



## SUPPLEMENT

<https://doi.org/10.15517/rev.biol.trop..v73iS1.63720>

## Marine cyanobacteria of Costa Rica: published records

Laura Brenes-Guillén<sup>1\*</sup>; <https://orcid.org/0000-0002-7185-4084>

Cindy Fernández-García<sup>2,3</sup>; <https://orcid.org/0000-0003-2808-4093>

Jorge Cortés<sup>2,3</sup>; <https://orcid.org/0000-0001-7004-8649>

1. Centro de Investigación en Biología Celular y Molecular (CIBCM), Universidad de Costa Rica, 11501-2060 San Pedro de Montes de Oca, San José, Costa Rica; laura.brenesguillen@ucr.ac.cr (\*Correspondence)
2. Centro de Investigación en Ciencias del Mar y Limología (CIMAR), Universidad de Costa Rica.
3. Escuela de Biología, Universidad de Costa Rica; Centro de Investigación en Biodiversidad y Ecología Tropical (CIBET), Universidad de Costa Rica; 11501-2060 San Pedro de Montes de Oca, San José, Costa Rica; cindy.fernandezgarcia@ucr.ac.cr, jorge.cortes@ucr.ac.cr

Received 22-X-2024.      Corrected 09-I-2025.      Accepted 28-I-2025.

### ABSTRACT

**Introduction:** Cyanobacteria, also known as blue-green algae, are photosynthetic bacteria that play a crucial role in the marine environment, including food and oxygen production, nitrogen fixation, yield antibiotics and other bioproducts which might be used by other members of the community. Cyanobacteria remain understudied, particularly in the marine environments of Central America. While research on cyanobacteria has been conducted in Costa Rica, most studies have focused on freshwater environments, leaving a significant gap in understanding their diversity in the region.

**Objective:** This study compiles the diversity of marine cyanobacteria in Costa Rica through a review of scientific publications and herbarium collections.

**Methods:** a review of the scientific literature and cyanobacterial specimens from the Pacific and Caribbean from 1936 to the present was conducted. In November 2023, the Dr Luis A. Fournier Origgi Herbarium at the University of Costa Rica was visited to examine the available specimens.

**Results:** We found 50 records of cyanobacteria in the references and herbarium collections, of which 10 belonged to Sections I and II, 26 to Section III, nine to Section IV and five to the unclassified category. Genomic data from two studies were found in public databases.

**Conclusions:** The diversity of marine cyanobacteria in Costa Rica represents a valuable resource for ecological and evolutionary studies. This work provides a baseline for future research and highlights the importance of continuing to explore and document the biodiversity of these bacteria.

**Key words:** marine biodiversity; herbarium; blue-green algae; microalgae; prokaryota.

### RESUMEN

#### Cianobacterias marinas de Costa Rica: registros publicados

**Introducción:** Las cianobacterias, también conocidas como algas verdeazuladas, son bacterias fotosintéticas que desempeñan un papel crucial en el ambiente marino, incluyendo la producción de alimento y oxígeno, la fijación de nitrógeno, la producción de antibióticos y otros bioproductos los cuales pueden ser utilizados por otros miembros de la comunidad. Las cianobacterias siguen siendo poco estudiadas, sobre todo en los ambientes marinos de América Central. Aunque en Costa Rica se han realizado investigaciones sobre cianobacterias, la mayoría de



los estudios se han centrado en ambientes de agua dulce, lo que deja un vacío importante en la comprensión de su diversidad en la región.

**Objetivo:** Este estudio recopila la diversidad de cianobacterias marinas en Costa Rica a través de una revisión de publicaciones científicas y colecciones de herbario.

**Métodos:** Se realizó una revisión de la literatura científica y de especímenes de cianobacterias del Pacífico y el Caribe desde 1936 hasta la actualidad. En noviembre de 2023, se visitó el Herbario Dr. Luis A. Fournier Origgi de la Universidad de Costa Rica para examinar los especímenes disponibles.

**Resultados:** Se encontraron 50 registros de cianobacterias en las referencias y colecciones del herbario, de los cuales 10 pertenecían a las Secciones I y II, 26 a la Sección III, nueve a la Sección IV y cinco a la categoría no clasificada. Se encontraron datos genómicos de dos estudios en bases de datos públicas.

**Conclusiones:** La diversidad de cianobacterias marinas en Costa Rica representa un recurso valioso para estudios ecológicos y evolutivos. Este trabajo proporciona una línea base para futuras investigaciones y resalta la importancia de continuar explorando y documentando la biodiversidad de estas bacterias.

