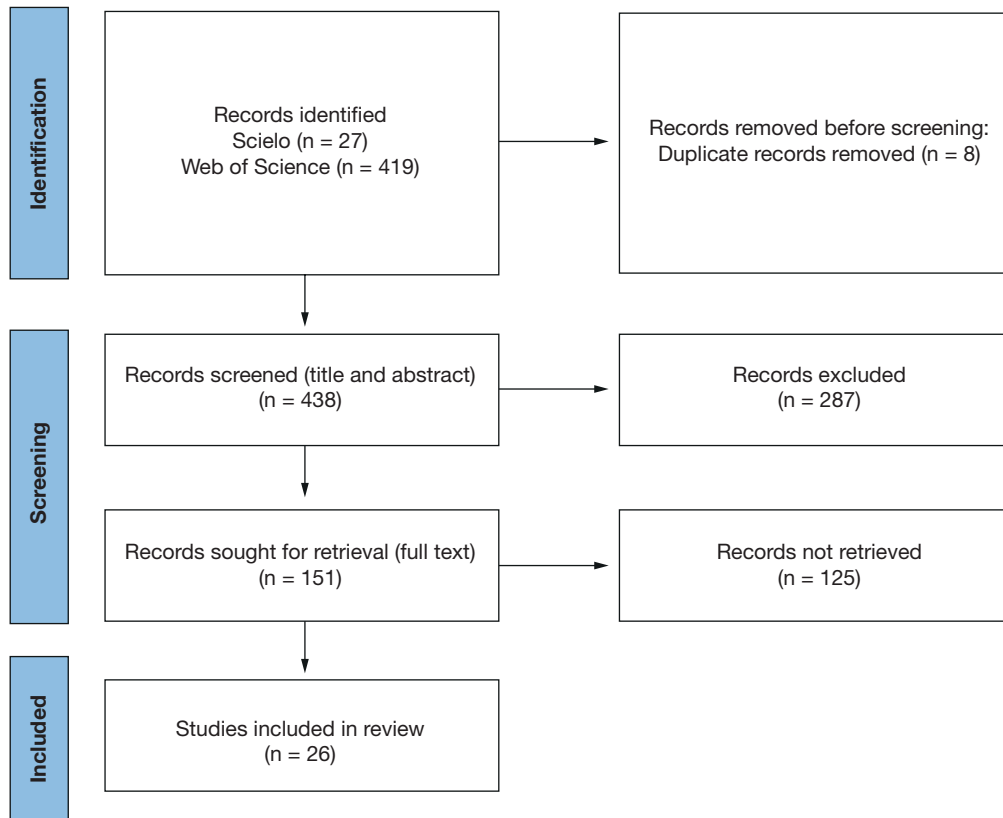


FIG. 1. — Flowchart of search methods for identification and selection of studies.

2000). The Brazilian authors also described new genera based only on morphological characters, such as *Streptostemon* Sant’Anna, Azevedo, Kaštovský & Komárek (Sant’Anna *et al.* 2010), *Sphaerocavum* M.T.P.Azevedo & Sant’Anna (Azevedo & Sant’Anna 2003) and *Cyanoaggregatum* Werner, Sant’Anna & Azevedo (Werner *et al.* 2008). *Streptostemon* was later confirmed as a separate genus by molecular analysis (Hentschke *et al.* 2016). *Sphaerocavum* turned out to belong to the Microcystis clade (Rigonato *et al.* 2018), and *Cyanoaggregatum* requires further molecular validation.

Based on 16S rRNA phylogenies, the first cyanobacterial genus described from Brazil was *Brasilonema* Fiore, Sant’Anna, de Paiva Azevedo, Komarek, Kaštovský, Sulek & Lorenzi (Fiore *et al.* 2007), and after that, many others were described using molecular tools. Currently there are more than thirty thousand sequences of 16S rDNA from Brazilian cyanobacterial strains in NCBI. Despite that, most of these cyanobacteria strains are taxonomically misidentified or represent new taxa that still lack proper characterization and documentation.

Based on that, in this paper we present a bibliographical review of the newly described Brazilian cyanobacterial genera, based on 16S rDNA analysis, and discuss their position according to the current classification system of Cyanobacteria. Also, to provide a better comprehension on the diversity of Brazilian 16S rDNA sequences deposited in GenBank (NCBI), we constructed a phylogeny based on an alignment of these sequences with cyanobacterial reference strains.

MATERIAL AND METHODS

BIBLIOGRAPHICAL REVIEW

To search for articles that described new cyanobacterial taxa in Brazil using molecular tools, we employed the Boolean operator “((Cyanobacteria) AND (Brazil)) AND ((taxonomy) OR (‘new genus’) OR (‘new genera’) OR (‘new species’) OR (diversity))” in the Scielo and Web of Science databases. For articles selection, we used the inclusion criterion of articles describing new taxa, while the exclusion criteria consisted of 1) the absence of 16S rDNA phylogeny; and 2) taxa not conforming to the guidelines of the *International Code of Nomenclature for algae, fungi, and plants* (Turland *et al.* 2018) or the *International Code of Nomenclature of Prokaryotes* (Parker *et al.* 2019).

This search was independently conducted by two of the authors (G.S.H and F.O.) between July 15th and July 30th, 2023. No restrictions were imposed regarding publication date or language. The information and outcomes extracted from each article included authorship, publication year, journal, impact factor, the methodology employed for taxon identification, described genera and species, type material details, herbarium numbers, reference strains, NCBI codes, habitat of the new taxa, taxonomical order, and the repository where the taxa are curated. The process is illustrated in Figure 1, and the results are presented in Appendix 1 (see results section).

16S rDNA SEQUENCES REVIEW

In order to locate Brazilian 16S rDNA sequences archived in GenBank (NCBI), we employed the operator “((Cyanobacteria) AND (16S) AND (Brazil))” on the NCBI website (<https://www.ncbi.nlm.nih.gov/>). To enhance the subsequent alignment and phylogenetic analyses, we filtered the sequences by selecting those encompassing a minimum of 1200 positions. After conducting preliminary alignment tests using all sequences collected on July 15th 2023, it was determined that Metagenomic Assembly Genomes (MAGs) should be excluded due to their shorter or fragmented nature.

