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The Diversity of Soil Cyanobacteria of the Dominican Republic

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Abstract:

This bachelor's thesis investigates the diversity of soil cyanobacteria in the Dominican Republic – a region that remains poorly studied in terms of this group of microorganisms. A total of 22 cyanobacterial samples from three different locations was analysed using molecular methods, including sequencing of the 16S rRNA gene and the 16S–23S ITS rRNA gene region, in order to assign the isolated strains to specific species or genera. Phylogenetic analysis divided the samples into nine distinct phylogroups. Strains from three of these phylogroups were identified into the species or genus level, while the remaining six could not be sufficiently identified, either due to a lack of reference sequences or inadequately corresponding morphological data. These groups likely represent new, previously undescribed species or genera. The results highlight not only the exceptional potential of tropical soils as reservoirs of cyanobacterial diversity, but also the need to revise current taxonomy, which often relies solely on morphological characteristics.

Key Words: 16S rRNA, 16S-23S ITS rRNA, Arid Regions, Biodiversity, Caribbean, Classification, Morphology, Phylogeny, Sequence Analysis, Taxonomy, Terrestrial Environments, Tropics.

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Abstrakt:

Tato bakalářská práce se zabývá diverzitou půdních sinic na území Dominikánské republiky, tedy oblastí, která je z hlediska výzkumu této skupiny mikroorganismů dosud málo probádaná. Celkem 22 vzorků sinic ze tří různých lokalit bylo analyzováno pomocí molekulárních metod, včetně sekvenování genu 16S rRNA a oblasti 16S-23S ITS rRNA, za účelem taxonomického určení do druhů či kmenů. Fylogenetická analýza rozdělila vzorky do devíti odlišných fyloskupin. Kmeny ze tří těchto fyloskupin bylo možné klasifikovat na úrovni druhů či rodů, zatímco zbývajících šest fyloskupin nebylo možné přesně zařadit, a to buď kvůli nedostatku referenčních sekvencí, nebo nedostatečně odpovídajícím morfologickým datům. Tyto skupiny pravděpodobně představují nové, dosud nepopsané druhy či rody. Výsledky ukazují nejen na výjimečný potenciál tropických půd jako rezervoáru sinicové diverzity, ale také na potřebu revize současné taxonomie, která se často spoléhá pouze na morfologické charakteristiky.

Klíčová slova: 16S rRNA, 16S-23S ITS rRNA, aridní oblasti, biodiverzita, fylogenetika, Karibik, morfologie, půdní ekosystémy, sekvenování, taxonomie, tropy.

Declaration

I hereby declare that this bachelor's thesis is my original work, written independently under the supervision of doc. Mgr. Petr Dvořák, Ph.D., and all sources of information and literature have been properly cited within the text and are listed in the reference section.

In Olomouc, on 15 May 2025 …….

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My deepest thanks go to my supervisor, Petr, for his expert guidance and thoughtful insight throughout the course of this thesis. His ability to combine scientific rigor with approachability made working under his supervision both productive and genuinely enjoyable.

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1 Introduction

Cyanobacteria are photosynthetic prokaryotes that play a fundamental role in terrestrial ecosystems by contributing to nitrogen fixation, primary production, and soil stabilization (Isichei, 1990). While their ecological significance is well documented in aquatic environments, the diversity of soil-dwelling cyanobacteria remains deficiently studied; particularly in tropical regions, where complex environmental gradients may support unique and largely undocumented microbial communities.

Despite the ecological richness of the Dominican Republic and its wide range of niches, research into the composition and taxonomy of its soil cyanobacteria remains scarce. Only a small fraction of cyanobacterial studies has focused on tropical environments globally, with just a handful marginally addressing the Dominican Republic — leaving a significant gap in our understanding of the diversity, distribution, and ecological roles of these organisms.

This study addresses this gap by examining the diversity of soil cyanobacteria in the Dominican Republic using a dual methodological framework: morphological analysis and molecular phylogenetics based on 16S rRNA gene 16S–23S rRNA gene region sequencing. Current records based solely on morphological data underestimate the true diversity of cyanobacteria in tropical environments, and discovery trends suggest that numerous species have yet to be identified (Sant´Anna et al., 2011). By focusing on cyanobacteria from soil environments across different microhabitats, this research seeks clearer understanding of their diversity and refine the taxonomic placement of isolated strains.

1.1 Aims and Objectives

The first aim of this thesis was to conduct a comprehensive literature review on cyanobacteria in tropical regions, with a particular focus on soil cyanobacteria in the Dominican Republic. It was done so using research literature relevant to the region. This review was intended to contextualize the experimental findings, highlight previous methodologies and broader studies, and identify gaps in current knowledge about tropical soil cyanobacterial diversity.

The thesis' second aim was to study the diversity of soil cyanobacteria in the Dominican Republic through a combination of molecular and morphological methods. Specifically, this involved the application of 16S rRNA gene and 16S–23S rRNA gene region sequencing to identify cyanobacterial taxa at the genetic level, complemented by morphological analysis using light microscopy. This dual approach exerted to provide a more accurate and holistic understanding of the cyanobacterial communities present in and on Dominican Republic's tropical soils.

2 Geographical Location

The Caribbean is a geographically diverse region between the continents of South and North Americas, comprising over a thousand islands as well as adjacent continental areas. It is often defined by the watersheds that drain into the Caribbean Sea and the Gulf of Mexico, forming what is known as the Greater Caribbean (Draper et al., 1994). The regional islands are grouped into three major archipelagos: the Greater Antilles (including Cuba, Hispaniola, Jamaica, and Puerto Rico), the Lesser Antilles (a chain of smaller islands stretching from the Virgin Islands to Grenada), and the Bahamas.

The Dominican Republic, located between 17° and 19° N latitude, occupies the eastern portion of the Caribbean island of Hispaniola. With a total area of 76 484 km², Hispaniola is one of the largest islands in the Caribbean, sharing geological characteristics with other Greater Antillean islands such as Cuba and Jamaica. The island's steep, rugged terrain developed during the Cretaceous period (130 million years ago) and the Oligocene-Miocene period (50 million years ago), while its valleys are composed from more recent Quaternary deposits (Cano et al., 2012). Dominant geological materials include karstic limestone, marls, and siliceous serpentine rocks (Lugo et al., 2012).

The Dominican Republic, which spans across 48 921 km², is largely mountainous — about 80% of its territory is covered by five northwest-to-southeast mountain ranges; Cordillera Central being the most prominent. This range is home to Pico Duarte (3 175 m above mean sea level), the highest mountain in the Caribbean, along with other notable peaks like La Pelona and La Rucilla. The island's complex topography and minor volcanic activity originate from its siting along the northern boundary of the Caribbean tectonic plate, which subducts beneath the North American plate, shaping its distinctive geological and geomorphological features (Carmona & Ortiz, 2012). In contrast to its towering peaks, the country's lowest point is Lago Enriquillo, lying 40 metres below mean sea level.

2.1 Tropical Climate and Weather Patterns

In attribution to the Dominican Republic's equatorial geographical position, the Sun passes directly overhead for most of the year, resulting in solar radiation levels nearly twice as intense as those experienced in temperate regions (Ortiz et al., 2015). The mean yearly temperatures generally span from 24 °C to 27 °C, with little to no seasonal fluctuation (Cano et al., 2012). The distribution of rainfall, however, shows strong

seasonal variation. Wet season, extending from May through November, is accompanied by unique weather patterns. One of these weather patterns is periodic hurricanes, which originate from the encounter of west and east trade winds along the equator, and ensure the delivery of moisture in the tropics (Guinn & Schubert, 1993). Areas supplied with higher rainfall are mountain ridges, where annual precipitation reaches above 2 500 mm, whereas midland wet seasons only last 2 months (Cano et al., 2012; Cano et al., 2014).

Interactions of all these climatic elements create a multitude of ecosystems. Humid montane vegetations and vast rainforests, as well as arid savannas, and semiarid bushlands (Sarmiento, 1976; Anadón-Irizarry et al., 2012). These, together with high mean temperature and abundant rainfall, create conditions that support a diverse range of biological life. The island's isolation from mainland insured that certain species had evolved exclusively and now exist nowhere else on the planet (Cano et al., 2013). Especially when it comes to local flora. The abundance of endemic species tends to rise with elevation, as higher altitudes provide specific ecological conditions that favour their growth. Highland regions shelter more extensive varieties compared to more uniform ecological settings found in the lowlands (Cano-ortiz et al., 2016). The fact that around 34% of plant species are endemic — most of them from the family *Melastomataceae*; highlights how important the island of Hispaniola is as a biodiversity hotspot (Myers et al., 2000; Cano et al., 2014).

3 Cyanobacteria

Cyanobacteria constitute a remarkably diverse group of photosynthetic prokaryotes capable of oxygenic photosynthesis using chlorophyll *a* (Cohen et al., 1986; Garcia-Pichel, 2009). They play a vital role in ecosystems and thrive in a wide range of habitats that are often inhospitable to other life forms (Whitton & Potts, 2000).

Cyanobacteria are some of the oldest life forms still living on Earth. Fossil evidence records their existence as early as 3.5 billion years ago (Schopf, 2006). During the Paleoproterozoic, approximately 2.4 billion years ago, one of the most significant changes in Earth's history occurred due to their ability to carry out oxygenic photosynthesis (Canfield et al., 2000; Lyons et al., 2014).

This process, in which cyanobacteria use solar energy to produce organic matter while releasing oxygen, had the biggest impact on the composition of the atmosphere (Fay, 1992). Oxygenic photosynthesis led to gradual release of molecular oxygen, which ultimately transformed the once anaerobic conditions, characterized by a high content of methane, to an oxygen-rich atmosphere (Pierson, 1994). This pivotal shift laid foundation for an environment fit for advanced life forms and opened the way for the evolution of aerobic organisms, which began to use oxygen for energy purposes. This "oxygen miracle" had far-reaching ecological and climatic consequences, as it significantly influenced the chemistry of the oceans and atmosphere, and thus the global climate (Bekker et al., 2004).

Their long evolutionary history has endowed them with remarkable resilience and adaptability, enabling them to achieve a (sub)cosmopolitan distribution, and even act as pioneers in colonizing new or extreme environments (Golubic et al., 2000; Ribeiro et al., 2018). They can withstand a broad spectrum of stressful conditions, including highly acidic or alkaline pH, temperature extremes from below freezing to above 110 °C, intense solar radiation or near pitch darkness, saturated salinity, and prolonged aridity (Stal, 2007).

Cyanobacteria inhabit common environments – soil, fresh water, marine ecosystems, plant surfaces, and rocks; as well as extreme environments, such as volcanic ash, glaciers, deserts, acidified soils, hot springs, and swamps (Jaag, 1945; Komárek, 1989; Dor & Danin, 1996; Whitton & Potts, 2000). For example, genus *Argonema* thrives in both Bohemian stream valleys and dry soils in western Antarctica, maintaining

an almost identical distribution pattern in these vastly different environments (Skoupý et al., 2022). Species belonging to the family *Oscillatoriaceae* have been observed growing on glaciers in Greenland (Uetake et al., 2010). *Arthrospira fusiformis* forms dense blooms on highly alkaline lakes in Kenya (Cirés et al., 2017). *Mastigocladus laminosus* prospers in thermal springs across the planet, from Karlovy Vary to Yellowstone National Park, and *Oscillatoria limnetica (Phormidium hypolimneticum*) was found in a hypersaline Egyptian lake with salinity reaching 15% and temperatures up to 55 °C (Komárek, 2003; Seckbach et al., 2007; Kaštovský & Johansen, 2008).

3.1 Morphology, Adaptations and Physiology of Cyanobacteria

Prokaryotic organisms are distinguished from eukaryotes by the absence of a defined nucleus and membrane-bound organelles. As a result, they lack complex internal structures, such as the Golgi apparatus, mitochondria, and endoplasmic reticulum. Instead, their genetic material, DNA fibrils, floats freely within the cytoplasm, not bound by a nuclear envelope. Their photosynthetic structures, known as thylakoids, are likewise not enclosed within chloroplasts, but exist unbound in the cytoplasm. Additionally, prokaryotes often carry small circular DNA molecules called plasmids, which provide adaptive advantages, such as antibiotic resistance or metabolic versatility, and their endosymbiotic origin is commonly traced back to cyanobacteria (Douglas, 1994; Hoek et al., 1995)

Cyanobacteria represent one of the most morphologically diverse groups of prokaryotes, earning them a reputation as exceptionally plastic microorganisms. They are capable of existing as simple unicellular forms, but also form colonies or more complex multicellular structures (Hoek et al., 1995). They take on a variety of shapes. From spherical, rod-shaped, and spiral to filamentous forms, which are often embedded in gelatinous or mucilaginous sheaths that protect them and also help them attach to surfaces (Singh & Montgomery, 2011). Cell sizes can range from no more than 0.3 μm up to 40 - 60 μm in diameter, and their thylakoid membranes, the site of photosynthesis, can be arranged in layered or spiral patterns within the cell (Albrecht et al., 2006; Schulz-Vogt et al., 2007).