**Palabras clave:** biodiversidad marina; herbario; algas verdeazuladas; microalgas; procariota.

## INTRODUCTION

Cyanobacteria, also known as blue-green algae, are a group of photosynthetic bacteria that play an important role in marine environments, as a source of food, oxygen production, nitrogen fixation, antibiotics production, and other bioproducts that are used by other community members (Hoffman, 1999). They are part of complex bacterial communities as biofilms (Zhong et al., 2024) and have been used as model organisms to study interactions with viruses in marine environments (Carlson et al., 2022). The picocyanobacteria *Synechococcus* and *Prochlorococcus* are the most abundant phototrophs in the global oceans, and account for a substantial fraction of marine primary production (Arias-Orozco et al., 2024; Flombaum et al., 2013).

There is a wide morphological, genetic, and functional diversity of marine cyanobacteria that is still poorly explored. They can be classified based on their morphological characteristics, including cell length and cell width of axenic culture. However, morphology does not provide sufficient taxonomic resolution and cyanobacteria with similar or identical morphology may have significantly different physiology (Nübel et al., 1997). Culturing strains is limited to replicating environmental conditions in the laboratory. Genetics and high-throughput sequencing techniques have allowed for

more detailed identification of their abundance and taxonomy in marine environments. Currently, there are 431 genera and 1 653 species valid under ICN and ICNP according to the CyanoDB database (<http://www.cyanodb.cz/>) (Hauer & Komárek, 2022).

Understanding the diversity of marine cyanobacteria is crucial for studying key ecological processes like upwelling and cyanotoxin production, which can have significant economic and health implications (Hallegraeff, 2010). Cyanobacteria have been successful in colonizing harsh environmental conditions such as salty environments and high radiation, using halophily and halotolerance as survival strategies. These characteristics, along with their role in oxygen production and the food chain, their functions in rhodolith beds or corals, and their symbiotic relationships with invertebrates such as sponges and ascidians, are interesting to study from both ecological and evolutionary perspectives (Cavalcanti et al., 2014; Donia et al., 2011; Mutualipassi et al., 2021).

In Central America, marine cyanobacteria have been poorly explored. Most studies of this group in Costa Rica focus on field observations, with few specimens in herbaria. Therefore, the objectives of this work were to compile cyanobacterial diversity in Costa Rican marine environments based on scientific publications and collections in herbaria as a baseline for future research.



## MATERIALS AND METHODS

Scientific articles and books from 1936 (the first record) to the present were reviewed, and a list of the genera and in some cases species of cyanobacteria reported from the Costa Rican Pacific and Caribbean Sea was compiled by location. In November 2023, the Dr. Luis A. Fournier Origgi Herbarium (USJ) at Escuela de Biología of the Universidad de Costa Rica was visited to review the cyanobacteria specimens. There are no other herbarium collections of marine cyanobacteria in the country.

The list of cyanobacteria was arranged according to the subdivisions proposed by Rippka et al. (1979), which are based on differences in morphological structure and development, allowing the recognition of five major sections among cyanobacteria (I, II, III, IV, and V). The taxonomic classification at the genus level was based on the system proposed in AlgaeBase (Guiry & Guiry, 2024). For each report, the taxonomic classification at the order, family, and genus levels, the collection site, and the references are provided.

The search for DNA sequences of marine cyanobacteria from Costa Rica was conducted in 2023 and 2024 using the NCBI (The National Center for Biotechnology Information), and ENA (European Nucleotide Archive) databases (Burgin et al., 2023), as well as scientific articles. We focused on nucleotide sequences, genomes, MAGs (Metagenome Assembled Genomes), and bioprojects.

## RESULTS

We found 50 records of cyanobacteria in the references and in the herbarium, 10 belong to Sections I and II, 26 in Section III, nine to Section IV and five under unclassified category. A total of 20 species are reported from the Pacific and 33 from the Caribbean with three species/genus in common, *Symploca hydnoides*, *Schizothrix calcicola* and *Spirulina* spp. *Trichodesmium erythraeum*, *Symploca* spp. and *Lynbya* spp. have the highest number of records,

with *Symploca* having the most herbarium accessions.

**Unicellular cyanobacteria (Section I and Section II):** We found ten species in these sections. Among the unicellular cyanobacteria reported in the literature are the genera *Merismopedia*, *Anacystis*, *Synechocystis*, *Synechococcus*, and *Prochlorococcus* (Table 1). Belonging to Section II, we find *Chamaecalyx* in the Orden Pleurocapsales. Chrococcales has the largest number of reported species, but the genera *Synechococcus* and *Prochlorococcus* have been reported from a greater number of sites. The reports of these groups were based on culture-independent techniques, while others were based on optical microscopy.

**Filamentous cyanobacteria without heterocysts (Section III):** This is the group of cyanobacteria with the most reports, there are 22 species in the Caribbean and seven species in the Pacific (Table 2). This reflects the higher sampling effort along the Caribbean coast. Oscillatoriales is the most reported order, followed by Coleofasciculace. These groups are characterized by being filamentous and are often the main phototrophic component of the biofilms. Interestingly, the genus *Spirulina*, which is widely used in the food industry, was reported from both coasts.