Guided by the metadata associated with the strains, our inclusion criterion was strains originating from Brazilian populations. An exclusion criterion was applied to sequences that could not be adequately aligned.

To extract the 16SrRNA gene sequences from genomes, a table containing all genome access identifiers (including both GenBank and RefSeq) for the Cyanobacteriota Phylum was downloaded. The downloaded data encompassed a total of 6122 genomes (July 24, 2023, available at NCBI Genome, <https://www.ncbi.nlm.nih.gov/genome/browse#!/overview/>). Redundant strains were excluded. Subsequently, the metadata of 3562 genomes were retrieved using the NCBI genome package datasets summary genome tool (<https://www.ncbi.nlm.nih.gov/datasets/docs/v2/how-tos/genomes/get-genome-metadata/>). After the application of the same inclusion/exclusion criteria (Fig. 2) the 16S rDNA of these genomes were identified using customized Python scripts (https://github.com/CNP-CIIMAR/bioinformatics-utilities/blob/main/run_barnap.py) to execute the Barrnap program (<https://github.com/tseemann/barrnap>).

PHYLOGENETIC ANALYSIS

The final dataset comprised 888 sequences, encompassing both Brazilian sequences and Cyanobacteria reference strains. Reference strains were retrieved from the original descriptions of cyanobacterial genera (personal database), as well as from other resources such as Cyanoseq (Lefler *et al.* 2023) and the review from Strunecký *et al.* (2023).

Sequence were aligned using Mafft (Katoh *et al.* 2002) algorithm and the optimal evolutionary model GTR was applied using MEGA11: Molecular Evolutionary Genetics Analysis version 11 (Tamura *et al.* 2021). Phylogenetic reconstruction was conducted using the FastTree method (Price *et al.* 2009), with a bootstrap value set to 1000. Tree topography was edited using iTol (Letunic & Bork 2021) and a system classification of tree labels was applied according to Strunecký *et al.* (2023).

RESULTS AND DISCUSSION

The bibliographic review results are summarized in Appendix 1, which shows all the papers selected after the application of inclusion and exclusion criteria in our search, as well as all the data extracted from them. The phylogeny containing the Brazilian sequences with the addition of Cyanobacteria reference strains is shown in Figure 3.

BIBLIOGRAPHICAL REVIEW

Brazilian cyanobacterial biodiversity

To this date, the *International Code of Nomenclature of Prokaryotes* (ICNP) recognizes a total of 431 validly described cyanobacterial genera worldwide, according to the Cyanodb website (July 2023) (Hauer & Komárek 2022). Until 2022, 232 of these genera have had their phylogenetic position confirmed through the use of the 16S rDNA sequencing method (Lopes *et al.* 2022). In the specific context of Brazil, molecular tools have been employed to characterize 28 genera by that year, constituting roughly 12% of the global Cyanobacteria biodiversity known, based on 16S rDNA phylogeny. In 2023, two additional genera were described (Loureiro de Araújo *et al.* 2023), culminating in a current total of 30 genera.

When considering the global distribution of genera across orders, up until 2022, molecular studies have confirmed the existence of 84 genera within the Nostocales order, 65 within Synechococcales (which encompasses Synechococcales, Lep- tolyngbyales, and Nodosilineales), 50 within Oscillatoriales (encompassing Oscillatoriales and Coleofasciculales), and approximately 20 within the Chroococcales + Chroococ- cidiopsidales (Lopes *et al.* 2022). Among these, Brazil has contributed to the identification of 11 genera in Nostocales, ten in Oscillatoriales, four in Synechococcales and three in Chroococcales. In the year 2023, an additional two genera were described within Synechococcales (De Araújo *et al.* 2022).

These representative numbers serve as indicators of the remarkable extent of Brazilian cyanobacterial biodiversity and reflect the endeavors of Brazilian institutions to enhance knowledge about cyanobacteria biodiversity, promoting its preservation and sustainable utilization. Whilst studies have been conducted across various Brazilian biomes, such as the Atlantic Rainforest, Amazon, Caatinga, and Pantanal (Appendix 1), it is important to acknowledge that these taxonomic investigations have been confined to relatively small segments of these regions. Because of that, the prospect of future sampling initiatives within these diverse Brazilian biomes holds the potential for substantially expanding the description of new genera of cyanobacteria in Brazil. In other places such as Pampa Biome (southern Brazil), molecular diversity of cyanobacteria remains entirely unexplored.

Concerning species, although currently there is no defined concept for this taxonomical level in Cyanobacteria (Johansen & Casamatta 2005; Pietrasiak *et al.* 2019), for Brazil, 52 new species were newly described using 16S rDNA and/or 16S-23S ITS data along with morphological and ecological analysis (Appendix 1).

Brazilian cyanobacteria and habitats

Regarding habitats, it is well established that cyanobacterial genera often present the capacity to grow in multiple environments. However, among the genera characterized from samples collected in Brazil or present within Brazilian culture collections, a notable proportion, 17 out of 30, have been isolated from terrestrial sources (Appendix 1). Furthermore, five genera are associated with marine ecosystems, and additional four are linked to freshwater environments (Appendix 1). It