Variations in cell morphology often correlate with ecological niches and environmental adaptations. For example, *Synechococcus* species are usually small and round, hence the name *coccus*; while *Oscillatoria* form long, almost thread-like filaments, and move in oscillating motion. Coccoid species tend to be smaller, and more

suited for pelagic environments, while sheathed filamentous forms, such as *Oscillatoria*, are adapted to harsher benthic habitats (Dvořák et al., 2017).

Cyanobacteria, like other Gram-negative bacteria, have a cell wall composed primarily of peptidoglycan, a mesh-like polymer made of sugars and amino acids, which provides mechanical strength, helps maintain the shape of the cells, and enables them to withstand external stress conditions, such as changes in osmotic pressure or physical damage (Hoek et al., 1995). In addition to this structural support, the internal cytoskeleton, made of specific proteins, also plays an important role in moulding the shape of cells. The presence or absence of these cytoskeletal elements affects whether cells are spherical, oval, or elongated; and thus their ability to move, organize into fibres, or adapt to a given environment (Springstein et al., 2020).

Cyanobacterial vegetative cells also possess the ability to form several types of specialized cells, that allow them to survive and thrive in different ecological conditions. Heterocysts are terminally differentiated cells with a thick outer layer that serve to fix nitrogen. This adaptation is essential for cyanobacteria living in environments where nitrogen is scarce, yet needed. Hormogonia are motile, filamentous structures that provide attachment to host organisms, such as plants and other microorganisms. When environmental conditions are favourable, hormogonia can rapidly expand and transform into new generations of filaments (Meeks & Elhai, 2002). Akinetes are dormant cells that retain viability even under adverse conditions, like drought. Once moisture returns, akinetes initiate formation of new vegetative cells, consequently allowing cyanobacteria to survive periods of extreme drought, and resume growth under more favourable conditions (Flores & Herrero, 2009).

Cyanobacteria reproduce asexually via binary fission or budding (Waterbury, 2006). In binary fission, individual cells enlarge and transversely divide into identical daughter cells inside the parent cell (Hoek et al., 1995). This method ensures efficient reproduction and colonization. Hormogonia and akinetes may also support the growth of new populations in less suitable and stress conditions.

Cyanobacteria contain pigments. Most notably chlorophyll *a*, carotenoids, phycocyanin, and phycoerythrin, that, through their light-harvesting functions, facilitate photosynthesis and give them their typical blue-green colour (Carr & Whitton, 1982). Chlorophyll *a* molecules are located within the thylakoid membranes, where they enable the process of oxygenic photosynthesis. Carotenoids provide protection against oxidative

stress, and phycocyanin and phycoerythrin are specific pigments that help cyanobacteria capture light even in lower light intensity or in various types of aquatic ecosystems (Saini et al., 2018).

3.1.1 Nitrogen Fixation

Cyanobacteria play a significant role in the nitrogen cycle through nitrogen fixation, diazotrophy, converting atmospheric nitrogen (N_2) into metabolically accessible forms like ammonia (NH_3) and ammonium (NH_4^+) (Fay, 1992). This process is needful for primary productivity in ecosystems, because plants need nitrogen as a precursor for DNA synthesis (Chamizo et al., 2018).

Cyanobacteria have adopted a plethora of mechanisms to accomplish nitrogen fixation. Given that the process is highly sensitive to oxygen, genera such as *Nostoc* and *Anabaena* differentiate specialized heterocysts. These cells, encased within thick, hyaline layers, forge a microenvironment free of oxygen, thereby safeguarding the nitrogen-fixing enzymes (nitrogenase complex) from oxidative damage and ensuring the uninterrupted flow of this vital biochemical pathway (Bustos-Díaz et al., 2019). On the other hand, non-heterocyst species like *Trichodesmium* sp. and *Crocosphaera* sp. use temporal separation of photosynthesis and nitrogen fixation. This mechanism prevents the formation of oxygen in the cells during fixation, effectively preventing its negative impact (Nawaz et al., 2024).

3.1.1.1 Symbiotic Relationships

Cyanobacteria form a variety of symbiotic relationships that perfect their nitrogen-fixing capacity and contribute to nutrient cycling in both natural ecosystems and agriculture. These partnerships allow cyanobacteria to thrive in diverse environments while providing their hosts with biologically available nitrogen (Villareal, 1992). One of the most notable examples is the symbiosis between the aquatic fern *Azolla* and the cyanobacterium *Trichormus azollae* (Peters, 1991). In this mutualistic relationship, the cyanobacterium resides in specialized leaf cavities of *Azolla*, supplying it with fixed nitrogen.

Symbiotic relationships are key to nitrogen fixation by some cyanobacteria. These microorganisms can exist either endophytically (living inside plant tissues), or as epiphytes (growing on plant surfaces), and their nitrogen fixation supports agricultural sustainability by reducing synthetic fertilizer dependence (Nawaz et al., 2024).

Endophytic cyanobacteria like *Nostoc punctiforme*, *Nostoc azollae*, and *Anabaena cycadae* inhabit plant species, spanning hornworts, ferns, and cycads. For example, *Nostoc azollae* symbiotically inhabits the leaf cavities of *Azolla*, while *Anabaena cycadae* resides in the coralloid roots of cycads. Some species of *Anabaena* and *Aphanothece* genera form symbiotic relationships with rice crops, and because they supply the crop with essential growth compounds, are used as biofertilizers (Dash et al., 2016).

Cyanobacterial symbioses promote biofertilization by directly transferring fixed nitrogen to plants. Beyond nitrogen fixation, these symbiotic relationships offer additional benefits by enhancing plants' ability to withstand environmental stress through phytohormone and antioxidant production (Álvarez et al., 2023; Nawaz et al., 2024).

Epiphytic cyanobacteria – *Gloeothece*, *Leptolyngbya*, and *Phormidium*, form colonies on plant roots and surfaces, adding to plant health through nutrient exchange and pathogen protection (Dey et al., 2022). Another well-documented symbiosis involves the genus *Nostoc* and *Ascomycota* fungi, resulting in the formation of cyanolichens (Rikkinen, 2015). Here, *Nostoc* sp. provides nitrogen to the fungal host while receiving protection and structural support for growth.

Cyanobacteria also establish symbiotic relationships with marine organisms, such as *Porifera* (sponges) and diatoms, contributing to oxygen production in aquatic ecosystems (Konstantinou et al., 2018). These associations are ecologically significant, supporting nutrient availability and productivity in otherwise nitrogen-poor environments. Unicellular cyanobacterium *Candidatus Atelocyanobacterium thalassa* is a major participant in the global marine diazotrophy, achieving high rates of biological nitrogen fixation at ocean surface through its symbiosis with single-celled algae (Vieyra-Mexicano et al., 2024).

3.2 Soil Cyanobacteria

Soil is a dynamic and complex system that serves as a habitat and gene reservoir (Blum, 2005). According to predictions by Locey and Lennon (2016), soil is home to more than 10^{12} microbial species, and soil cyanobacteria are a specialized group, which lives on or within terrestrial surfaces, exposed to the atmosphere such as rocks, soils, or plant litter.

Although cyanobacteria have mainly garnered attention for ecological importance in aquatic systems, their roles in terrestrial ecosystems are equally significant. Beyond decomposition – primarily carried out by fungal hyphae, soil cyanobacteria improve soil structure by binding particles and supporting key processes like nitrogen fixation and carbon availability all of which contribute to overall ecosystem stability (Wen et al., 2023). Cyanobacteria also play a vital role as primary producers in the food chain. By releasing organic acids, exopolysaccharides, and bioactive compounds, they provide energy sources for other bacteria, fungi, and invertebrates, and stimulate activity in the soil matrix (Newton, 2007; Sudharsanam et al., 2019).

As obligate photoautotrophs, cyanobacteria rely exclusively on light to oxidize inorganic substrates and fix carbon dioxide, a process that underpins their high densities in the upper soil layers where sunlight is most accessible. This density tends to decrease with depth, as light availability diminishes (Belnap & Lange, 2001; Román et al., 2018). The distribution of cyanobacteria in these upper layers creates a unique vertical stratification, fostering the development of microhabitats that support diverse soil microbiota (see Fig. **1**). These microhabitats play a crucial role in the formation of biological soil crusts (BSCs), mats, and biofilms, which are essential components of soil ecosystem services (Sanchez, 2019).

Soil cyanobacteria show remarkable resilience to extreme environmental pressures. Their ability to thrive under a wide range of stressors, including prolonged drought, extreme temperature fluctuations and intense UV radiation, makes them dominant in arid tropical regions. In these regions, they colonize not only soils but also subaerial spaces – cavities, cracks, and pores in rocks; and act as pioneers on exposed, susceptible surfaces, where they help combat erosion, pollution caption, stabilisation, and support nutrient cycling (Rampelotto, 2013). However, climate change and increasing environmental stressors pose a threat to their ecological functions.

Genera *Leptolyngbya*, *Microcoleus*, *Nostoc*, and *Scytonema* are widespread across heterogeneous soil habitats, each displaying unique adaptations that enable their survival and function within the soil matrix (Dvořák et al., 2015; Roncero-Ramos et al., 2022). And cyanobacterium *Gloeocapsa* sp. can settle in weathering cracks in limestone sediments, and over time contributes to substrate decomposition and new ecosystem development (Czerwik-Marcinkowska et al., 2015).

3.2.1 Biological Soil Crusts

Biological soil crusts (BSCs) are surface communities formed by soil biota and found in deserts, savannas, temperate zones, and polar regions. Cyanobacteria, along with algae, lichens, bryophytes, and microfungi weave throughout the top few millimetres of soil, binding together soil particles (Belnap & Lange, 2001). Biological soil crusts can be classified into three main forms: hypermorphic – found above ground, perimorphs at ground level, and cryptomorphic forms, which are hidden beneath the soil surface (Eldridge & Greene, 1994). A topographic classification of biological crusts further divides them into four types: smooth, rugose, pinnacled, and rolling, based on surface features and predominant organisms.

Smooth crusts, found in hot deserts with non-freezing soils, primarily consist of endedaphic (living in soil) cyanobacteria, algae, and fungi. Rugose crusts, typically formed in moister temperate regions, feature scattered clumps of lichen and moss, though can also be dominated by filamentous blue-green algae. Pinnacled and rolling crusts are typically seen in regions with frozen soils, where frost heaving gives rise to unique coverings of moss and lichen (Belnap & Lange, 2001).

Like biofilms, biological soil crusts endure frequent wet-dry cycles. Moisture promotes microbial activity, photosynthesis, and soil stabilization, while dry periods lead to dormancy, reducing metabolic activity and making the crusts more vulnerable to erosion. These cycles are essential for the resilience and function of BSCs in arid ecosystems, where they typically form after monsoon rains, as cyanobacteria undergo dormancy in response to dry season (Büdel, 2011).

Biological soil crusts cover up to 12% of the land, and cyanobacteria play a central role in their formation and function. They dominate the early stages of ecological succession, stabilizing the soil and preventing erosion through the production of polysaccharide sheaths (Büdel et al., 2016; Chen et al., 2023). They also enhance soil

fertility by fixing carbon and nitrogen. Beyond soil stabilization, they regulate water retention, reduce erosion, and promote biodiversity by creating homes for other organisms (Warren et al., 2021). They can also function as networks for nutrient transport.

Biocrust cyanobacteria can be categorized into three distinct groups based on their roles and habitat preferences (Ullmann & Büdel, 2003). Filamentous cyanobacteria, such as *Calothrix* and *Microcoleus*, stabilize soils and are responsible for biocrust primary formation. These cyanobacteria tend to thrive in fine-textured soils, where their polysaccharide sheaths act both as protective shields and adhesives that bind soil particles together. These cyanobacteria successfully pioneer in the biostabilization process (Garcia-Pichel & Wojciechowski, 2009). According to Johansen and Shubert (2001), *Microcoleus vaginatus* is the most abundant species in crusts and often acts as the first colonizer for other species to appear.