**Filamentous cyanobacteria with heterocysts and true branching (Section IV):** The genera *Isactis*, *Calothrix*, *Rivularia*, *Anabaena*, *Bachytrichia*, and *Nodularia* were found within the Order Nostocales, each belonging to different families (Table 3). All these genera possess heterocysts, which makes them potential nitrogen fixers. Nitrogen-fixing cyanobacteria play an important role in transforming elemental nitrogen into bioavailable nitrogen, which is of great importance for food chains.

**Unclassified cyanobacteria:** Investigations carried out in the Pacific using light microscopy or independent culture techniques reported five samples as unclassified cyanobacteria (Table 4).

**Table 1**

Marine cyanobacteria that belong to the orders Chroococcales, Synechococcales and Pleurocapsales (Sections I and II) and its geographic distribution in Costa Rica.

| Order           | Family             | Genus/species   | Biogeographic distribution   | References  |
|-----------------|--------------------|---|--|---|
| Chroococcales   | Chamaesiphonaceae  | <i>Stichosiphon sansibaricus</i> (Hieronymus) F.E.Drouet & W.A.Daily, 1956  | Caribbean: Piuta, Isla Uvita, Puerto Vargas, Puerto Viejo, Manzanillo                                      | Muñoz-Simon (2012)  |
|                 | Chroococcaceae     | <i>Chroococcus</i> sp. Nägeli, 1849   | Caribbean: Piuta, Isla Uvita, Puerto Vargas, Puerto Viejo, Manzanillo                                      | Muñoz-Simon (2012)  |
|                 | Cyanothrichaceae   | <i>Johannesbaptistia pellucida</i> (Dickie) W.R.Taylor & Drouet, 1938   | Caribbean: Isla Uvita  | Muñoz-Simon (2012), Muñoz-Simon et al. (2020)   |
|                 | Microcystaceae     | <i>Anacystis</i> sp. Meneghini, 1837<br><i>Merismopedia glauca</i> (Ehrenberg) Kützing, 1845<br><i>Merismopedia elegans</i> A.Braun ex Kützing 1849<br><i>Synechocystis</i> sp. Sauvageau, 1892 | Pacific: Golfo de Papagayo<br>Pacific: Bahía Culebra<br>Pacific: Gulf of Nicoya<br>Caribbean: Isla Uvita   | Loza-Álvarez et al. (2018)<br>Cortés et al. (2012), Drouet, (1936)<br>Calvo Vargas et al. (2014)<br>Muñoz-Simon et al. (2020) |
| Pleurocapsales  | Hyellaceae         | <i>Chamaecalyx leibleiniae</i> (Reinsch) Komárek & Anagnostidis, 1986   | Caribbean: Piuta, Isla Uvita, Puerto Vargas, Puerto Viejo, Manzanillo                                      | Muñoz-Simon (2012)  |
|                 | Synechococcaceae   | <i>Synechococcus</i> sp. Nägeli, 1849   | Pacific: Costa Rica Thermal Dome   | Ahlgren et al. (2014), Cox et al. (2014), Gutiérrez-Rodríguez et al., (2014), Saito et al. (2005)                             |
| Synechococcales | Prochlorococcaceae | <i>Prochlorococcus</i> sp. Chisholm, Frankel, Goericke, Olson, Palenik, Waterbury, West-Johnsrud & Zettler ex Komárek et al., 2020  | Pacific: Isla del Coco National Park; Open ocean, 30 miles from Isla del Coco; and Costa Rica Thermal Dome | Ahlgren et al. (2014), Cortés (2012), Cox et al. (2014), Gutiérrez-Rodríguez et al. (2014), Williamson et al. (2008)          |

The taxonomic classification is based on Algae Base.

**Table 2**

Marine cyanobacteria belonging to the orders Oscillatoriales, Leptolyngbyales, Pseudanabaenales, Coleofasciculales, Geitlerinematales, Spiruliniales and Gomontiellales (Section III) and its geographic distribution in Costa Rica.

| Order             | Family             | Genus/species   | Biogeographic distribution  | References  |
|-------------------|--------------------|---|---|---|
| Coleofasciculales | Coleofasciculaceae | <i>Coleofasciculus chthonoplastes</i> (Gomont) M.Siegesmund, J.R.Johansen & T.Friedl 2008 | Caribbean: Piuta, Isla Uvita, Puerto Vargas, Puerto Viejo, Manzanillo   | Muñoz-Simon (2012)  |
|                   |                    | <i>Symploca</i> sp. Kützing ex Gomont, 1892   | Caribbean: Piuta, Isla Uvita, Puerto Vargas, Puerto Viejo, Manzanillo   | Muñoz-Simon (2012)  |
|                   |                    | <i>Symploca hydnoides</i> Kützing ex Gomont, 1892   | Caribbean: Vicinity of Puerto Limón, Portete, Parque Nacional Cahuita Pacific: Isla Bolaños, Bahía Salinas, Playa Sámara, Cangrejal, Península de Nicoya, Isla del Caño | Dawson (1962); USJ-73046, USJ-73108, USJ-73152, USJ-73305, USJ-73341, USJ-73498, USJ-73528, USJ-73537, USJ-73570, USJ-73686 |