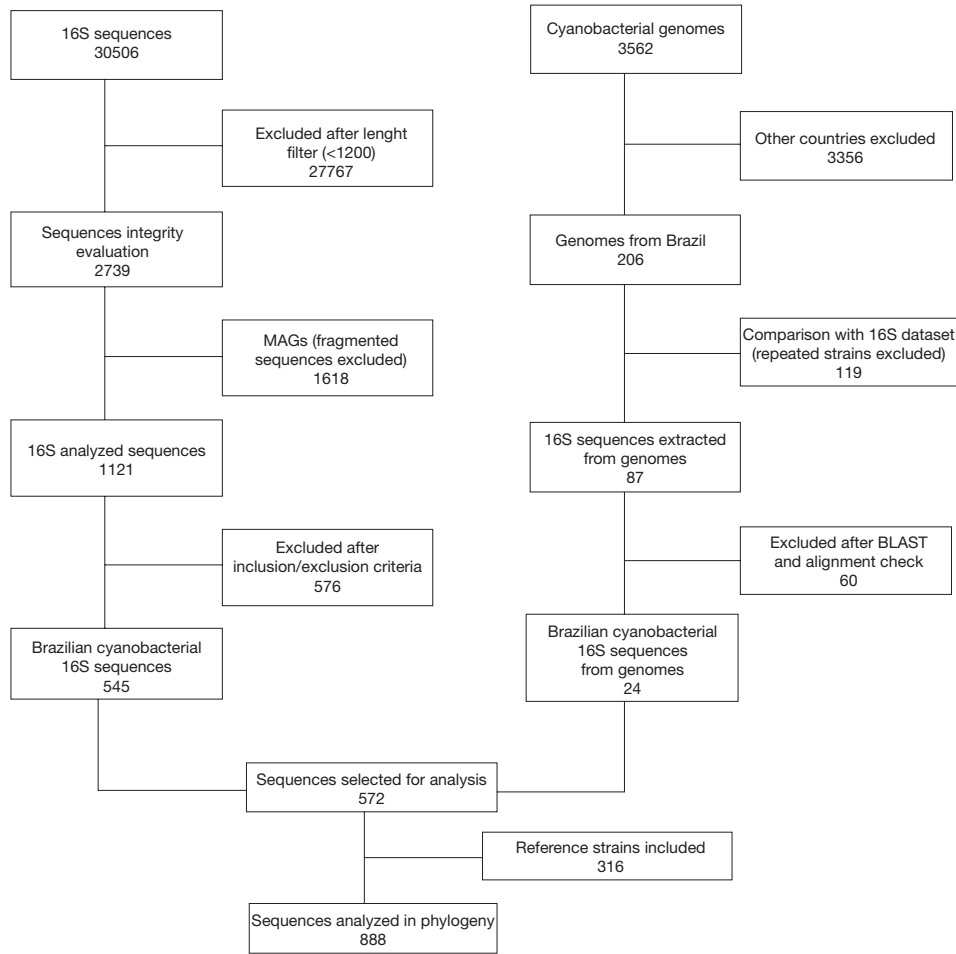


Fig. 2. — Flowchart of search methods for identification and selection of Brazilian 16S rDNA sequences from GenBank (NCBI).

is worth highlighting that three genera have been described exclusively from extreme environments, such as saline alkaline lakes found within the Pantanal Biome (Appendix 1). These lakes exhibit interesting dynamics and are primarily dominated by populations of *Anabaenopsis* V.V.Miller and *Arthrospira* Stizenberger ex Gomont (Santos *et al.* 2011). They have remained relatively underexplored despite their potential significance, thus presenting a promising source for uncovering novel biodiversity.

The prevalence of descriptions for terrestrial genera can be attributed to the focus and endeavors of research groups led by Dr. Célia Leite Sant’Anna and Dr. Marli Fiore (Instituto de Botânica de São Paulo (IBt) and Centro de Energia Nuclear na Agricultura (CENA)), who have conducted important sampling within the Atlantic Rainforest, Cerrado, and Caatinga Biomes. Certain groups, such as those at “Universidade Estadual de Feira de Sant’Anna” (Bahia State), have concentrated more on studying marine cyanobacterial biodiversity. When considering Brazil’s expansive coastline with a diverse range of habitats (Caires *et al.* 2018), research in these areas holds great importance and are promising for unveiling cyanobacterial biodiversity, due to the lack of knowledge about these areas. Likewise, investigations into terrestrial and freshwater

cyanobacteria have the potential to continue yielding numerous new taxa, given the array of habitats within the Brazilian Biomes, as discussed earlier.

When comparing Brazilian data to numbers globally, up until 2022, molecular analyses had validated 110 genera for terrestrial habitats worldwide, 118 for freshwater environments, and 53 for marine environments (Lopes *et al.* 2022). Significantly, in the context of terrestrial habitats, Brazil has made substantial contributions to Cyanobacteria taxonomy, accounting for 16% of the genera validated through molecular tools. Similarly, Brazil has played a significant role in marine biodiversity studies, contributing to 10% of the genera confirmed by molecular investigations (Appendix 1). In particular, it should be emphasized that, in terms of proportion, marine Cyanobacteria constitute the least explored group in molecular analysis, as shown by Lopes *et al.* (2022). Globally, only 49% of marine genera have been validated through molecular analysis, whilst for terrestrial and freshwater environments, the proportions stand at 68% and 60%, respectively (Lopes *et al.* 2022).

Concerning freshwater environments, the relatively modest representation of genera described from Brazil (4%) is primarily attributed to the fact that Brazilian research groups

have predominantly directed their focus toward terrestrial and marine Cyanobacteria. The majority of recent Brazilian studies concerning freshwater environments predominantly employ traditional (morphological) taxonomy, in general biodiversity studies.

In extreme environments, Brazil has made a notable impact by contributing four out of the 20 genera confirmed through molecular analysis, representing 20% of the total. All of these genera were isolated from Pantanal saline and alkaline lakes.

Within all those habitats, we found that among the holotypes of the new Brazilian terrestrial new genera, seven are from soil samples and six are epiphytic on tree leaves. Terrestrial genera are also described from rocks (one) and wood (two). The marine genera are all benthic, and for freshwater habitats, two genera are benthic and other two are planktonic (Appendix 1).

Culture collections and publications

Publications of new cyanobacterial taxa are considered valid when described under the *International Code of Nomenclature for algae, fungi, and plants*, and later also under the *International Code of Nomenclature of Prokaryotes* due to their prokaryotic nature. Regarding to that, among the newly described Brazilian taxa, we found that *Adonisia turfiae* Walter *et al.* (Walter *et al.* 2017), was invalidly published, and because of that, it was excluded from our Appendix 1. The species is not formally described, and no holotype and reference strain were formally designated. The 16S rRNA sequence is still included in our phylogenetic analysis (Fig. 3).

The first publication considering molecular data of Brazilian Cyanobacteria was in 2007 (Fiore *et al.* 2007), describing *Brasilonema*, and the peak was reached in 2015 and 2016 with four publications in each of those years. Since then, at least one genus has been published per year (mean 2.75). However, there seems to have been a decreasing trend in these numbers over the last four years (Appendix 1).