As biocrusts mature, the microbial community shifts; cyanobacterial decline in abundance, while fungi, mosses, and other bacteria – *Geodermatophilaceae* and *Bacillaceae*, become more prominent (Tirkey & Adhikary, 2005; Maier et al., 2018). Some cyanobacteria do not partake in the creation of these biocrusts and only use them as sanctuaries, while still contributing to nitrogen cycling and decomposition. These are generally spherical in form and habitual in coarser substrates (Hakkoum et al., 2021). Examples include *Chroococcidiopsis*, *Scytonema*, and *Stigonema*. Lastly, cyanobacteria that only randomly occur in biocrusts, possibly originating from other habitats, for instance aquatic environments or lichen symbiosis. This group includes *Chroococcus* sp., *Gleocapsa* sp., *Gloeocapsopsis* sp., *Cylindrospermum* sp., *Tolypothrix* sp., and many *Phormidium* species (Bhatnagar et al., 2008).

Cyanobacterial biodiversity in temperate soils is best documented in the forest zones of Eurasia. In oak and pine forests, common species include *Desmonostoc muscorum*, *Nostoc punctiforme*, *Microcoleus autumnalis*, and *Leptolyngbya foveolarum*. In contrast, broad-leaved forests are dominated by species *Trichocoleus hospita* and *Myxosarcina* cf. *tatrica* (Komárek & Anagnostidis, 1995; Anagnostidis, 2001).

In colder climates mosses are the leading inhabitants of soil crusts, playing a leading role in their structure and function, and otherwise common crust-forming genera like *Nostoc*, *Scytonema*, or *Stigonema* are present in smaller quantities. According to Namsaraev (2010), cyanobacteria may once again dominate phototrophic crusts in the extreme polar regions, including both the Arctic and Antarctic, which together

encompass approximately 14% of the Earth's biosphere. Remarkably, these resilient organisms have been found to survive even in the permafrost as deep as 15 metres below the surface (Friedmann & Ocampo, 1976).

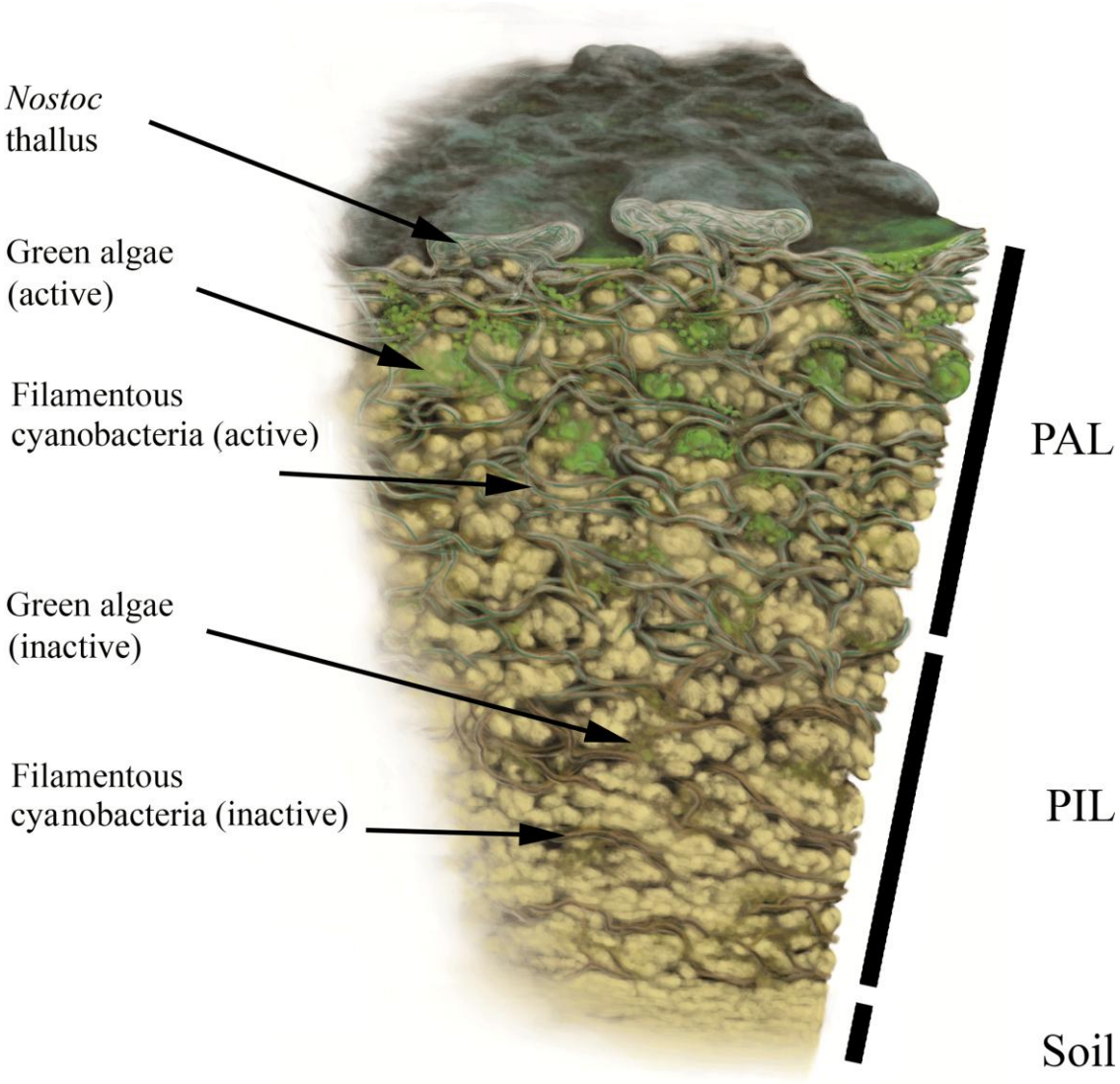

Figure **1**: Illustration of a vertical cross-section of a BSC showing photosynthetically active (PAL) and inactive forms of microorganisms (PIL). Reproduced from Jung et al. (2018).

3.2.2 Environmental Factors and Soil Cyanobacteria

3.2.2.1 pH

Soil pH is a critical factor influencing the growth, establishment, and diversity of cyanobacteria (Hoffmann, 1989). Cyanobacteria generally thrive in poor, sandy soils with a neutral to slightly alkaline pH levels. In soils with alkaline conditions (pH 9 - 10), representative cyanobacterial genera such as *Microcoleus*, *Phormidium*, and *Nostoc commune* are frequently observed, particularly in regions of the former USSR (Gaysina et al., 2019). In contrast, cyanobacteria are generally absent from strongly acidic soils, especially those with pH values below 4 - 5. Nevertheless, several extremophilic filamentous taxa, including members of *Oscillatoria*, *Limnothrix*, and *Spirulina* genera, have been reported in highly acidic habitats, such as Bavarian lakes, where pH levels can drop as low as 2.9 (Seckbach et al., 2007).

3.2.2.2 Water

The growth and ecological performance of soil cyanobacteria are closely tied to the presence and dynamics of water. Even minimal hydration – from dew, fog, or light rainfall; can activate photosynthesis, once soil moisture exceeds 14%. Yet, their metabolic response is not solely about water presence; it's also shaped by how often and how much water is available, as well as local factors, such as soil structure and surface variation (Strong et al., 2013).

Cyanobacteria in gravel substrates are well-equipped to endure dry conditions, employing features like protective sheaths and dormancy to survive until moisture returns. In regions like semi-deserts, species such as *Nostoc flagelliforme* often remain in a dormant state during short-lived wet periods, unable to complete their life cycles until more favourable conditions arise (Whitton & Potts, 2007).

3.2.2.3 UV

As a result of their invasion of terrestrial habitats, cyanobacteria tolerate a broad range of photosynthetically active radiation, from intense sunlight to dimly lit caves, where they are often the only phototrophs capable of colonizing. While UV-A radiation (320 - 400 nm) is very important for the production of oxygen, thus for the process of photosynthesis, UV-B (280 - 320 nm) radiation damages DNA molecules by forming lesions, for instance cyclobutane pyrimidine dimers (CPDs) in pyrimidine nucleobases,

that impair DNA replication and transcription (Garcia-Pichel & Castenholz, 1993; Rastogi et al., 2014).

To survive harsh conditions, cyanobacteria use several strategies to protect themselves from UV damage. One is avoidance and migration by negative photokinesis, i.e. away from irradiation. Second is production of special UV-blocking compounds. These compounds include mycosporine-like amino acids, pigment scytonemin, enzymes, and non-enzymatic defences (Rastogi et al., 2014).

MAAs, mycosporine-like amino acids, act like sunscreen metabolites which form a protective layer around the cell. These compounds are always present, but become active when exposed to UV light at around 320 nm (Sommaruga et al., 2009). Another compound, the pigment scytonemin, found in the extracellular sheath, has been confirmed to function as a UV sunscreen by absorbing a broad spectrum of ultraviolet and violet wavelengths.

Antioxidative enzymes – superoxide dismutase and catalase (CAT); help protect cells from damage caused by reactive oxygen radicals. Superoxide dismutase first converts harmful superoxide radicals into hydrogen peroxide (H_2O_2) and oxygen. Catalase then breaks down the hydrogen peroxide into water and oxygen. Together, these enzymes prevent oxidative damage and help maintain cellular health (Pathak et al., 2019). And non-enzymatic defences, in form of vitamin A, C, E, and carotenoids, reduce oxidative stress and stabilise cell structures (Garcia-Pichel & Castenholz, 1993). Along with UV-absorbing sheath pigments, they help cyanobacteria survive in exposed environments (Carr & Whitton, 1982).

3.2.2.4 Temperature

Soil cyanobacteria demonstrate physiological sensitivity to temperature, with optimal growth typically ranging between 21 °C to 30 °C. As desert temperatures drop sharply in late autumn, soil cyanobacteria must level with certain fluctuations that happen in winter months. These shifts can be detrimental when temperatures fall below −5 °C, as intracellular water may freeze and harm cellular structures. Gradual exposure to repeated temperature fluctuations led to successful acclimation (Wang et al., 2013). This adaptive process seems to rely on three key strategies: raised production of extracellular polysaccharides (EPS) to shield cells from thermal extremes. These EPS are polymers consisting of monosaccharide or disaccharide units connected by glycosidic bonds,

and can take on various morphological forms, such as capsules that surround individual cells and soil particles, or loose sheaths and slime layers, that envelop entire colonies (Mager & Thomas, 2011). Then shifting the balance of light-harvesting pigments to ensure efficient light capture for photosynthesis while minimizing UV damage, and upregulation of antioxidant defences. Notably, cyanobacterial soil crusts with lighter pigmentation have higher tolerance to these temperature shifts, compared to their darker counterparts (Wang et al., 2013).

3.2.2.5 Phosphorus

Phosphorus is an important nutrient for vital metabolism function for soil cyanobacteria, but its availability is oftentimes limited for low solubility. Despite soils containing significant amounts of phosphorus, only a small portion (<2.5%) is accessible to plants and microbes. Cyanobacteria have evolved mechanisms to efficiently accumulate inorganic phosphate and utilize it in their metabolic pathways. In conditions of phosphorus deficiency, cyanobacteria outcompete other bacteria and break down mineral phosphate rocks to form phthalic acid, which helps them solubilize the phosphorus they need for growth. Additionally, they synthesize polyphosphates, which not only help them store phosphorus for future use, but also promote healthy plant root growth (Afkairin et al., 2021).

3.3 Cyanobacteria in Tropics

The rich diversity of habitats in the tropics provides life for not only endemic species but also for a wide range of non-endemic organisms (Lugo et al., 2012). Both aquatic and terrestrial ecosystems enable the development of a wide variety of microorganisms, with cyanobacteria among them. The tropical warmth and irradiation promote exceptional photosynthetic activity and growth rates, which allow these microorganisms to thrive together with other primary producers such as phytoplankton (Vasconcelos & Pereira, 2001). Despite their importance, they remain understudied compared to other microbial groups. According to Dvořák et al. (2015), out of a total of 9 066 scientific papers on cyanobacteria, only about 3% focus on their tropical diversity, indicating a significant research gap in this area (see Fig. **2**).