| Order             | Family             | Genus/species  | Biogeographic distribution  | References   |
|-------------------|--------------------|--|---|--|
|                   |                    | <i>Symploca hydnoides</i> var.<br><i>fasciculata</i> Gomont, 1892  | Caribbean: Portete  | Dawson (1962)  |
|                   |                    | <i>Symploca thermalis</i> Gomont, 1892   | Pacific: Isla del Caño  | USJ-73837  |
| Geitlerinematales | Geitlerinemataceae | <i>Geitlerinema cf. exile</i> (Skuja)<br>Anagnostidis, 1989  | Caribbean: Piuta, Isla Uvita,<br>Puerto Vargas, Puerto<br>Viejo, Manzanillo                                     | Muñoz-Simon (2012)   |
| Gomontiellales    | Gomontiellaceae    | <i>Borzia</i> sp. Cohn ex Gomont,<br>1892  | Caribbean: Piuta, Isla Uvita,<br>Puerto Vargas, Puerto<br>Viejo, Manzanillo                                     | Muñoz-Simon (2012)   |
| Leptolyngbyales   | Leptolyngbyaceae   | <i>Leptolyngbya</i> sp.<br>Anagnostidis & Komárek,<br>1988, nom. et typ. cons.   | Caribbean: Piuta, Isla Uvita,<br>Puerto Vargas, Puerto<br>Viejo, Manzanillo                                     | Muñoz-Simon (2012)   |
|                   | Trichocoleusaceae  | <i>Schizothrix</i> sp. Kützing ex<br>Gomont, 1892  | Caribbean: Cahuita<br>National Park   | USJ-73851  |
|                   |                    | <i>Schizothrix calcicola</i> var.<br><i>symplociformis</i> Hansgirg ex<br>Elenkin, 1949  | Caribbean: Vicinity of<br>Puerto Limón<br>Pacific: Playa Manuel<br>Antonio (reported as Playa<br>Manuel Garcia) | Dawson (1962)  |
| Oscillatoriales   | Microcoleaceae     | <i>Blennothrix cantharidosma</i><br>(Gomont)<br>Anagnostidis & Komárek,<br>1988 as <i>Hydrocoleum</i><br><i>cantharidosmum</i> | Pacific: Bahía Culebra  | Cortés et al., 2012; Drouet,<br>1936   |
|                   |                    | <i>Leibleinia gracilis</i><br>(Rabenhorst ex Gomont)<br>Anagnostidis & Komárek,<br>1988  | Caribbean: Piuta, Isla Uvita,<br>Puerto Vargas, Puerto<br>Viejo, Manzanillo                                     | Muñoz-Simon (2012)   |
|                   |                    | <i>Lyngbya</i> sp. C.Agardh ex<br>Gomont, 1892, nom. et typ.<br>cons.  | Caribbean: Isla Uvita   | Muñoz-Simon (2012)   |
|                   |                    | <i>Lyngbya majuscula</i> Harvey<br>ex Gomont, 1892   | Caribbean: Vicinity of<br>Puerto Limón  | Dawson (1962)  |
|                   |                    | <i>Lyngbya sordida</i> f.<br><i>bostrychicola</i> Gomont, 1892   | Caribbean: Portete, Vicinity<br>of Puerto Limón   | Dawson (1962)  |
|                   |                    | <i>Lyngbya subconfervoides</i><br>O.Borge, 1918  | Caribbean: Cahuita<br>National Park   | Bernecker & Wehrmann,<br>(2009)  |
|                   |                    | <i>Microcoleus chthonoplastes</i><br>Thuret ex Gomont, 1892  | Caribbean: Puerto Vargas  | Dawson (1962)  |
|                   |                    | <i>Trichodesmium erythraeum</i><br>Ehrenberg ex Gomont, 1892   | Pacific: Bahía Culebra, Gulf<br>of Nicoya, Caldera  | Calvo Vargas et al. (2014),<br>Calvo Vargas et al. (2016),<br>Vargas-Montero (2004),<br>Vargas-Montero & Freer<br>(2004) |
|                   |                    | <i>Oscillatoria</i> sp. Vaucher ex<br>Gomont, 1892   | Caribbean: Isla Uvita   | Muñoz-Simon (2012), Muñoz-<br>Simon et al. (2020)  |
|                   | Oscillatoriaceae   | <i>Oscillatoria corallinae</i><br>Gomont, 1890   | Caribbean: Vicinity of<br>Puerto Limón  | Dawson (1962)  |