Regarding culture collections, all newly published genera types are currently held in Brazilian culture collections, primarily at the Centre for Nuclear Energy in Agriculture (CENA) in Piracicaba, with ten type strains (Appendix 1). The Culture Collection of the Institute of Botany (CCIBt) follows with eight type strains. Since 2021, Brazil has signed the Nagoya Protocol, and as a consequence, it is probable that the country's borders will be more open to foreign researchers for sampling and studying our biodiversity. This may lead to increased access to international researchers interested in studying Brazilian biodiversity.

PHYLOGENETIC ANALYSIS OF GENERA DESCRIBED FROM BRAZIL

The taxonomical classification of the genera described from Brazil is presented in Appendix 1 and Figure 3, according to Strunecký *et al.* (2023).

The genera *Marmoreocelis* Machado-de-Lima & Branco, *Monilinema* C.F.S.Malone, Genuário, M.G.M.V.Vaz, M.F.Fiore & Sant'Anna, *Insularia* V.L.Araújo, A.S.Schnadelbach, J.M.C.Nunes & T.A.Caires and *Microlinema* V.L.Araújo,

A.S.Schnadelbach, J.M.C.Nunes & T.A.Caires were not revised by the authors and are discussed below.

Marmoreocelis (Machado-de-Lima & Branco 2020) is a filamentous homocytous genus and was described for the order Oscillatoriales *sensu* Komárek *et al.* (2014), as a sister clade of *Gracilinea* N.M.Machado-de-Lima & Branco, which is currently positioned in Coleofasciculales (Strunecký *et al.* 2023). In our phylogeny, in which we have included more sequences (total 888) and reference strains compared to the original description (Machado-de-Lima & Branco 2020), *Gracilinea* is confirmed in Coleofasciculales, but *Marmoreocelis* is related to the Gomontielales genera such as *Crinalium* Crow, *Starria* Lang, *Komvophoron* Anagnostidis & Komárek and *Chamaesiphon* Braun & Grunow. This order includes unicellular and filamentous genera and according to Strunecký *et al.* (2023), the order is monophyletic and presents heterogenous morphology, which is in agreement with our findings. Currently there is not enough data to transfer *Marmoreocelis* to Gomontielales, but our results suggest that further studies are needed to clarify its taxonomical position.

Monilinema (Malone *et al.* 2020) is a *Leptolyngbya*-like genus described for the family Leptolyngbyaceae (Synechococcales) *sensu* Komárek *et al.* (2014). Our findings confirm this genus in this family, being closely related to *Leptolyngbya* Anagnostidis & Komárek, *Plectolyngbya* A.Taton, A.Wilmotte, J.Smarda, J.Elster & Komárek, *Tapinothrix* Sauvageau and *Pinocchia* P.Dvorak, Jahodarova & P.Hasler. The Leptolyngbyaceae family changed the taxonomical status to Leptolyngbyales (Strunecký *et al.* 2023), and considering that our results are in agreement with the revision of Strunecký *et al.* (2023), it is natural to move this genus from Oscillatoriales (Leptolyngbyaceae), to the order Leptolyngbyales (Leptolyngbyaceae).

Insularia (Loureiro de Araújo *et al.* 2023) was described for the family Pseudanabaenaceae *sensu* Komárek *et al.* (2014), owing to its phylogenetic relationship with *Pseudanabaena* YACCYB277 (MH683727) and *Pseudanabaena galeata* SP44 (HQ658458). These strains are not related to the reference strains *Pseudanabaena* PCC6903 and *P. catenata* SAG 1464-4 (KM020005) (true *Pseudanabaena* Lauterborn), but even though *Insularia* was positioned in that order. Moreover, the morphological and ultrastructural observations don't relate *Insularia* to Pseudanabaenales. Although slightly constricted, *Insularia* filaments are morphologically similar to Leptolyngbya. The parietal thylakoid position is congruent with Synechococcales and Spirulinales *sensu* Komárek *et al.* (2014) and also Acaryochloridales *sensu* Strunecký *et al.* (2023). In our phylogeny, *Insularia* is in the Acaryochloridales clade, closely related to *Acaryochloris* Miyashita & Chihara and *Thainema* Rasouli-Dogaheh & Hauer, also not revised by Strunecký *et al.* (2023), as well as to the Brazilian sequences MF084982, M084983 and M084981, which must be described as a new genus. So far, we don't have enough evidences to transfer *Insularia* to Acaryochloridales, but our findings indicate that a revision of the taxonomical classification of this genus must be done. The same situation occurs with *Thainema* (Rasouli-Dogaheh *et al.* 2022), which was originally described as part