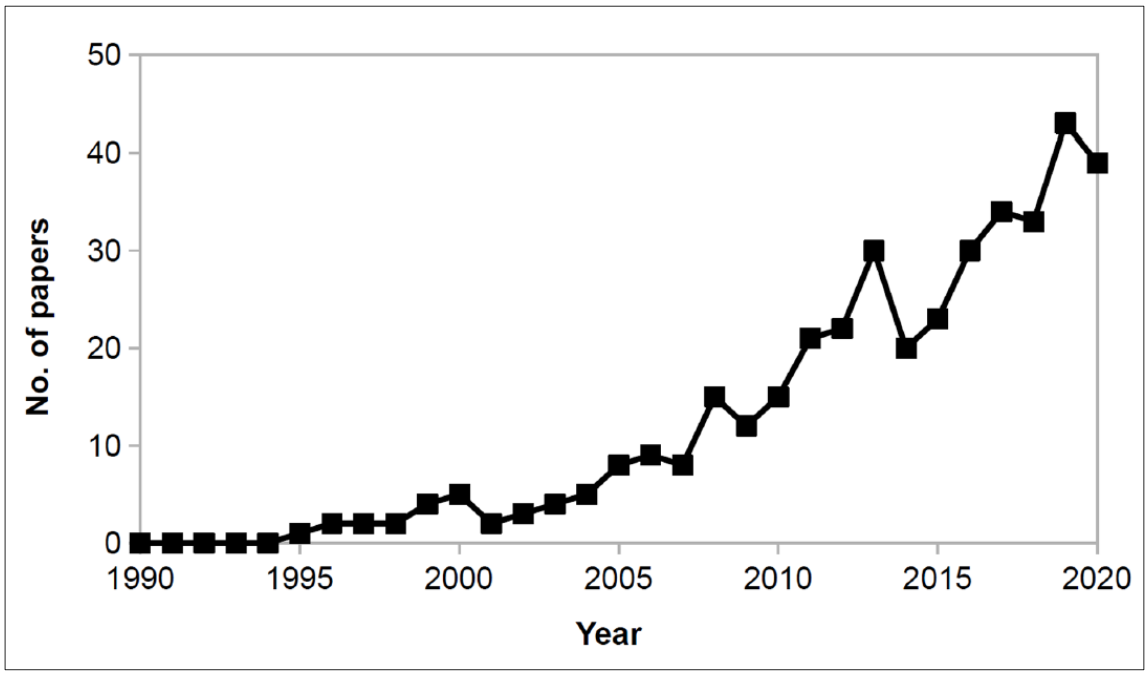

Figure **2**: Annual number of Web of Science publications on tropical cyanobacterial diversity (as of February 2021). Adapted from Dvořák et al. (2021).

3.3.1 Tropical Marine Cyanobacteria

Although presence of cyanobacteria in the Caribbean region helps the ecological equilibrium, they are more likely be associated with their negative impact. Such as black band disease and algal blooms.

Black band disease (BBD) occurs as a coral disease where a black circular mat forms on coral surfaces and exudated cyanobacterial toxins cause tissue necrosis. The infection is triggered by a consortium of filamentous cyanobacteria, in main measure the species *Phormidium corallyticum* and *Roseofilum reptotaenium* (Frias-Lopez et al., 2003; Casamatta et al., 2012). The presence of anthropogenic impacts like urban development and pollution from agricultural runoff has caused eutrophication in numerous Caribbean water bodies, and excessive accumulation of nutrients leads to harmful algal blooms (Wielgus et al., 2010).

In tropical coastal waters nutrient runoff, especially phosphorus from agriculture, has become a powerful trigger for dangerous cyanobacterial blooms. Species such as *Nodularia spumigena* and *Anabaena circinalis* cause hundreds of kilometres long bloom veils in Western Australia and the Baltic Sea. These blooms destabilize aquatic ecosystems, and through cyanobacterial toxins threaten fish mortality and human health, and due to El Niño events and climate change, that alter water flushing rates, are expected to dramatically increase (Griffith & Gobler, 2020).

Studies show the presence of 76 genera and 119 species in Caribbean marine waters alone (Vargas et al., 2023). Notable marine cyanobacteria genera include *Aliterella, Caldora*, *Capilliphycus*, *Dapis*, *Jacksonvillea*, *Lyngbya*, *Nunduva*, *Okeania*, *Phormidium*, *Symploca*, *Richelia*, and *Zehria* (Gosliner, 2004; Thacker & Paul, 2004; Komárek & Anagnostidis, 2005; Komárek et al., 2014; Engene et al., 2015; Gutiérrez Salcedo et al., 2015; Rigonato et al., 2016; Hašler et al., 2017; Engene et al., 2018; Gonzalez-Resendiz et al., 2018; Caires et al., 2019). These genera have been associated with various aquatic habitats, from coral reefs, coastal bays and mudflats, marshes, to mangrove ecosystems. Species of *Lyngbya*, *Okeania*, *Phormidium*, and *Spirulina* genera have been documented as regular contributors to algal blooms (Acosta, 2014). And other species causing large-scale blooms in the Caribbean include *Schizothrix mexicana*, *Cyanothece* strains related to *Synechococcus* and *Bradyrhizobium jicamae*, and the red alga *Metapeyssonnelia corallepida* (Ballantine et al., 2008; Olson & Lesser, 2013; Vargas et al., 2023).

Cyanobacteria are an indispensable part of the biodiversity of the Caribbean region, especially in marine ecosystems, where they spearhead the nitrogen fixation frontier, and provide nutrients for phytoplankton and zooplankton (Anadón-Irizarry et al., 2012).

3.3.2 Tropical Freshwater Cyanobacteria

Cyanobacteria are widely distributed across the tropical freshwater bodies and brackish ecosystems. They are especially successful in shallow aquatic environments – marshes, lakes, rivers, and streams; where sunlight can penetrate to the bottom (Paerl, 1996; Scott & Marcarelli, 2012). Although *Planktothrix rubescens* can grow in light-deprived depths (Walsby et al., 2004).

Freshwater cyanobacteria frequently establish varying microbial communities, referred to as periphyton or biofilms (Azim & Asaeda, 2005). Such communities adhere to different submerged surfaces: stones, aquatic vegetation, and sediments. In some situations, fragments of these attached communities become buoyant and form surface-floating microbial layers (Zohary et al., 1998).

Planktonic blooms are quite common; for instance, heavy rainfall can lead to surges in *Trichodesmium* populations (Fogg, 1991). This red-pigmented species is responsible for blooms across the whole region, including in Belize, Puerto Rico, Mexico, and Colombia (Hoffmann, 1999; Navarro et al., 2000; Hernández-Becerril et al., 2007; Webb et al., 2022).

Genera such as *Calothrix*, *Dolichospermum*, *Hapalosiphon*, *Leptolyngbya*, *Limnothrix*, *Microcystis*, *Nodosilinea*, *Nostoc*, *Phormidium*, *Scytonema*, *Schizothrix*, and *Symploca* appear in benthic freshwater bodies of the Dominican Republic (Komárek & Anagnostidis, 2005; Vargas et al., 2023; Fernandez et al., 2025). *Leptolyngbya* and *Schizothrix* are typically found in marshes, often alongside *Trichodesmium*. The genus *Phormidium* is prevalent in shallow waters (Komárek & Anagnostidis, 2005); while *Microcystis* is more commonly observed in lakes, where it lends to nitrogen balance. *Nodosilinea* and *Symploca* species are generally free-floating, but may also adhere to submerged rocks (Perkerson III et al., 2011). *Calothrix* often graces wet rocks (Jones, 1992).

3.3.3 Tropical Soil Cyanobacteria

Biological soil crusts are present everywhere, but strikingly frequent in arid and semi-arid regions; however, the composition of microorganisms within them varies with climate. In extremely dry environments, such as the Sahara and Atacama deserts, cyanobacteria are the predominant crust-formers, while in more humid regions, their role is gradually overtaken by mosses and lichens (Connon et al., 2007).

Soil-associated cyanobacteria display a diverse array of morphological forms, with the predominant population comprising coccoid morphologies, belonging to the order *Chroococcales*, and filamentous structures, classified within the orders *Oscillatoriales* and *Nostocales* (Whitton & Potts, 2007; Singh et al., 2016).

In tropical sandy soils of arid regions, biological soil crusts are dominated by cyanobacterial taxa including *Klebsormidium*, *Zygogonium*, *Symplocastrum purpurascens*, and *Nostoc commune*. Common soil-dwelling cyanobacterial species in the Caribbean region also include *Phormidium* sp., *Oscillatoria* sp., *Scytonema* sp., *Microcoleus* sp., *Calothrix* sp., *Schizothrix* sp., *Lyngbya* sp., and *Pseudanabaena* sp. (Anagnostidis, 2001; Maya & López-Cortés, 2002; Komárek & Anagnostidis, 2005).

In Caribbean BSCs, species from the genera *Microcoleus*, *Scytonema*, and *Chroococcidiopsis* reign in abundance (Godínez-Alvarez et al., 2012). In desert crusts from these tropics, regularly observed cyanobacterial taxa include *Microcoleus vaginatus*, *Schizothrix calcicola*, *Nostoc spp. (commune*, *muscorum*, *paludosum*, *punctiforme)*, *Phormidium minnesotense*, *Leptolyngbya tenuis*, *Trichormus variabilis*, and *Tolypothrix tenuis*, while species such as *Coleofasciculus* sp. and *Schizothrix calcicola* are paramount in local neotropical savannas (Johansen, 1993; Sanchez, 2019; Cantón et al., 2020).

Identification of soil crust cyanobacteria is challenging due to their simple morphologies and molecular tools are necessary to uncover their hidden diversity. Recent studies using advanced techniques like metabarcoding have revealed new tropical genera *Gracilinea*, *Konicacronema*, and *Roholtiella*, and highlighted the continuous discovery of cryptic species (Bohunická et al., 2015; Machado-De-Lima & Branco, 2020; Patova et al., 2023).

4 Taxonomy

4.1 Basic Taxonomy

Taxonomy is an important discipline within biology. It is concerned with the identification, description, classification, and naming of organisms, and provides a structured framework for organizing biological diversity and serves as a basis for communication about life forms across scientific disciplines (Fee & Matson, 1992). At its core, taxonomy aims to create coherent systems that reflect the natural relationships between organisms, both extant and extinct (Thomson et al., 2018).

The historical roots of taxonomy can be traced to 18th century, to early naturalists like Linnaeus, who classified organisms like blue-green algae based on observable morphological traits (Skulberg et al., 1993). This initial visual sorting marked the beginning of formal classification systems grounded in perceived similarities. Over time, taxonomy developed into a more refined and methodologically rigorous science. As defined by Trüper and Krämer (1981), it comprises three essential components – classification (grouping organisms based on shared characteristics), nomenclature (assigning standardized names to taxa), and identification (determining the taxonomic position of a specimen).

Far from being a fixed discipline, taxonomy is constantly changing—an evolving science shaped by the ongoing interplay of theory and discovery. As new data emerge, particularly from molecular biology, phylogenetics, and evolutionary studies, traditional taxonomic boundaries are being tested, revised, and often redrawn (Wheeler, 2008). This current shift is not simply a refinement of old frameworks, but a transformation of how species and higher taxa are conceptualized. In response, taxonomy should remain open to innovation yet stay anchored in the clarity and consistency to secure meaningful classification. The future of taxonomy depends on how well it can combine new scientific tools with its core goal: organizing and making sense of the diversity of life on Earth.

4.2 Taxonomy of Cyanobacteria

The taxonomy of cyanobacteria has a complex and evolving history. Originally grouped with algae because of their shared ability to carry out oxygenic photosynthesis and similar ecological roles, cyanobacteria have been referred to as "blue-green algae" for a long time. However, their prokaryotic nature has been recognized for over a century (Anand et al., 2019).

Historically, cyanobacteria were classified using botanical principles, which focused primarily on their observable physical traits. Geitler's 1932 monograph classified cyanobacteria based on morphological characteristics, such as cell shape, colour, and structure (Geitler, 1932). However, cyanobacteria can alter their morphological and functional traits in response to environmental stimuli. This phenomenon is known as phenotypic plasticity and makes morphological traits unreliable for identifying true evolutionary relationships (Koch et al., 2017). As a result, these taxonomical systems often placed genetically unrelated organisms into the same group – crating a problem known as polyphyly. This issue is especially common in genera *Synechococcus* and *Leptolyngbya* (Dvořák et al., 2018).