| Order            | Family            | Genus/species   | Biogeographic distribution  | References                                    |
|------------------|-------------------|---|---|---|
|                  |                   | <i>Phormidium</i> sp. Kützing ex Gomont, 1892                                   | Caribbean: Isla Uvita   | Muñoz-Simon (2012), Muñoz-Simon et al. (2020) |
|                  |                   | <i>Phormidium crosbyanum</i> Tilden, 1909                                       | Caribbean: Undefined site   | Dawson (1962)                                 |
|                  |                   | <i>Phormidium monile</i> Setchell & Gardner, 1930 as<br><i>Lyngbya gracilis</i> | Pacific: Bahía Culebra  | Taylor (1945)                                 |
| Pseudanabaenales | Pseudanabaenaceae | <i>Pseudanabaena</i> sp. Lauterborn, 1915                                       | Caribbean: Piuta, Isla Uvita, Puerto Vargas, Puerto Viejo, Manzanillo   | Muñoz-Simon (2012)                            |
| Spirulinales     | Spirulinaceae     | <i>Spirulina</i> sp. Turpin ex Gomont, 1892                                     | Caribbean: Piuta, Isla Uvita, Puerto Vargas, Puerto Viejo, Manzanillo<br>Pacific: Mangrove sediments, Golfo Dulce | Medeanic et al. (2008); Muñoz-Simon (2012)    |
|                  |                   | <i>Spirulina subsalsa</i> Oersted ex Gomont, 1892                               | Caribbean: Parque Nacional Cahuita  | Hargraves & Víquez (1981)                     |

The taxonomic classification is based on Algae Base. Codes correspond to USJ-Herbaria Collection number, Universidad de Costa Rica.

**Table 3**

Marine cyanobacteria belonging to the Order Nostocales (Section IV) and its geographic distribution in Costa Rica.

| Order      | Family             | Genus/species   | Biogeographic distribution  | References             |
|------------|--------------------|---|---|------------------------|
| Nostocales | Aphanizomenonaceae | <i>Anabaena</i> sp. Bory ex Bornet & Flahault, 1886, nom. cons.       | Pacific: Mangrove sediments, Golfo Dulce                              | Medeanic et al. (2008) |
|            | Nodulariaceae      | <i>Nodularia harveyana</i> Thuret ex Bornet & Flahault, 1886          | Caribbean: Piuta, Isla Uvita, Puerto Vargas, Puerto Viejo, Manzanillo | Muñoz-Simon (2012)     |
|            | Nostocaceae        | <i>Nostoc commune</i> (Vaucher ex Bornet et Flahault 1888)            | Caribbean: Punta Manzanillo   | USJ-28295              |
|            | Rivulariaceae      | <i>Calothrix</i> C. Agardh ex Bornet & Flahault, 1886                 | Caribbean: Piuta, Isla Uvita, Puerto Vargas, Puerto Viejo, Manzanillo | Muñoz-Simon (2012)     |
|            |                    | <i>Calothrix crustacea f. simulans</i> F.S.Collins, 1907              | Caribbean: Vicinity of Puerto Limón                                   | Dawson (1962)          |
|            |                    | <i>Calothrix pilosa</i> Harvey ex Bornet & Flahault, 1886             | Caribbean: Vicinity of Puerto Limón                                   | Dawson (1962)          |
|            |                    | <i>Isactis plana</i> (Harvey) Thuret ex Bornet & Flahault, 1886       | Pacific: Bahía Culebra  | Taylor (1945)          |
|            |                    | <i>Rivularia</i> sp. C. Agardh ex Bornet & Flahault, 1886, nom. cons. | Pacific: Mangrove sediments, Golfo Dulce                              | Medeanic et al. (2008) |
|            | Scytonemataceae    | <i>Brachytrichia quoyi</i> Bornet & Flahault, 1886                    | Caribbean: Puerto Vargas  | Dawson (1962)          |

The taxonomic classification is based on Algae Base. Codes correspond to USJ-Herbaria Collection number, Universidad de Costa Rica.



**Table 4**  
Unclassified marine cyanobacteria of Costa Rica and its geographic distribution.

| Order              | Family             | Genus/specie       | Biogeographic distribution  | References                 |
|--------------------|--------------------|--------------------|---|----------------------------|
| unc. Cyanobacteria | unc. Cyanobacteria | unc. Cyanobacteria | Pacific: Isla del Coco National Park  | Fernández (2008)           |
|                    |                    | unc. Cyanobacteria | Pacific: Área de Conservación Guanacaste  | Cortés & Joyce (2020)      |
|                    |                    | unc. Cyanobacteria | Pacific: Coral reefs and submerged pinnacles around Isla del Caño Biological Reserve; coastal rocky reefs and islets along the Osa Peninsula, including Corcovado National Park | Friedlander et al. (2022)  |
|                    |                    | unc. Cyanobacteria | Pacific: Golfo Dulce  | Steinsdóttir et al. (2022) |
|                    |                    | unc. Cyanobacteria | Pacific: In front of Punta Copal, Isla Bolaños, Bahía Salinas, Guanacaste   | USJ-73735                  |

The taxonomic classification is based on Algae Base. Codes correspond to USJ-Herbaria Collection number, Universidad de Costa Rica.