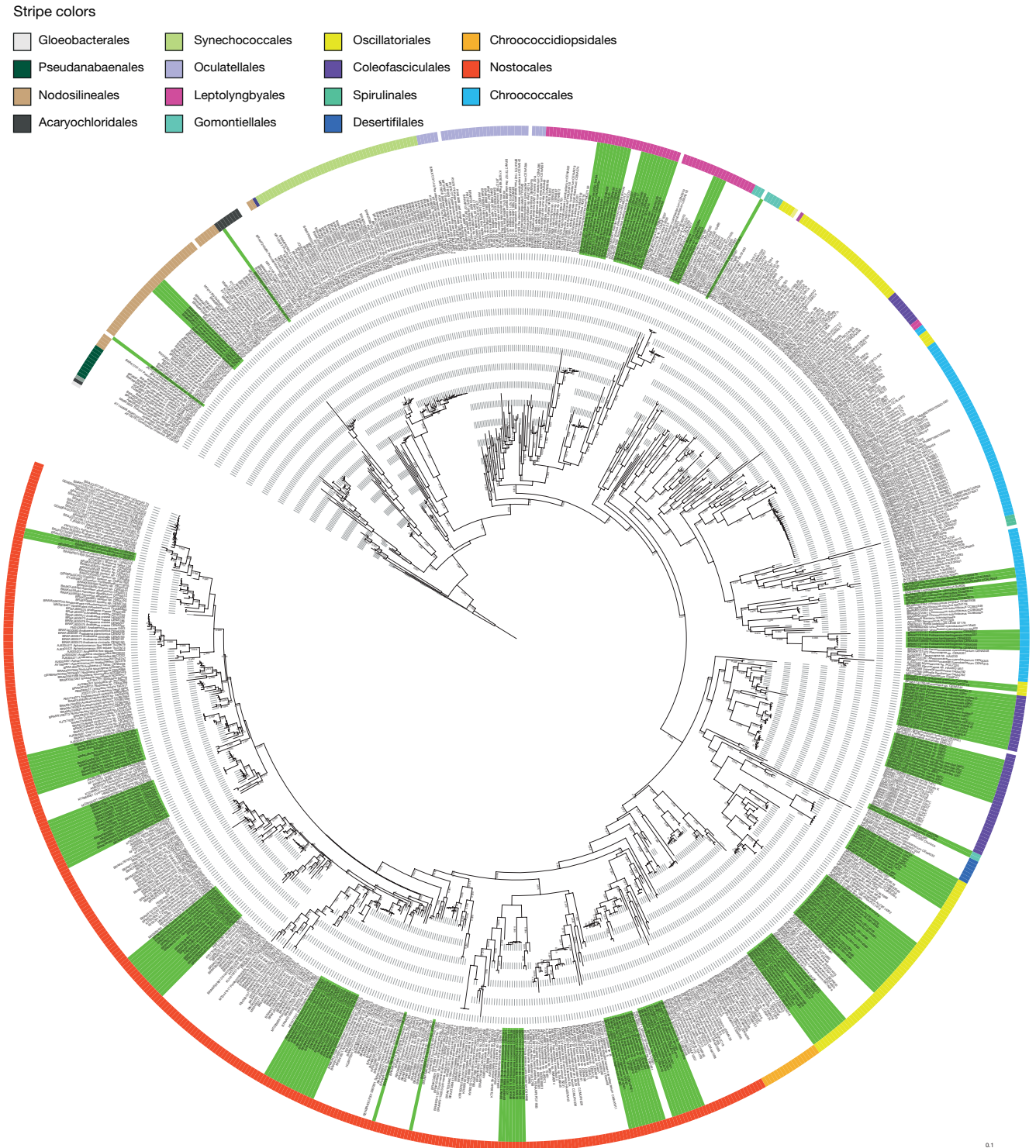


FIG. 3. — Phylogenetic reconstruction of 16S rDNA of Brazilian strains and reference strains of Cyanobacteria. The strains marked in **green** are Brazilian genera. The **stripe colors** represent taxonomical orders.

of Leptolyngbyaceae *sensu* Komárek *et al.* (2014), though our results suggest that should be included in the Acaryochloridales.

Microlinema is also a *Leptolyngbya*-like genus described for Leptolyngbyaceae *sensu* Komárek *et al.* (2014). In our phylogeny the genus is in the monophyletic Nodosilineales clade, closely related to *Haloleptolyngbya* P.K.Dadheech,

H.Mahmoud, K.Kotut & L.Krienitz, *Marileptolyngbya* Zhou & Ling and Brazilian sequences such as KC695849, which must be described as a new genus. The parietal thylakoids are in agreement with Nodosilineales (Strunecký *et al.* 2023), but further studies are needed to validate this genus in this order.

Most of the Brazilian genera are monophyletic with the exception of *Brasilonema* which has been shown to be paraphyletic and *Capilliphycus* T.A.Caires, Sant'Anna & J.M.Nunes, which is polyphyletic. Among *Brasilonema* sequences, are found *Iphinoe* Lamprinou & Pantazidou and *Symphyonemopsis* Tiwari & Mitra type sequences (Lamprinou *et al.* 2013). In order to test these incongruences, we built a smaller ML tree, using 63 sequences and 1170 positions analyzed (Trifinopoulos *et al.* 2016), including our Nostocales set of reference strains, and consequently we obtained the same results, shown in Figure 4, with *Iphinoe* and *Symphyonemopsis* among *Brasilonema* strains. These three genera present parallel arrangement of filaments, but considering other characters, *Brasilonema* is very different from the others. *Brasilonema* is characterized by scytonematoid filaments with few false branches (Fiore *et al.* 2007), while *Iphinoe* and *Symphyonemopsis* present true branching (Lamprinou *et al.* 2013). Clearly, we cannot treat these genera as a singular entity. However, our phylogenetic findings suggest that further investigations, potentially involving phylogenomic analyses, are imperative to clarify the placement of these strains. Conducting new 16S rDNA sequencing for *Iphinoe* and *Symphyonemopsis* type strains is essential to ensure the absence of contamination in the existing known sequences. Furthermore, it is worth noting that the bootstrap support for the *Brasilonema* clade is relatively low (72), thus warranting a comprehensive reevaluation of this genus.

Capilliphycus was found to be polyphyletic in our phylogeny with 888 sequences. This genus was originally described with two species: *C. salinus* T.A.Caires, Sant'Anna & J.M.Nunes and *C. tropicalis* T.A.Caires, Sant'Anna & J.M.Nunes. The type species, *C. salinus*, is alone in its own branch and is closely related to the genus *Lyngbya* C.Agardh ex Gomont, represented here by the reference strain PCC7419 (Castenholz 2011; Engene *et al.* 2018). However, *C. tropicalis* forms a sister clade to the *Capilliphycus*/*Lyngbya* cluster, indicating that it can be a different genus. To confirm this, we conducted an additional phylogeny using 52 sequences and 1226 analyzed positions (Fig. 5). The resulting tree is more robust compared to the phylogeny of Caires *et al.* (2018), in which the genus was originally described, considering that it includes more nucleotide positions analyzed.

In our additional phylogeny (Fig. 5), *C. salinus* remains isolated in its own clade as a distinct and coherent genus. However, *C. tropicalis* appears distant from this clade, in an uncertain position within a cluster containing *Neolyngbya* Caires, Sant'Anna & J.M.C.Nunes, *Sirenicapilaria* Berthold, Lefler & Laughinghouse, *Limnospira* Nowicka-Krawczyk, Müh- lsteinová & Hauer, *Tigrinifilum* D.E.Berthold, Lefler & Laughinghouse, *Affixifilum* Lefler, D.E.Berthold & Laughinghouse, *Lyngbya*, *Limnoraphis* J.Komárek, E.Zapomelová, J.Smarda, J.Kopecky, E.Rejmánková, J.Woodhouse, B.A.Neilan & J.Komárková and *Capilliphycus*. The bootstrap values within this cluster are low, primarily due to the high sequence similarity (p-distance) between these sequences, which have a mean of 97%. Considering this, we conclude that a reevaluation of these genera is necessary, and *C. tropicalis* should be described as a new genus, separate from *Capilliphycus*. Furthermore,

there are three additional *Capilliphycus* strains (coded PMC) situated at the base of the *Lyngbya*-like cluster, which also warrant description as new genera.