At the same time, bacteriological methods began to emerge and focused more on studying cyanobacteria at the strain level. These approaches emphasized the observation of pure laboratory cultures and led to nomenclature on laboratory characteristics such as growth patterns, cellular structure, and biochemical properties (Rippka et al., 1979; Komárek & Anagnostidis, 1999). Though this shift also overlooked natural diversity and focused on characteristics observable in isolation rather than ecological contexts. Drouet (1981) advocated for minimizing taxonomic complexity by suggesting many morphological differences were temporary forms.

4.2.1 Issues with Taxonomy

Blurred definitions between different international naming systems lead to confusion in classifying cyanobacteria. Cyanobacterial taxonomy has historically been shaped by two parallel classification systems. Komárek and Anagnostidis adopted a botanical framework, whereas Castenholz and Waterbury, in *Bergey's Manual*, adhered to the International Code of Nomenclature of Bacteria, organizing cyanobacteria into five primary morphological subsections (Anagnostidis & Komárek, 1985; Castenholz et al., 2001; Palinska & Surosz, 2014). Although the botanical system has inherent limitations, it provided a foundational scheme for grouping cyanobacteria based on phenotypic characteristics (Komárek, 2016). Cyanobacterial nomenclature is currently mainly regulated by the International Code of Nomenclature for Algae, Fungi, and Plants (ICN) (Komárek et al., 2014; Pinevich & Averina, 2024).

Recent molecular approaches particularly DNA sequencing and phylogenetic analysis, including ITS (Internal Transcribed Spacer) and *rbcL* (Ribulose-bisphosphate carboxylase) genes, offer better phylogenetic resolution. In cyanobacterial taxonomy

and phylogenetics, the ITS region, located between the 16S and 23S ribosomal RNA genes, evolves rapidly, making it easier for identifying closely related or cryptic species or genera, though the identification is not always perfect (Kauff & Büdel, 2011). The *rbcL* gene, which evolves at a moderate rate, serves as a molecular marker for differentiating species and lineages. Metagenomics and species delimitation algorithms help identify uncultured diversity but often conflict with morphology-based systems (Handelsman, 2004).

Despite the widespread use of the 16S rRNA gene in defining species and genera, its low resolution often fails to distinguish very closely related or cryptic species. The whole 16S-23S ITS rRNA region provides greater variability and helps distinguish species in genera like *Oculatella*, which was previously identified as *Leptolyngbya* (Zammit et al., 2012; Dvořák et al., 2024). However, in others like *Argonema*, ITS is insufficient, requiring whole-genome data (Skoupý et al., 2022).

In some cases, multiple rRNA gene copies within a single genome exhibit greater variability than those found between distinct species, highlighting the potential for extensive cryptic diversity. Whole-genome sequencing has proven valuable in clarifying such complexity, leading to the identification of new genera such as *Moorena*, *Elainella*, and *Argonema* (Engene et al., 2012; Jahodářová et al., 2017; Skoupý et al., 2022; Dvořák et al., 2024). However, despite these advances, genome-based taxonomic studies remain relatively scarce.

To refine species delimitation, recent efforts have incorporated population genomics, which provides higher resolution for understanding diversity. Though originally developed for eukaryotes, population genomics now helps investigate genome-wide variation, recombination, and speciation in asexual prokaryotes. Forces like geographical isolation, gene flow, and ecological selection shape both core and accessory genomes. In *Laspinema*, genome sequencing revealed distinct cryptic lineages with limited gene flow and ecological differentiation, supporting species-level recognition (Dvořák et al., 2024). Sequencing archived herbarium type materials could also provide valuable insights that connect past and present understandings of cyanobacterial evolution (Skoupý et al., 2024).

Although estimates suggest there may be up to 8 000 cyanobacterial species, current databases list only around 2 700 (Dvořák et al., 2018). This discrepancy is largely assigned to misidentification, insufficient sampling, and the limitations of morphology-

based classification systems, which can lead to both over- and under-representation in sequence datasets. Blending phenotypic and genotypic data offers the potential to resolve these issues and establish more accurate evolutionary relationships among the reliably identified species.

The attempt to classify soil cyanobacteria also presented complications. In 1935, Petersen classified them based on habitat, distinguishing soil forms by moisture (Elster, 2002). Tiffany later included cyanobacteria growing on rocks or vegetation. In the 1960s, Shields and Durrell, and Gollerbach and Shtina tried incorporating ecological, physiological, and taxonomic data, though efforts were often limited by region or language (Metting, 1981).

Efforts to reconcile molecular and phenotypic data are still early. Species described under one code may not be recognized under another. Cyanobacterial taxonomy is undergoing major changes as molecular tools – such as DNA barcoding, metagenomics, and whole genome sequencing; become increasingly integrated with classical approaches. However, challenges like missing reference sequences, phenotypic variability, and inconsistent taxonomy continue to limit the full potential of next generation sequencing in biodiversity studies (Mishra, 2020). These methods revealed that morphological evolution in cyanobacteria often does not correspond to genetic evolution.

Revisiting *Synechococcus* as an example. Its composition of morphologically similar yet genetically distinct lineages clearly indicates that the taxon has independently evolved at least twelve times over the past three billion years (Dvořák et al., 2014). This repeated divergence has led to the recognition of polyphyletic lineages and the reclassification of these groups into new genera. Recent studies have highlighted the importance of employing advanced microscopy techniques to elucidate the fine structural details that differentiate species within genera. For example, a study of five species showed that while shape and structure can help with identification, they aren't enough for accurate classification because different species can look similar due to evolution (Dvořák et al., 2015).

In summary, the taxonomy of cyanobacteria has journeyed from the surface-level simplicity of morphological traits to the genomic depth that reveals their true evolutionary relationships. Continued refinement through molecular tools, standardized nomenclature, and comprehensive sampling will be key to resolving remaining taxonomic ambiguities of this ancient lineage.

5 Materials and Methods

5.1 Origin of Samples

Cyanobacterial samples were collected in June 2024 by doc. Mgr. Petr Dvořák, Ph.D., from various moist soil cyanobacterial crusts and mats within and around the city of Santo Domingo, Dominican Republic (see Fig. **3**). The aim was to isolate and explore often overlooked cyanobacteria inhabiting soil substrates where moisture lingered after rainfall. A total of five soil samples was collected from diverse locations, including a wet fountain wall, a rain puddle, an area of wet soil on the campus, and two distinct roadside sites (see table **1**). These sites were deliberately chosen to reflect a gradient of hydrological conditions of tropical cyanobacteria. Each soil sample was collected using a sterile sampling spatula, immediately placed in a sterile zip-lock bag to prevent contamination, and then stored in a cool, dark place until transportation to the Department of Botany at Palacký University. Although my initial attempts were made to culture cyanobacteria from all five sites, samples from only three locations successfully proliferated without contamination. Thus, for the purposes of this bachelor's thesis, only those three locations (IDs 2, 3 and 4 in Table **1**) will be analysed and discussed.

The collected samples were categorized into three subsets: Dr4, Dr2, and Dr5A/5B. The prefix "Dr" denotes that the samples originate from the Dominican Republic, while the number corresponds to one of the five original cell culture plates used during the initial cultivation phase, each plate associated with a distinct sampling location. The alphanumeric code following the dash (e.g. A1, B5, C5) identifies the specific well within the respective plate from which each cyanobacterial strain was successfully isolated and cultured. These identifiers were consistently used to trace the origin and cultivation history of each isolate throughout the study.

The subset of Dr4 samples was obtained from shallow, stagnant puddle located at 18°26.8415' N, 69°36.52528' W. Another subset, Dr2, was collected from moist soil adjacent to a water fountain at 18°29.38337' N, 69°57.49934' W. The Dr5A and Dr5B sample subset was isolated from persistently wet soil on the Instituto Tecnológico de Santo Domingo (INTEC) campus grounds at 18°29.26087' N, 69°57.84165' W. The sampled sites exhibited varying degrees of soil moisture, ranging from temporarily waterlogged substrates to constantly damp soils with limited drainage. These differing

moisture conditions provided suitable environments for soil-dwelling cyanobacteria, particularly those adapted to thrive in wet, but not permanently flooded, soils.

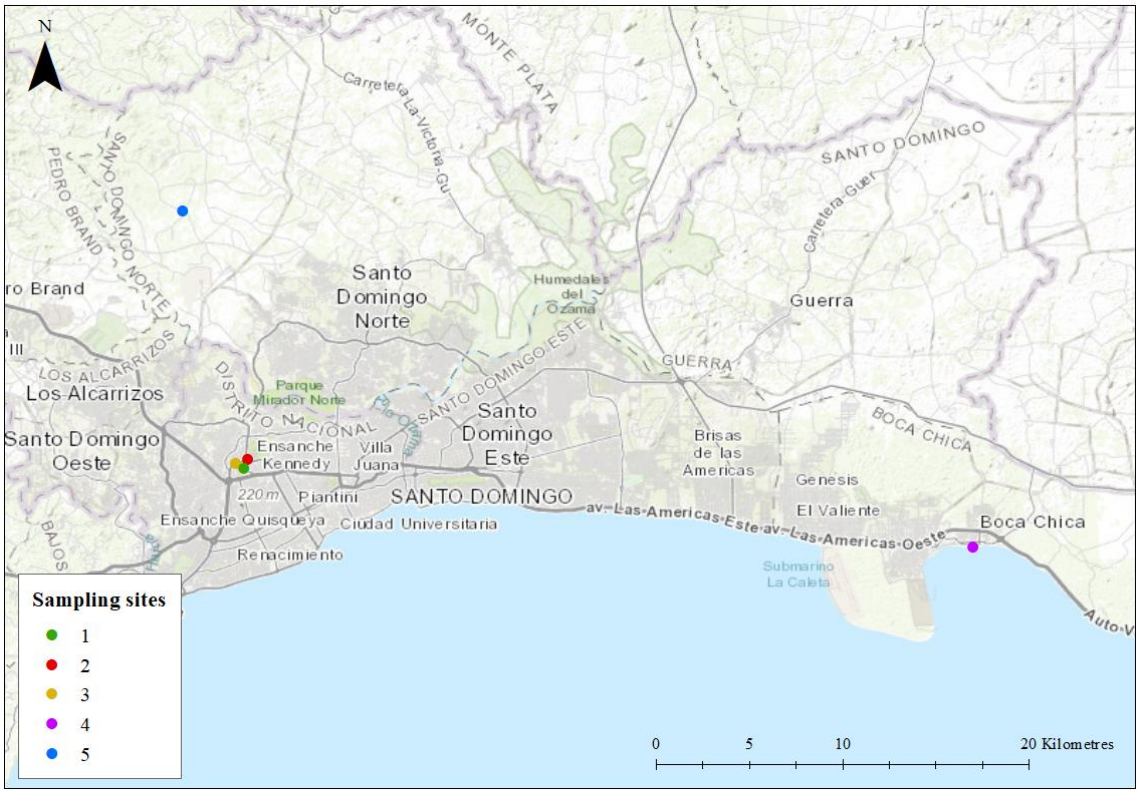

Figure **3**: Sampling locations in Santo Domingo area, Dominican Republic. The map was constructed using ArcGIS Desktop 10.8 (ESRI, USA).

Table **1**: Overview of GPS Coordinates of All Sampling Points.

LOCATION ID	LATITUDE	LONGTITUDE	SITE DESCRIPTION
1	18°29.11600' N	69°57.61149' W	Roadside soil
2	18°29.38337' N	69°57.49934' W	Fountain wall
3	18°29.26087' N	69°57.84165' W	Wet soil on INTEC campus
4	18°26.84150' N	69°36.52528' W	Puddle
5	18°36.6301' N	69°59.3900' W	Roadside soil

5.2 Laboratory Work After Field Sampling

From each soil sample taken, a small portion of the cyanobacterial mat was placed into test tubes with liquid Zehder's (Z) medium, and allowed to grow for several days (Staub, 1961). I then transferred small portions of the resulting biomass onto 6cm Petri dishes containing solidified agar medium. These plates were afterwards incubated in a phytotron under controlled conditions, maintained at 22 ± 1 °C with a 16-hour light and 8-hour dark photoperiods, to promote natural growth.