**Table 5**  
DNA sequences of cyanobacteria in the NCBI and ENA databases.

| Site/Bioproject                                  | Accesion ID | Taxonomic classification      | Reference             |
|--|-------------|-------------------------------|-----------------------|
| Costa Rica Dome Upwelling Zone (8 m depth)       | EF102542    | unclassified Cyanobacteria    | Zehr et al. (2007)    |
|  | EF102614    | unclassified Cyanobacteria    | Zehr et al. (2007)    |
|  | EF102613    | unclassified Cyanobacteria    | Zehr et al. (2007)    |
|  | EF102612    | unclassified Cyanobacteria    | Zehr et al. (2007)    |
|  | EF102611    | unclassified Cyanobacteria    | Zehr et al. (2007)    |
|  | EF102590    | unclassified Cyanobacteria    | Zehr et al. (2007)    |
|  | EF102573    | unclassified Cyanobacteria    | Zehr et al. (2007)    |
| Stomach content of the crab <i>Paralomis</i> sp. | HE974904    | Uncultured Cyanobacterium sp. | Niemann et al. (2013) |

We found two studies that focused on cyanobacterial genome analysis (**Table 5**). Zehr et al. (2007) investigated the genomic diversity of tropical oceanic nitrogen-fixing cyanobacteria in the Dome Upwelling Zone in Pacific Costa Rica, obtaining cultures and amplifying the region encoding the cytochrome C gene using Sanger sequencing. The second study by Niemann et al. (2013) examined the bacterial communities associated with the decapod *Paralomis*.

## DISCUSSION

Published reports of cyanobacteria from the Pacific and the Caribbean of Costa Rica do not have photographs, and most of these reports lack data on temperature, salinity, pH,

substrate type, or other metadata, which limits our understanding of the ecology of these group. Additionally, these cyanobacteria are not associated with herbarium specimens. There are only 14 cyanobacterial samples in the herbarium collection. The improvement of herbarium records and sample conservation would support the training of future scientists. High-quality collections serve as invaluable resources for teaching taxonomy, systematics, ecology, and fostering the development of new expertise in these fields. Plus, it increases the knowledge of the marine biodiversity of the country.

Due to traditional sampling techniques, where larger micro-organisms are more likely to be studied, unicellular cyanobacteria or pycocyanobacteria are probably among the least studied. The classification of cyanobacteria



is undergoing rapid change due to advances in 16S rRNA gene and genome sequencing, independent and dependent culture techniques can now be used to characterize them, as well as other groups of cyanobacteria (Chen et al., 2021; Doré et al., 2023). Taxonomic studies must be polyphasic, incorporating morphological data such as cell size and shape, presence or absence of a mucilaginous sheath, and shape of apical cells, among others (Hauer & Komárek, 2022). The integration of genomic data is essential for conclusively defining the taxonomic clades of many cyanobacterial genera. The morphological similarity between some groups, such as the *Leptolyngbya* clade in Section III (Brenes-Guillén et al., 2021; Komarek, 2007), could be studied in marine environments to understand the coexistence of phylogenetic closely and ecologically similar cyanobacterial species.

There are several studies that summarize the cyanobacteria found in the region. Vargas et al. (2023) carried out a review of the diversity in the Caribbean region and reported 76 genera and 119 species of cyanobacteria associated with different environments such as coral reefs, ascidians, mangroves and others. In that study, *Lyngbya confervoides* is the only cyanobacteria mentioned for Costa Rica (based on the report by Bernecker & Wehrmann, 2009), unlike our research where we report 33 species for the Caribbean. Studies in Honduras and Belize indicate that new genera similar to the genera *Lyngbya* and *Symploca* may be found in marine environments (Engene et al., 2015). In Panama, studies on marine cyanobacteria have focused on the extraction of metabolites to identify novel treatments for neglected parasitic diseases such as malaria. The Panama International Cooperative Biodiversity Group (ICBG) programme has investigated secondary metabolites mainly from *Leptolyngbya*, *Symploca*, *Lyngbya* and *Oscillatoria* (Linington et al., 2007; McPhail et al., 2007; Medina et al., 2008; Simmons et al., 2006; Vining et al., 2015). Additionally, Diaz et al. (2007) found *Oscillatoria spongiae* associated with marine sponges in the Caribbean Sea of Panama.