PHYLOGENETIC ANALYSIS OF BRAZILIAN STRAINS

From the 20 orders proposed by Strunecký *et al.* (2023), the Brazilian strains are classified in 13 of them. In our tree (Fig. 3), we found 243 Brazilian strains in the order Nostocales, 65 in Chroococcales, 62 in Oscillatoriales, 44 in Synechococcales, 41 in Coleofasciculales, 41 in Leptolyngbyales, 33 in Nodosilineales, 15 in Oculatellales, 11 in Chroococciopsidales, six in Pseudanabaenales, four in Acaryochloridales, two in Gomontiellales and one strain in Desertifilales. Three are undefined or positioned differently from the original description such as *Marmoreocelis xerophila* CATCB5 (MT311247), *Pseudanabaenaceae cyanobacterium* CENA510 (KF246480), *Microlinema* sp. ALCB132774 (MW024865), which are discussed in other sections of our paper.

Part of this diversity is already taxonomically identified, but some clades formed by the Brazilian strains are clearly not related to any type or reference strains, and must be described as new genera. To evaluate this, we considered the phylogenetic results and identity of 16S rDNA using BLAST (NCBI). Sequences with less than 95% of identity with any already described genus were considered probable new genera (Stackebrandt & Ebers 2006).

In the order Nodosilineales, the strain *Leptolyngbya* CENA155 (KC695849) is a sister clade of *Nodosilinea* R.B.Perkerson & D.A.Casamatta (Nodosilineales), but presents only 94% of 16S rDNA identity (BLAST) with this genus. The strains identified as *Phormidesmis* CENA317 (KT731138), CENA316 (KT731137), CENA332 (KT731152), CENA318 (KT731139), CENA335 (KT731154) and CENA339 (KT731156) are a monophyletic sister clade of *Cymatolege* Konstantinou & Gkelis, but presents only 91% of identity with this genus.

In the Acaryochloridales, the strains CENA553 (MF084983), CENA554 (MF084982) and CENA555 (MF084983) are in a monophyletic clade, sister to *Insularia* and *Thainema*, but presents only 92% of 16S rDNA similarity with these genera.

In the Synechococcales, the Brazilian strains morphologically identified as *Limnothrix* LEGE 15497 (MF629814), CENA545 (KF246506), CENA217 (MN551904), CENA109 (EF088335), CENA111 (EF088338), CENA110 (EF088336) are in a monophyletic clade not related with the reference strain *Limnothrix redekei* (Goor) Meffert (CCAP 1443/1) (Pseudanabaenales) (Strunecký *et al.* 2023) and are in a monophyletic clade among Synechococcales.

In the Oculatellales, the strain *Pseudanabaenaceae cyanobacterium* CENA319 (KT731140) is a sister clade of *Toxifilum* Zimba, Huang, Foley & Linton, but presents only 93% of 16S rDNA identity with this genus. The strain *Leptolyngbya* CENA129 (KP835533) is a sister clade of *Calenema* Ramos, Brito & Kaštovský, but presents only 93% of 16S rDNA identity with this genus. The strains CENA340 (KT731157), CENA350 (KR137571), CENA364 (KR137585), CENA321 (KT731142), CENA342 (KT731159) are in a monophyletic sister clade of *Pegethrix* Mai, J.R.Johansen & Bohunická which