After approximately five days of incubation, proliferating cyanobacterial filaments were examined under an inverted microscope. Using sterile inoculation needles, individual filaments were isolated and transferred into designated wells of 24-well culture plates containing Z medium. A total of five culture plates was prepared, each corresponding to one of the five original sampling locations (see Table **1**). This arrangement ensured that each well contained a single filament, allowing the development of monoclonal cultures appropriate for further molecular and morphological analyses.

The cultures were routinely monitored, and Z medium was added as needed to sustain growth. To minimize medium evaporation, each plate was sealed with Parafilm before incubation in the phytotron or fridge. Once substantial biomass had developed, a portion of each culture was aseptically transferred into sterile test tubes containing fresh Z medium for continued cultivation. Test tubes were labelled according to the number of the source culture plate and the specific well position from which the biomass (filament) originated.

To ensure culture preservation and eliminate the risk of sample loss, duplicates of each test tube culture were prepared by transferring a portion of the biomass into new sterile test tubes. These backup cultures served as a safeguard for experimental procedures.

After sufficient growth had been achieved, most of the samples were microscopically observed. Samples that were not included in the observations showed either evident contamination or failed to develop viable biomass for meaningful analysis. Microscopic observations were performed using a light microscope (Axio Imager, Carl Zeiss Microscopy GmbH, Germany) with camera (AxioCam ERc 5s camera, Carl Zeiss Microscopy GmbH, Germany) and equipped with a Neofluar 40×/1.3 NA objective lens and an Apochromat 100×/1.4 NA oil immersion objective lens. Image processing and

analysis were carried out using AxioVision Rel. 4.8.3 software (Carl Zeiss Microscopy GmbH, Germany).

Genomic DNA (50 mg per reaction) was extracted from the biomass of each specimen sample using the DNeasy UltraClean Microbial Kit (Qiagen, Germany), following the protocol of the manufacturer. The quality of the extracted DNA was evaluated by electrophoresis on a stained 1.3% agarose gel. DNA concentrations were quantified using a NanoDrop 1 000 spectrophotometer (ThermoFisher Scientific, USA).

Amplification of a partial 16S rRNA gene and 16S-23S ITS rRNA region sequence was carried out via polymerase chain reaction (PCR). Each 40 µl PCR reaction contained 20 µl of EmeraldAMP Master Mix (Takara Bio Europe SAS, France), 17 µl of H_2O, 1 µl of primer I, 1 µl of primer II, and 1 µl of template DNA. A total of 24 samples was processed, along with one negative control containing H_2O.

Purification of the PCR products was carried out using the E. Z. N. A. Cycle Pure Kit (Omega Bio-Tek, USA), and done so in lockstep to the manufacturer's guidelines. Once purified, each sample was supplemented with primers P1, P2, P5, and P8, then carefully stored at −20 °C to preserve integrity prior to sequencing. The sequencing process, conducted via Sanger method by Macrogen Europe B.V. (Amsetrdam, The Netherlands), generated high-quality reads of both 16S rRNA gene and 16S-23S ITS rRNA gene region. Sequence assemblies and refinements were performed using Sequencher 5.0 (Gene Codes Corporation, USA).

Multiple sequence alignment was conducted in AliView (Larsson, 2014) using the MUSCLE (Edgar, 2004) algorithm, which ensured precise alignment across datasets. Two sample sequences were excluded from the analysis for observed irregularities during multiple sequence alignment. Phylogenetic relationships were then inferred using the maximum likelihood method implemented in IQ-TREE (Trifinopoulos et al., 2016). To put the tree's branches to the test, 2 000 ultrafast bootstrap replicates were unleashed (Minh et al., 2013). This provided solid statistical support for the reconstructed topology. The phylogenetic tree was then visually brought to life using FigTree v. 1.4.4. (Rambaut, 2018); with final graphic refinements crafted in Inkscape (Inkscape Project, open source).

6 Results

Figure **4**: The phylogenetic tree based on the 16S rRNA gene and 16S-23S ITS rRNA gene region sequences. Observed strains are divided into 9 phylogroups. Asterisks at the nodes represent >95% ultrafast bootstrap support values.

6.1 Phylogenetic Tree

The phylogenetic analysis based on 16S rRNA gene and 16S-23S ITS rRNA gene region sequences resolved the cyanobacterial strain isolates from Dominican Republic soil samples (Dr2, Dr4, Dr5A and Dr5B) into nine distinct phylogroups (as seen in Fig. **4**) within the orders *Leptolyngbyales*, *Oscillatoriales* and *Pseudanabaenales*. All major branches displayed strong bootstrap support (>95%), indicating robust clustering of the sequences into distinct lineages.

Phylogroup 1 includes strain Dr5A–D3, which clustered within a clade containing members of the families *Ocullatelaceae* and *Pseudanabaenaceae*. Phylogroup 2, which contains strain Dr4-A1, and Phylogroup 3, that hosts strain Dr4-A3, form a distinct lineage within or adjacent to the genus *Kovacikia* and species of *Stenomitos* spp. Phylogroups 4 through 7 formed the most extensive and strongly supported portion of the phylogenetic tree and included the majority of analysed strains from Dr2, Dr4, Dr5A, and Dr5B.

Based on phylogenetic analysis, the strains Dr5B-B2, Dr5A-B6, Dr5A-D1, Dr5A-B5, Dr4-B6, Dr4-A2, Dr4-D4, Dr4-C2, Dr4-D1, Dr5A-D4, Dr4-A4, and Dr5A-C5 were assigned to Phylogroup 4. Singular strain Dr5B-C5 forms Phylogroup 5, while Dr5A-A5 constitutes Phylogroup 6. Phylogroup 7 also contains a single strain, Dr2-D1. These phylogroups grouped into a cohesive clade alongside reference sequences attributed to species from genera *Floridaenema, Hillbrichtia*. *Lyngbya*, *Microcoleus*, *Oscillatoria, Phormidium* and *Potamosiphon*. Notably, some Dr5B strain from Phylogroup 5 clustered more closely with *Microcoleus vaginatus* and *Microcoleus* sp. Phylogroup 8 consists of an individual strain Dr4–B1, which forms a distinct, moderately supported branch in close proximity to sequences of *Geitlerinema* sp. and *Ancylothrix* sp. Finally, Phylogroup 9 encompasses strains from Dr4, namely Dr4-C4, Dr4-A6, and Dr4-A5), which cluster within a moderately supported lineage containing *Geitlerinema* species.

Taken together, the phylogenetic reconstruction reveals that the soil cyanobacteria from the Dominican Republic represent a phylogenetically diverse group of filamentous cyanobacteria. They group into five principal lineages:

(1) a *Pseudanabaenaceae* lineage - Phylogroup 1;

(2) a *Leptolyngbyaceae* lineage – Phylogroups 2 and 3;

(3) an *Oscillatoriaceae-Microcoleaceae* lineage – Phylogroups 4, 5, 7, 9;

(4) an *Aerosakkonemataceae* lineage – Phylogroup 6;

(5) a *Geitlerinemataceae* lineage – Phylogroup 8.

6.2 Morphological Observation

The morphological characteristics of each of the 22 strains — including cell shape and size, pigmentation, the presence and thickness of the mucilaginous sheath, calyptra and filament apex morphology, intracellular granules, and other distinctive structural features, were determined using the identification guide by Komárek and Anagnostidis (2005).

6.2.1 Phylogroup 1

Strain Dr5A-D3 was assigned to Phylogroup 1 based on phylogenetic analysis (**A** in Fig. **5**). Morphologically, this strain exhibited a filament composed of a uniseriate row of cylindrical to slightly rectangular cells, measuring approximately 3.05 µm in width and 2.8 µm in length. The cells were green with small intracellular granules present. A very thin mucilaginous sheath surrounded the filament, with clear constrictions between adjacent cells. The apex was rounded, and no specialized terminal structures, such as calyptra, heterocytes, or akinetes, were observed.

6.2.2 Phylogroup 2

Strain Dr4-A1 was classified within Phylogroup 2 (**B** in Fig. **5**). This strain displayed filaments composed of uniseriate trichomes formed by cylindrical to slightly barrel-shaped cells, with cell widths ranging from 5.05 µm to 5.79 µm, and length from 1.87 µm to 4.05 µm. The cells were green and showed visible intracellular granules. A thin mucilaginous sheath was present, and individual cells were separated by distinct septa. Most filament apices were rounded, although one apex exhibited a conical shape. No heterocytes or akinetes were detected.

6.2.3 Phylogroup 3

Strain Dr4-A3 belonged to Phylogroup 3 (**C** in Fig. **5**). Its filaments were composed of uniseriate trichomes consisting of cylindrical cells with width around 5.2 µm and length from 1.95 µm to 2 µm. The cells contained green pigmentation and fine intracellular granules. A delicate, thin mucilaginous sheath enveloped the filaments, with prominent

septa separating the cells. The apex of the filaments was rounded, and the terminal cell displayed a slightly cap-like shape. No calyptra, heterocytes, or akinetes were present.

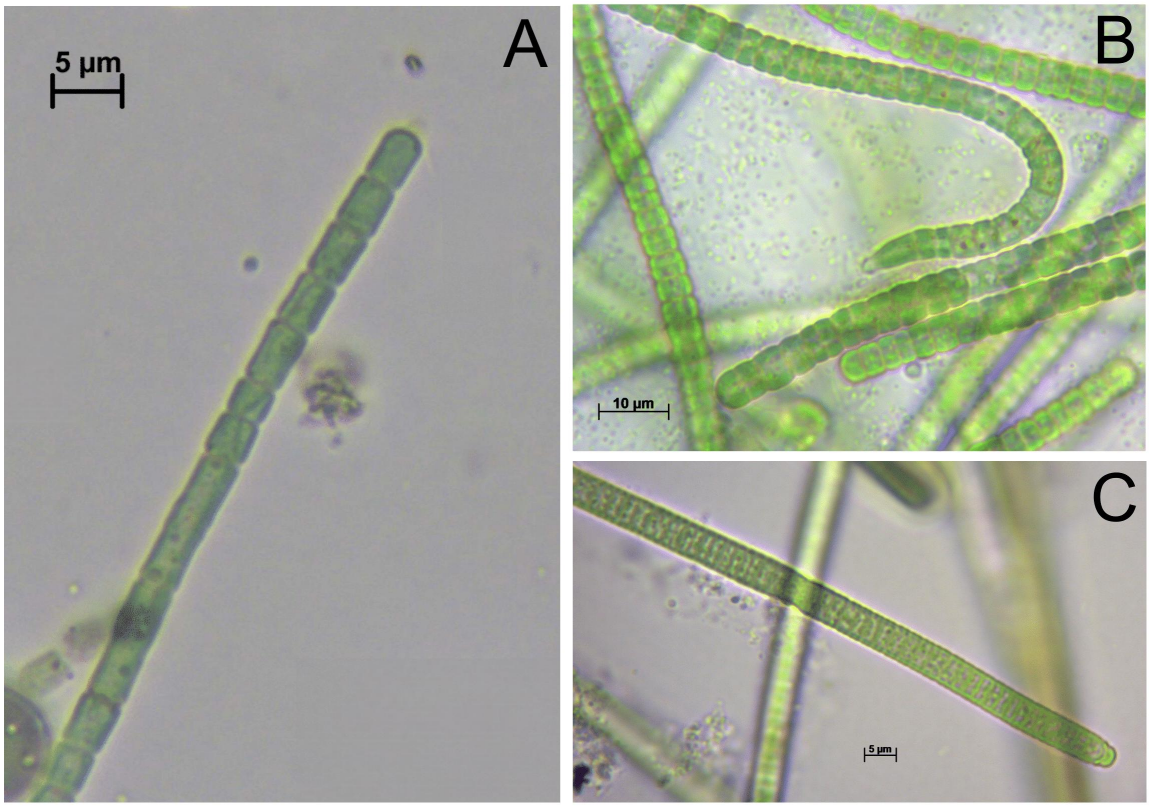

Figure **5**: Microscopic observations of filaments from isolated cyanobacterial strains belonging to different phylogroups. **A**: Dr5A-D3 strain from Phylogroup 1; **B**: Dr4-A1 strain from Phylogroup 2; **C**: Dr4-A3 strain from Phylogroup 3.