Some groups of marine cyanobacteria are symbionts of protozoa, macroalgae, seagrasses, sponges, ascidians, and other invertebrates, altering the host's metabolism (Carpenter & Foster, 2003; Konstantinou et al., 2018; Mutali-passi et al., 2021). In addition, they possess cellular and molecular strategies that enable them to withstand nutrient limitation, temperature fluctuations, increased UV radiation, and high salinity (Li et al., 2019; Rastogi et al., 2014; Reignier et al., 2023). These characteristics suggest that these bacteria may have promising biotechnological applications. Current evidence shows the presence of marine cyanobacteria on both coasts of Costa Rica, highlighting their importance, but the morphological and genetic diversity of cyanobacteria in Costa Rican and Central Americans marine environments remains largely unknown. In order to improve our understanding of the taxonomic and functional diversity of cyanobacteria, it is essential to conduct studies focusing on morphological and genetic analysis, either using molecular markers such as 16S gene amplicons or whole genome sequencing. This will provide information on the microscopic characterization of cyanobacteria, their biogeographic distribution, temporal variations in abundance and the genetic reservoir. This publication will serve as a basis and motivation for future research.

**Ethical statement:** the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

## ACKNOWLEDGMENTS

LB and CF thank Dr. Luis A. Fournier Origgi Herbarium (USJ), Escuela de Biología, Universidad de Costa Rica for facilitating access to specimens. JC thanks the University of Costa



Rica for its support of marine biodiversity research over many decades.

## REFERENCES

- Ahlgren, N. A., Noble, A., Patton, A. P., Roache-Johnson, K., Jackson, L., Robinson, D., McKay, C., Moore, L. R., Saito, M. A., & Rocap, G. (2014). The unique trace metal and mixed layer conditions of the Costa Rica upwelling dome support a distinct and dense community of *Synechococcus*. *Limnology and Oceanography*, 59(6), 2166–2184. <https://doi.org/10.4319/lo.2014.59.6.2166>
- Arias-Orozco, P., Zhou, L., Yi, Y., Cebrián, R., & Kuipers, O. P. (2024). Uncovering the diversity and distribution of biosynthetic gene clusters of prochlorosins and other putative RiPPs in marine *Synechococcus* strains. *Microbiology Spectrum*, 12(1), e03611-23. <https://doi.org/10.1128/spectrum.03611-23>
- Bernecker, A., & Wehrtmann, I. S. (2009). New records of benthic marine algae and Cyanobacteria for Costa Rica, and a comparison with other Central American countries. *Helgoland Marine Research*, 63, 219–229. <https://doi.org/10.1007/s10152-009-0151-1>
- Brenes-Guillén, L., Vidaurre-Barahona, D., Morales, S., Mora-López, M., Sittenfeld, A., & Uribe-Lorío, L. (2021). Novel cyanobacterial diversity found in Costa Rican thermal springs associated with Rincon de la Vieja and Miravalles volcanoes: A polyphasic approach. *Journal of Phycology*, 57(1), 183–198. <https://doi.org/10.1111/jpy.13077>
- Burgin, J., Ahamed, A., Cummins, C., Devraj, R., Gueye, K., Gupta, D., Gupta, V., Haseeb, M., Ihsan, M., & Ivanov, E. (2023). The European nucleotide archive in 2022. *Nucleic Acids Research*, 51(D1), D121–D125. <https://doi.org/10.1093/nar/gkac1051>
- Calvo-Vargas, E., Boza-Abarca, J., & Berrocal-Artavia, K. (2014). Efectos de El Niño y La Niña sobre el comportamiento del microfitoplancton marino y las variables fisicoquímicas durante el 2008 a 2010 en el Golfo de Nicoya, Costa Rica. *Revista de Ciencias Marinas y Costeras*, 6, 115–133. <https://doi.org/10.15359/revmar.6.8>
- Calvo-Vargas, E., Berrocal-Artavia, K., & Boza-Abarca, J. (2016). Floraciones algales nocivas durante el periodo 2008-2010 en el Golfo de Nicoya, Costa Rica. *Revista de Ciencias Marinas y Costeras*, 8(1), 129–149. <https://doi.org/10.15359/revmar.8.1.9>
- Carlson, M. C. G., Ribalet, F., Maidanik, I., Durham, B. P., Hulata, Y., Ferrón, S., Weissenbach, J., Shamir, N., Goldin, S., Baran, N., Cael, B. B., Karl, D. M., White, A. E., Armbrust, E. V., & Lindell, D. (2022). Viruses affect picocyanobacterial abundance and biogeography in the North Pacific Ocean. *Nature Microbiology*, 7, 570–580. <https://doi.org/10.1038/s41564-022-01088-x>
- Carpenter, E., & Foster, R. A. (2002). Marine cyanobacterial symbioses. In: A. N. Rai, B. Bergman, & U. Rasmussen (Eds.), *Cyanobacteria in Symbiosis* (pp. 11–17). Springer. [https://doi.org/10.1007/0-306-48005-0\\_2](https://doi.org/10.1007/0-306-48005-0_2)
- Caivalcanti, G. S., Gregoracci, G. B., Dos Santos, E. O., Silveira, C. B., Meirelles, P. M., Longo, L., Gotoh, K., Nakamura, S., Iida, T., & Sawabe, T. (2014). Physiologic and metagenomic attributes of the rhodoliths forming the largest  $\text{CaCO}_3$  bed in the South Atlantic Ocean. *The ISME Journal*, 8(1), 52–62. <https://doi.org/10.1038/ismej.2013.133>
- Chen, M. Y., Teng, W. K., Zhao, L., Hu, C. X., Zhou, Y. K., Han, B. P., Song, L. R., & Shu, W. S. (2021). Comparative genomics reveals insights into cyanobacterial evolution and habitat adaptation. *The ISME Journal*, 15(1), 211–227. <https://doi.org/10.1038/s41396-020-00775-z>
- Cortés, J. (2012). Marine biodiversity of an Eastern Tropical Pacific oceanic island, Isla del Coco, Costa Rica. *Revista de Biología Tropical*, 60(Suppl. 3), 131–185. <https://doi.org/10.15517/rbt.v60i3.28356>
- Cortés, J., & Joyce, F. (2020). BioMar-ACG: A successful partnership to inventory and promulgate marine biodiversity. *Biotropica*, 52(6), 1103–1106. <https://doi.org/10.1111/btp.12841>
- Cortés, J., Vargas-Castillo, R., & Nivia-Ruiz, J. (2012). Marine biodiversity of Bahía Culebra, Guanacaste, Costa Rica: published records. *Revista de Biología Tropical*, 60(Suppl. 2), 39–71. <https://doi.org/10.15517/rbt.v60i2.19962>
- Cox, A. D., Noble, A. E., & Saito, M. A. (2014). Cadmium enriched stable isotope uptake and addition experiments with natural phytoplankton assemblages in the Costa Rica Upwelling Dome. *Marine Chemistry*, 166, 70–81. <https://doi.org/10.1016/j.marchem.2014.09.009>
- Dawson, E. (1962). Additions to the marine flora of Costa Rica and Nicaragua. *Pacific Naturalist*, 3(13), 375–395.
- Díaz, M. C., Thacker, R. W., Rützler, K., & Piantoni Dietrich, C. (2007). Two new haplosclerid sponges from Caribbean Panama with symbiotic filamentous cyanobacteria, and an overview of sponge-cyanobacteria associations. In: M. R. Custódio, G. Löbo-Hajdu, E. Hajdu, & G. Muricy (Eds.), *Porifera Research: Biodiversity, Innovation and Sustainability* (Serie Livros 28, pp. 31–39). Smithsonian Libraries and Archives.
- Donia, M. S., Fricke, W. F., Partensky, F., Cox, J., Elshahawi, S. I., White, J. R., Phillippe, A. M., Schatz, M. C., Piel, J., & Haygood, M. G. (2011). Complex microbiome underlying secondary and primary metabolism in the tunicate-*Prochloron* symbiosis. *Proceedings of the National Academy of Sciences of the United States of America*, 108(26), 10533–10538. <https://doi.org/10.1073/pnas.1103400108>