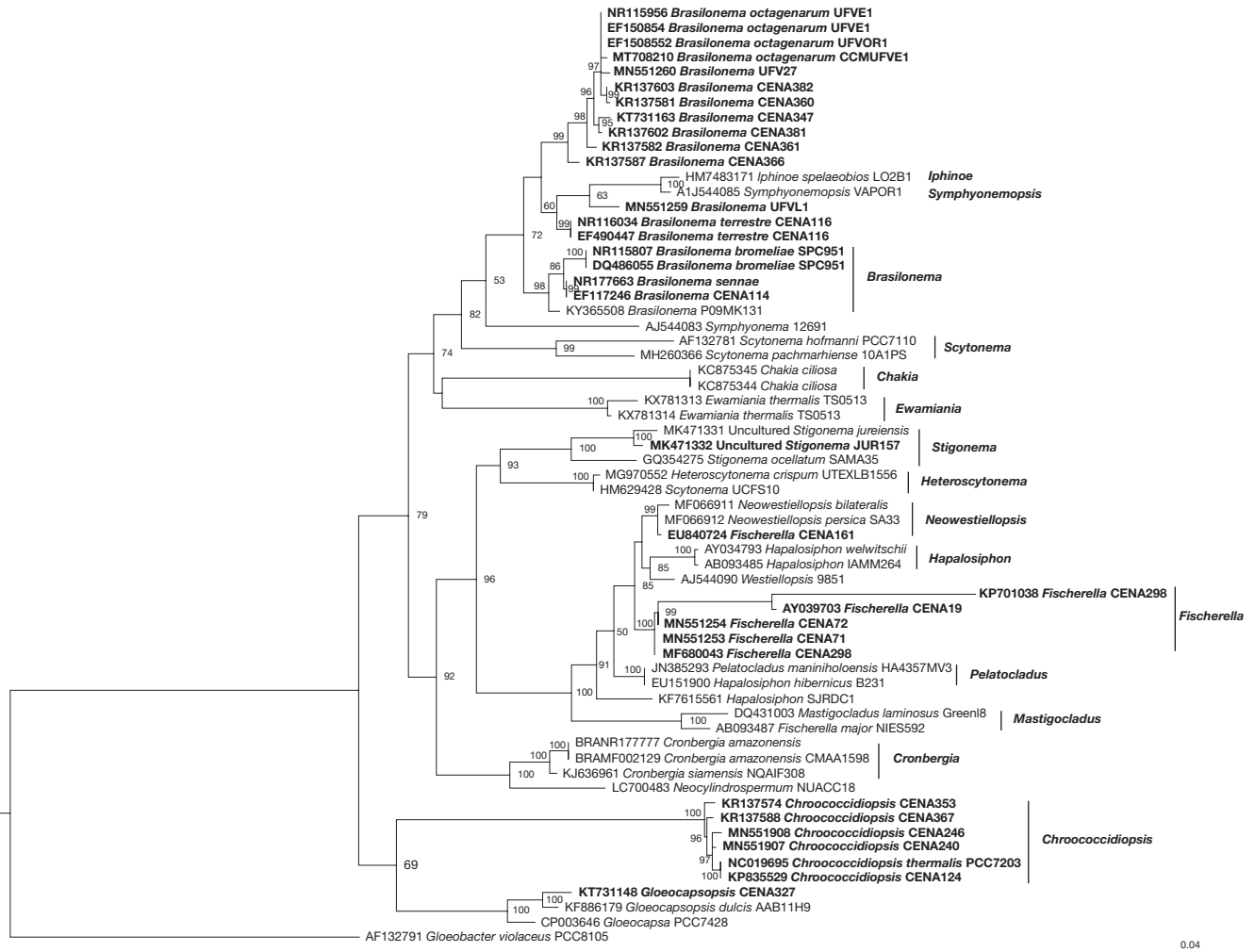


Fig. 4. — Phylogenetic analysis of *Brasilonema* Fiore, Sant'Anna, de Paiva Azevedo, Komarek, Kaštovský, Sulek & Lorenzi and other Cyanobacteria reference strains. Brazilian strains are in **bold**.

presents 95% of 16S rDNA identity with this clade. Although the similarity reaches 95%, it is common that phylogenetically distant genera share this identity level. The strains CENA385 (KR137606) and CENA359 (KR137580) are a sister clade of *Albertania* Zammit which presents only 92% of 16S rDNA identity with this genus.

In the Leptolyngbyales, the strains CENA519 (KF246486), CENA518 (KF246485) are a monophyletic sister clade of *Romeriopsis* Hentschke which presents only 89% of 16S rDNA identity with this genus. *Romeriopsis* was originally described for the family Leptolyngbyaceae (Synechococcales) (Komárek *et al.* 2014), but currently this family is positioned in the order Leptolyngbyales (Strunecký *et al.* 2023). *Romeriopsis* should be transferred to Leptolyngbyales.

In the Oscillatoriales, the strains CENA556 (F084984) and CENA552 (MF084980) are in a monophyletic sister clade of *Sodalinema* Cellamare, Charlotte Duval, Touibi, Djediat & Cécile Bernard which presents only 94% of 16S rDNA identity with this genus.

In the Nostocales, the strain CMAA1611 (MN334196) is a sister clade of *Mastigocladus* Cohn Ex Kirchner and *Fischerella*

(Bornet & Flahault) Gomont, but presents only 94% of 16S rDNA identity with these genera. The strains identified as *Fischerella* CENA298 (KP701038) and *Fischerella* CENA19 (Y039703) are in a monophyletic clade separated from this genus and sharing only 90% of 16S rDNA identity with it. The same occurs with *Fischerella* CENA72 (MN551254), CENA71 (MN551253), CENA298 (MF680043), which are even more distant to the genus. The strain CCMUFV006 (MT708211) is phylogenetically related to *Dulcicalothrix* Saraf, Suradkar, Dawda, Gaysina, Gabidullin, Kumat, I. Behere, Kotulkar, Batule & Prashant, but presents only 92% of 16S rDNA identity with this genus. Moreover, many strains identified as *Nostoc* Vaucher ex Bornet & Flahault, *Scytonema* C. Agardh ex É. Bornet & Flahault, and *Calothrix* Bornet & Flahault are scattered among Nostocales genera and need to be revised.

Finally, the strain *Pseudanabaenaceae cyanobacterium* CENA510 (KF246480) is phylogenetically closely related to *Metis* Philippi, but share only 89% of 16S rDNA identity. Both genera are in an unresolved position between Acaryochloridales, Nodosilineales and Synechococcales.