6.2.4 Phylogroup 4

This Phylogroup's strains can be seen in Fig. **6**. Morphological characterization of this group revealed that all strains exhibited uniseriate trichomes composed of cylindrical cells, typically organized in a straight or gently curved row. Cell widths varied across samples, ranging from as narrow as 4.83 µm (Dr4-D4) to as wide as 10.47 µm (Dr5A-B6), with most strains showing moderate variability in cell length, approximately 1.15 - 2.57 µm. This variation resulted in observable differences in cell aspect ratios among the filaments. The cell pigmentation across all strains was consistently green, though strain Dr5B-B2 exhibited a violet hue. In all cases, intracellular granules were present and typically scattered finely throughout the cytoplasm, contributing to a subtly

textured internal appearance. Cell segmentation was clearly visible in all filaments, with well-developed septa separating the cells and giving rise to a distinctly segmented morphology.

The apices of the trichomes were typically broadly rounded, with no significant structural modification of the terminal cell. A few strains, such as Dr5B-B2 and Dr5A-B5, showed a slightly tapered or enlarged terminal cell, yet no specialized apical structures such as calyptra were observed in any case. Furthermore, across all strains, no heterocytes or akinetes were present, indicating a uniform absence of these differentiated cell types in this phylogroup.

A thin mucilaginous sheath surrounded the trichomes in every specimen, though the visibility and distinctness of the sheath varied. In strain Dr4-C2, Dr4-D4, Dr5A-B6, and Dr5A-B5, the sheath was more clearly delineated, whereas in others like Dr5A-D4 and Dr5A-C5, it was barely noticeable. All strains of this phylogroup show uniform filament morphology, reinforcing their phylogenetic relation.

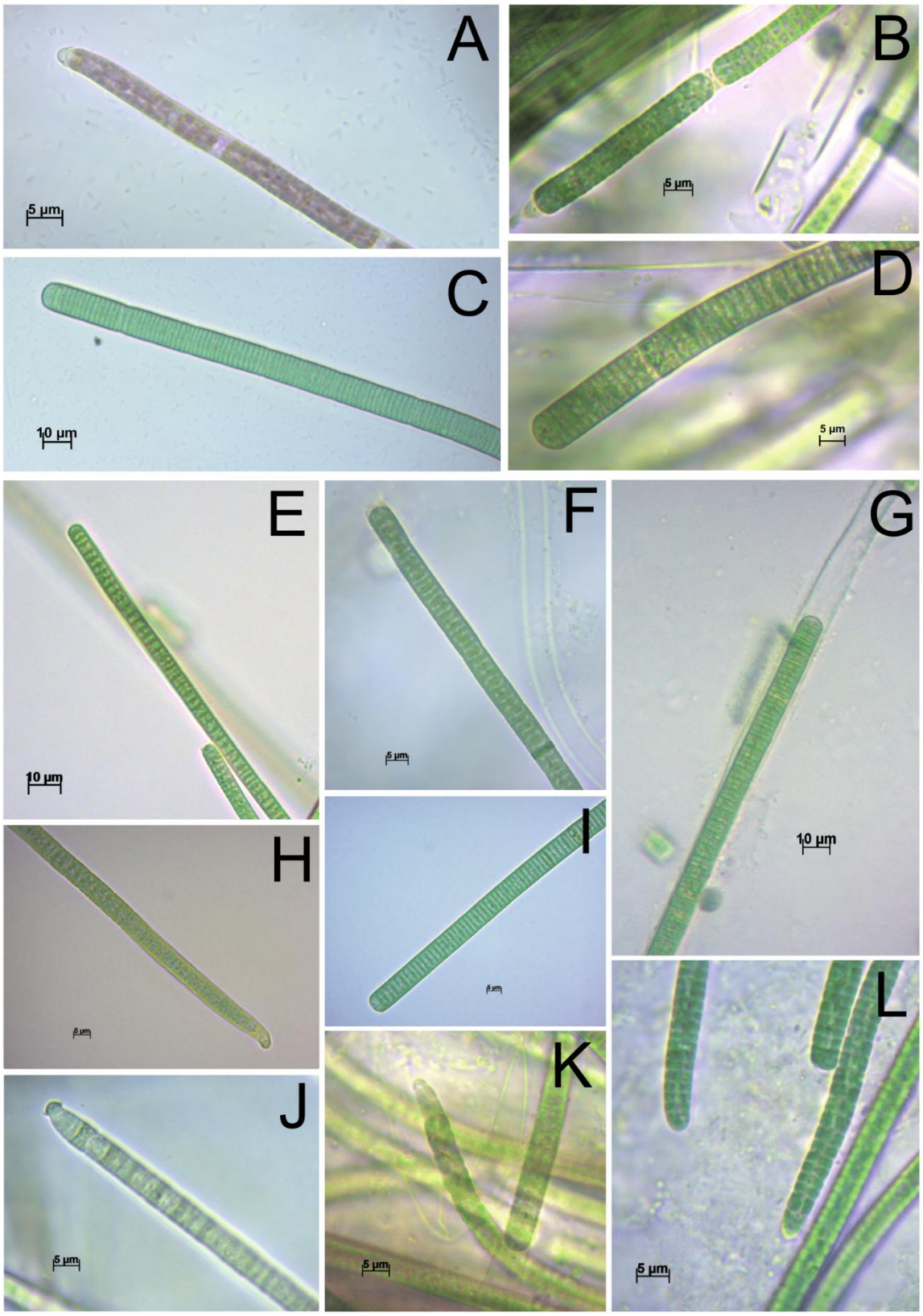

Figure **6**: Microscopic observations of filaments from isolated cyanobacterial strains belonging to Phylogroup 4. Strain: **A**: Dr5B-B2; **B**: Dr4-A2; **C**: Dr5A-B6; **D**: Dr5A-D1; **E**: Dr4-B6; **F**: Dr4-D1; **G**: Dr5A-B5; **H**: Dr4-A4; **I**: Dr5A-D4; **J**: Dr5A-C5; **K**: Dr4-C2; **L**: Dr4-D4.

6.2.5 Phylogroup 5

Observed strain, Dr5B-C5 (see **B** in Fig. **7**), possesses robust trichomes composed of barrel-shaped to slightly elongated cells arranged neatly in a uniseriate pattern. These cells range widely in size, lending the filament a striking structural variability. From just 1.03 µm up to 3.3 µm in length, and 10.68 µm to 11.73 µm in width. Pigmentation transitions from light yellowish green to a muted brownish-green, and the cytoplasm is textured by coarse, scattered granules, adding visual depth under the microscope. Each cell is crisply separated by well-defined septa, creating a distinctly segmented appearance along the length of the trichome. A delicate mucilaginous sheath encases the filament, though it remains faintly visible. At the filament's apex, the broadly rounded tip blends seamlessly with the rest of the structure, and the terminal cell shows no remarkable deviation in form. Much like in prior observed strains, this microscoped filament lacks heterocytes, akinetes, or apical specializations of calyptra.

6.2.6 Phylogroup 6

The phylogroup's strain, Dr5A-A5 (see **C** in Fig. **7**), exhibits slender, uniseriate trichomes composed of elongated cylindrical cells. The cell widths remain relatively uniform, ranging from 1.85 µm to 1.95 µm, while the lengths extend considerably from 8.93 µm to 9.68 µm, resulting in a distinct, stretched morphology. Each cell is imbued with consistent green pigmentation, and the cytoplasm is subtly textured by finely dispersed granules. The entire filament is lightly enveloped in a mucilaginous sheath, barely perceptible. Well-developed septa delineate the cells, creating a clearly segmented appearance along the trichome. The filament apices terminate in smooth, rounded tips, and the terminal cells seamlessly mirror neighbouring cells in both form and size. No evidence of heterocytes, akinetes, or calyptra structures was found, too.

6.2.7 Phylogroup 7

Strain Dr2-D1 (**A** in Fig. **7**) presents a slender filament made up of cylindrical cells organized in a single, unbranched trichome. The cells exhibit a high degree of dimensional consistency, with widths of 1.6 µm and lengths of about 1.76 µm. Cytoplasmic pigmentation is consistently green, and the presence of finely dispersed intracellular granules imparts a subtle granular texture visible under light microscopy. No mucilaginous sheath was discernible during observation. Individual cells are distinctly separated by prominent septa, producing a clearly segmented appearance along

the trichome. At the apex, the filament terminates in a broadly rounded tip, with the terminal cell showing only slight morphological variation from adjacent cells, thereby maintaining structural continuity. No evidence of specialized cells was detected during observation.

6.2.8 Phylogroup 8

Strain Dr4-B1 (**D** in Fig. **7**) is characterized by a trichome of cylindrical cells arranged in a rather precise, uniseriate alignment. Cell dimensions exhibit minimal variation, reflecting consistent uniformity along the filament, with lengths measuring approximately 1.27 µm and widths around 4.81 µm. The cells display intense green pigmentation, and the cytoplasm is textured by numerous small, dispersed intracellular granules. Encasing the trichome is a very thin mucilaginous sheath, which remains nearly imperceptible under light microscopy. Distinct septa sharply define each cell, producing a clearly segmented filament structure. The filament apex is broadly rounded, with the terminal cell appearing slightly larger yet maintaining continuity with the cylindrical morphology of the trichome. No specialized structures, including heterocytes, akinetes, or calyptra, were observed in the examined material.

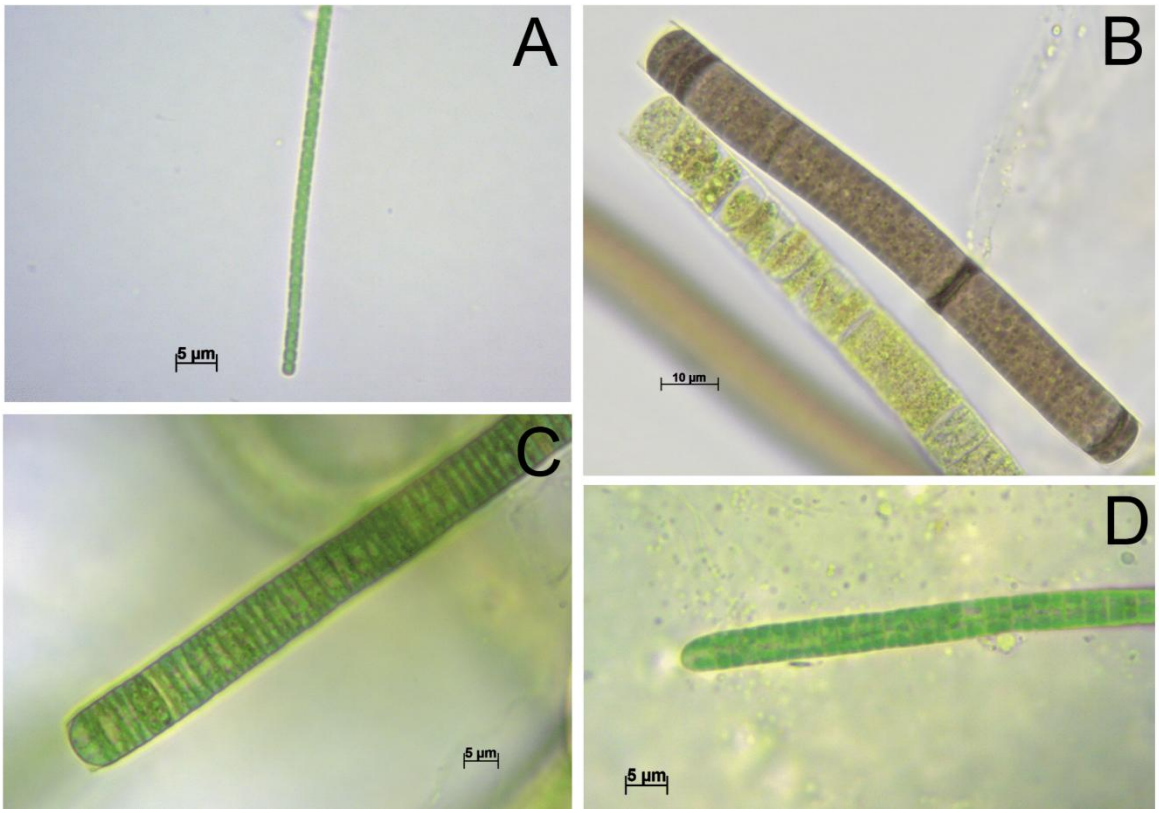

Figure **7**: Microscopic observations of filaments from isolated cyanobacterial strains belonging to different phylogroups. **A**: strain Dr2-D1 from Phylogroup 7; **B**: strain Dr5B-C5 from Phylogroup 5; **C**: strain Dr5A-A5 from Phylogroup 6; **D**: strain Dr4-B1 from Phylogroup 8.

6.2.9 Phylogroup 9

While varying slightly in dimensional features, all Dr4 strains in this Phylogroup share a common morphological framework characterized by trichomes composed of cylindrical and barrel cells aligned in a single row (see Fig. **8**). Cell dimensions across the specimens exhibit moderate heterogeneity. In strains Dr4-C4 and Dr4-A5, the width ranges from 5.4 µm to 5.87 µm, while the width in strain Dr4-A6 is 4.83 µm. Lengths of 1.87 µm (Dr4-A6), 2.2 µm (Dr4-A5), and 2.31 µm (Dr4-C4) were observed. The cell length in Dr4-A6 further ranges from 3.42 µm to 5.46 µm, suggesting a wider size variability within this group. Despite these differences, all cells display uniform green pigmentation, with finely scattered intracellular granules imparting a subtly textured appearance to the cytoplasm.

A thin mucilaginous sheath encloses each filament, remaining faintly visible under light microscopy. Well-defined septa consistently separate individual cells across all three specimens, creating a distinctly segmented filament structure. At the apex,

the filaments typically terminate in a broadly rounded tip, though Dr4-C4 occasionally displays a slightly pointed or elongated terminal cell, particularly in smaller trichomes. In Dr4-A6, the apical cell appear slightly cap-like, but this remains subtle and continuous with the cylindrical form of the rest of the trichome. Across all examined material, no calyptra, heterocytes, or akinetes were detected, indicating a lack of specialized cells.

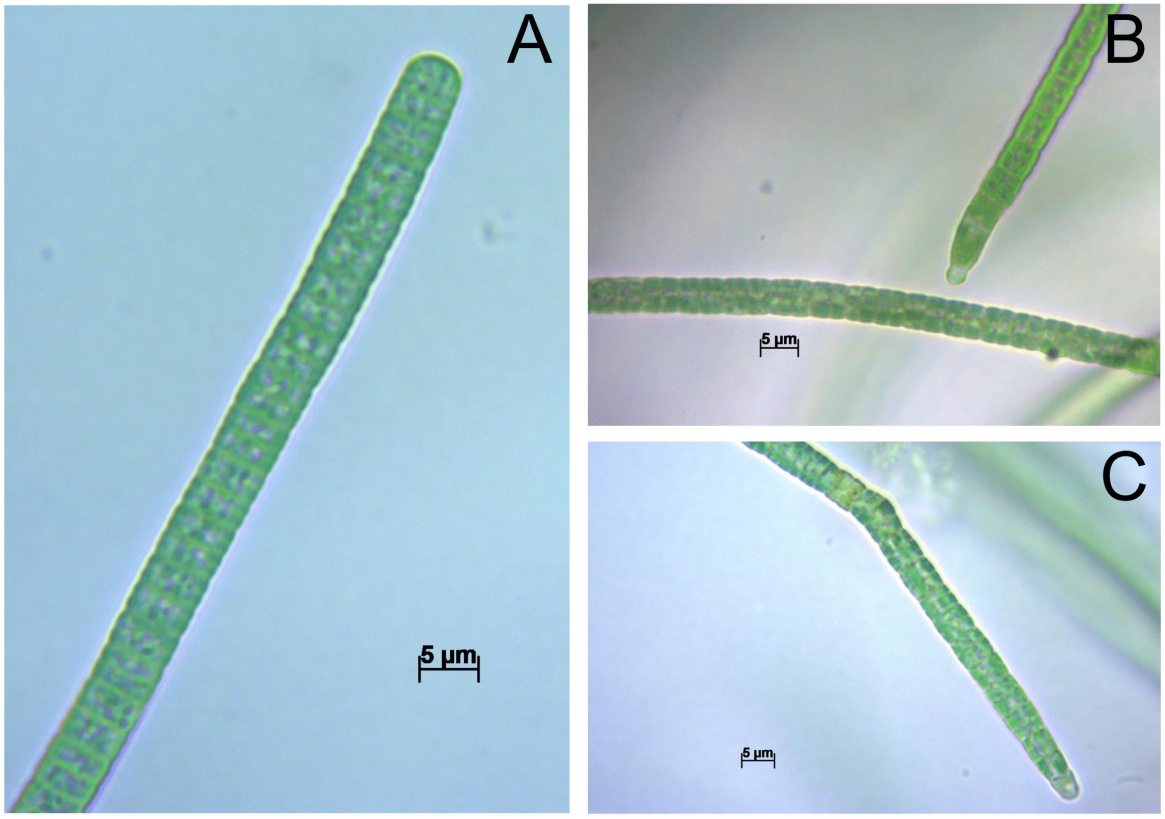

Figure **8**: Microscopic observations of filaments from isolated cyanobacterial strains belonging to Phylogroup 9. Strain: **A**: Dr4-A5; **B**: Dr4-C4; **C**: Dr4-A6.

7 Discussion

Tropical regions host the greatest biological diversity on the planet, not only among higher plants but also within microbial communities, including cyanobacteria. Despite this richness, tropical microbial diversity remains largely unexamined and inadequately researched, particularly in the context of soil cyanobacteria (Santillán et al., 2021). To contribute to filling this gap, I investigated cyanobacterial diversity in samples collected from the Dominican Republic. My approach combined sequencing data with morphological analysis of the isolated strains in 9 distinct phylogroups in the phylogenetic tree.

Strain Dr5A-D3 (Phylogroup 1) shows close phylogenetic affinity to an uncharacterized member of the family *Oculatellaceae* and an uncultured cyanobacterial lineage. The genus *Oculatella*, described within this family, forms narrow trichomes, at most 3 µm wide, in achromatic sheaths. This genus usually grows as mats or biofilms on limestone surfaces (Zammit et al., 2012). These morphological characters closely resemble those observed in strain Dr5A-D3, suggesting a plausible affiliation. However, *Oculatella* also exhibits unique characters, such as a prominent violet-red pigmentation and a photosensitive orange spot at the apex of the trichomes, neither of which were observed in Dr5A-D3. Thus, although this strain possibly belongs to the family *Oculatellaceae*, it is probably not a member of the genus *Oculatella*, and its exact taxonomic identity remains undetermined, suggesting it may represent a new species.

Although the strain from Phylogroup 2 is phylogenetically closest to the species Kovacikia muscicola, it remains evolutionarily distant. The phylogenetic branch connecting them is long and poorly supported, suggesting a possible long-branch attraction artifact (Bergsten, 2005). The genus *Kovacikia* includes filamentous cyanobacteria that form floating mats on water surfaces or in soils. Its trichomes consist of fine, cylindrical cells that typically measure 0.9 - 2.2 µm in length and 1.1 - 1.3 µm in width, and often contain prominent granules (Shen et al., 2022). The genus is characterized by Visible constriction at cross wall, as well as rounded apical cells and the absence of heterocysts. The trichomes are enclosed in thin sheaths. While the observed strain shares some morphological features with *Kovacikia*, it differs in key aspects. Notably, its cells are significantly wider, and one apical cell is conical rather than rounded. These differences, together with phylogenetic evidence, suggest that the strain, although

related to the genus *Kovacikia*, likely represents a distinct lineage within the family *Leptolyngbyaceae*. Given that *Kovacikia* has a tropical distribution and was originally isolated from a cave in Hawaii, the discovery of this distinct strain further supports the presence of previously undescribed diversity of tropical soil cyanobacteria (Miscoe et al., 2016).

The strain Dr4-A3 from Phylogroup 3 is strongly supported phylogenetically as closely related to *Stenomitos terricola*, a soil-dwelling cyanobacterium. This species typically forms green filaments that can form compact mats or irregularly interwoven structures (Lee et al., 2023). The thin, tightly enveloped sheaths are visible only when empty. Cells are generally longer than wide, with polar granules, measuring approximately 2.5 μm in length and 1.4 μm in width. While some morphological features of my strain resemble those of *S. terricola*, major discrepancies in cell shape and dimensions prevent definitive classification.

Phylogroup 4 comprises a diverse set of strains, making precise phylogenetic classification more complex. Despite strong bootstrap support, the strains appear to represent novel species closely related to *Floridaenema evergladense*. According to Moretto et al. (2025), *F. evergladense* is characterized by cell widths ranging from 14 to 21 μm, slight constrictions at cross-walls, sheaths that are sometimes open at the apex and may contain multiple trichomes, and the presence of aerotopes inside blue-green cells. Calyptra is often present. None of these features were present in the strains I examined. The filamentous strain DR5B-B2 does not match the usual characteristics of *Chroococcidiopsis*, suggesting that *Chroococcidiopsis* clade was likely misidentified in the phylogenetic analysis. Instead, the morphological features of phylogroup's strains align more closely with those within the *Aerosakkonemataceae* family.

The Dr5B-C5 strain from Phylogroup 5 clusters closely with *Microcoleus vaginatus*, with strong bootstrap support. The strong phylogenetic proximity between the species, along with morphological characteristics described by Komárek and Anagnostidis (2005) and ecological evidence of adaptation to mat-forming lifestyles typical of desert crusts, supports its classification as *M. vaginatus*.

Strain Dr5-A5 (Phylogroup 6) shows some phylogenetic proximity to the undetermined *Oscillatoriaceae cyanobacterium BETA 8*, although this relationship is not strongly supported by bootstrap. Evolutionarily, it is somewhat more distant from

Potamosiphon australiensis, yet still shows a notable connection. Morphological characteristics – such as filament structure, sheath texture, and cell shape; suggest a possible affiliation with the family *Aerosakkonemataceae*, potentially within the genus *Limnonema*, but not *Potamosiphon*, as the species' morphology differs from my observed strain (Song et al., 2023). Taken together, the phylogenetic distance and morphological traits point toward a tentative placement in *Aerosakkonemataceae* family.

Strain Dr2-D1 from Phylogroup 7 exhibits both phylogenetic proximity and strong morphological resemblance to *Hillbrichtia pamiria*. This species is characterized by filamentous morphotypes with narrow green trichomes, cells slightly constricted at the cross-walls, and a lack of sheath, though sometimes embedded in mucilage. Strains may also display prominent intracellular granules (Jasser et al., 2022). Given the strong genetic similarity and the matching morphological traits observed in Dr2-D1, it can be identified as a strain of *Hillbrichtia pamiria*.

Strain Dr4-B1 (Phylogroup 8) shares morphological features with its phylogenetically close relative, *Ancylothrix* sp. According to Martins et al. (2016), this filamentous cyanobacterium is commonly found forming biofilms both on the surface and within soil layers. Its trichomes consist of cylindrical cells, typically 4.5 - 7.0 µm in width, that are shorter than they are wide and may show slight constrictions at the cross-walls. Sheaths are rarely observed and, when present, are extremely thin and achromatic. The cells lack aerotopes. At the ends of the filaments, apical cells are either gently rounded or tapered with a conical shape, notably without a calyptra. Strong bootstrap support in phylogenetic analysis suggests that Dr4-B1 belongs to the genus *Ancylothrix*.

Taxonomic identification of the strains in Phylogroup 9 remains uncertain. Even though they showed minor similarities to paraphyletic *Planktothrix* sp., main morphological characteristics were completely different. Therefore, these strains are likely to represent a new, yet unidentified genus.

8 Conclusions

This study provides new insight into the poorly documented diversity of soil-dwelling cyanobacteria in tropical regions, focusing on samples collected from the Dominican Republic. Through a combined phylogenetic and morphological approach, I identified nine distinct phylogroups, some of which (Phylogroup 5, 7, and 8) were classified to known species. Others, however – particularly strains within Phylogroup 1, 2, 3, 4, 6, and 9; remain unresolved due to insufficient genetic support, morphological ambiguity, or the absence of closely related reference sequences.

The presence of such uncertain lineages, coupled with consistent deviations from known morphological patterns, suggests the existence of previously undescribed taxa and highlights the cryptic diversity of cyanobacteria in tropical soils. These findings highlight the need for more comprehensive studies in tropical environments, which remain significantly underrepresented in global cyanobacterial research.

Further molecular analyses, including whole-genome sequencing and broader comparative datasets, will be essential to resolve the taxonomic placement of several strains and to confirm the discovery of potentially novel species or genera. This research represents a step toward filling the gap in our understanding of tropical soil cyanobacterial diversity and contributes to the broader effort of cataloguing microbial life in ecologically vital yet scientifically overlooked regions, where cyanobacteria remain among the least understood inhabitants.

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