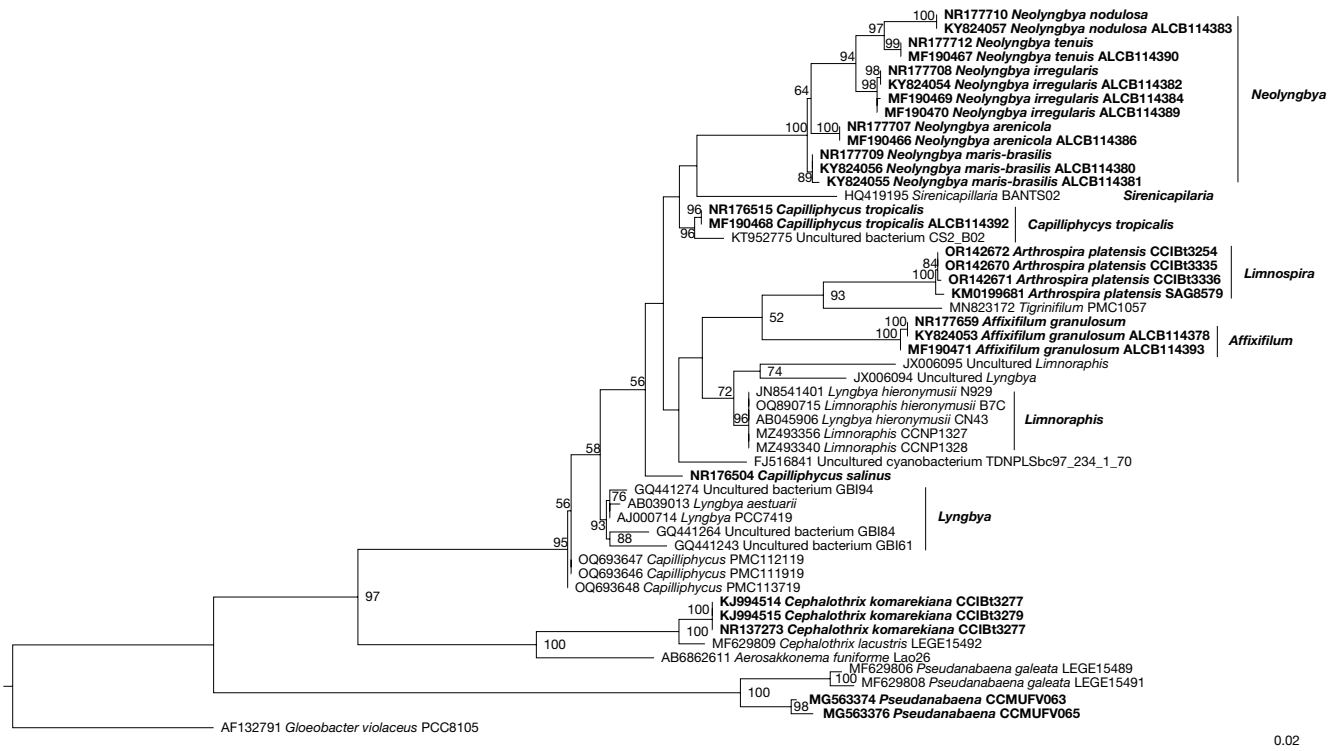


FIG. 5. — Phylogenetic analysis of *Capilliphycus* T.A.Caires, Sant’Anna & J.M.Nunes and other Cyanobacteria reference strains. Brazilian strains are in bold.

Based on the data from this review, we found that even with reduced sampling efforts in small parts of some Biomes, there are many strains in Brazilian culture collections that are still not taxonomically studied. Based on 16S rRNA gene sequences, in our analysis, at least 15 monophyletic clades represent new genera from Brazil, which must be described in the future (Fig. 3). This data reinforces the fact that the Brazilian cyanobacterial diversity is underestimated.

PHYLOGENETIC ANALYSIS OF CYANOBACTERIA

Because of the methodological limitations of our phylogeny (16S rDNA FastTree) (Fig. 3), we cannot make much progress in discussions about order level. Nonetheless, we observed a notably congruent topology between our tree and the phylogenies presented in the review by Strunecký *et al.* (2023). It is evident that the order Nostocales is monophyletic and closely related to Chroococcidiopsidales. The orders Aegeococcales, Thermostrictales and Pseudanabaenales are in a basal phylogenetic position. However, the order Oscillatoriales displays a marked polyphyletic pattern in our phylogeny. This aligns with Komárek *et al.* (2014) but contradicts the findings of Strunecký *et al.* (2023). It is worth highlighting that in the last-mentioned review, the authors employed a more robust phylogenetic approach (ML) utilizing 120 protein sequences to establish the current classification. The 16S rDNA tree presented in that study was built with a constrained topology that is not explicitly specified, making direct comparison with our phylogeny unfeasible.

Nevertheless, the reference strains in our tree are coherent with the currently Cyanobacteria system, considering the order level. Some exceptions can be noticed, such as Spirulinales genera among Chroococcales. In fact, these orders have close phylogenetic relationship according to Strunecký *et al.* (2023). The order Geitlerinematales among Oscillatoriales genera are not a surprise, considering that *Geitlerinema* (Anagnostidis & Komárek) Anagnostidis was former classified in this order by Komárek & Anagnostidis (2005).

LIMITATIONS AND CONCLUSIONS

A limitation of our work is that the FastTree method used to perform our tree is not as accurate as Bayesian analysis. The size of the dataset makes it impossible to run this analysis. Nevertheless, our tree presented a very similar topology at the base, compared to the current classification system.

In order to have better resolution in our phylogeny, we selected only the Brazilian sequences with more than 1200 nucleotides and, because of that, it is obvious that the diversity we presented in this paper is a portion of the total diversity of Brazilian sequences present in GenBank. However, the results we achieved from these data are reliable.

Another limitation was that some 16S rDNA sequences and genomes in NCBI do not have the country of origin indicated in metadata. Because of that these sequences were not retrieved. Also, many sequences of Brazilian strains were MAGs and fragmented, not aligning properly. Because of

that, they were excluded. Another problem with Brazilian genomes was that after BLAST search, we found that many 16S sequences were not Cyanobacteria.

In conclusion, our study reveals the genetic relationships among all the genera found in Brazil, along with a significant number of 16S rDNA sequences derived from Brazilian strains. Based on our phylogenetic analysis, there are strong indications that the diversity of cyanobacteria in Brazil is much greater than previously estimated, and numerous new genera within Brazilian culture collections warrant description. Additionally, we propose that *Capilliphycus* be divided into two separate genera. Another noteworthy aspect is that, considering the limited sampling across Brazilian biomes and the complete absence of molecular tool application in the Pampa biome, targeted sampling efforts could considerably increase the number of newly described taxa. This could have a significant impact on advancing our understanding of cyanobacteria diversity.

Acknowledgements

The authors thank the reviewers and the editor for their careful evaluation of the article.

Statement

During the preparation of this work the authors used ChatGPT/OpenAI in order to correct the English language in some parts of the text. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Authors' contributions

GSH wrote the whole article, performed the bibliographical and sequences review, performed the phylogenies, prepared the tables and figures.

KRSS wrote part of "Introduction" section and revised the text.

LM searched for Cyanobacteria genomes, filtered Brazilian genomes, extracted 16S rDNA sequences and wrote part of "Material and methods" section.

FO worked on the bibliographical review and Appendix 1.

VMV worked on the final revision and found the funding.

Funding

GSH is funded by Programa de Recuperação e Resiliência Português (PRR), Blue Bioeconomy Innovation Pact, Call 02/C05-101/2022, application number C632741873-00467082, and FCT projects UIDB/04423/2020 and UIDP/04423/2020.

Availability of data and materials

Considering that this is a bibliographic review article, the data that support the findings of this study are available in NCBI, Scielo and Web of Science (ISI).

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Submitted on 21 August 2023;
accepted on 14 February 2024;
published on 12 July 2024.

APPENDIX

APPENDIX 1. — Characterization of publications describing new Cyanobacteria taxa from Brazilian samples and culture collections. https://doi.org/10.5852/cryptogamie-algologie2024v45a6_s1