- National Academy of Sciences, 108(51), E1423–E1432. <https://doi.org/10.1073/pnas.1111712108>
- Doré, H., Guyet, U., Leconte, J., Farrant, G. K., Alric, B., Ratin, M., Ostrowski, M., Ferrieux, M., Brillet-Guéguen, L., Hoebeke, M., Siltanen, J., Le Corguillé, G., Corre, E., Wincker, P., Scanlan, D. J., Eveillard, D., Partensky, F., & Garczarek, L. (2023). Differential global distribution of marine picocyanobacteria gene clusters reveals distinct niche-related adaptive strategies. *The ISME Journal*, 17(5), 720–732. <https://doi.org/10.1038/s41396-023-01386-0>
- Drouet, F. (1936). Myxophyceae of the G. Allan Hancock Expedition of 1934, collected by Wm. R. Taylor. *Allan Hancock Pacific Expeditions*, 3, 15–32.
- Engene, N., Tronholm, A., Salvador-Reyes, L. A., Luesch, H., & Paul, V. J. (2015). *Caldora penicillata* gen. Nov., comb. Nov. (Cyanobacteria), a pantropical marine species with biomedical relevance. *Journal of Phycology*, 51(4), 670–681. <https://doi.org/10.1111/jpy.12309>
- Fernández, C. (2008). Flora marina del Parque Nacional Isla del Coco, Costa Rica, Pacífico Tropical Oriental. *Revista de Biología Tropical*, 56(Suppl. 2), 57–69.
- Flombaum, P., Gallegos, J. L., Gordillo, R. A., Rincón, J., Zabala, L. L., Jiao, N., Karl, D. M., Li, W. K., Lomas, M. W., & Veneziano, D. (2013). Present and future global distributions of the marine Cyanobacteria *Prochlorococcus* and *Synechococcus*. *Proceedings of the National Academy of Sciences*, 110(24), 9824–9829. <https://doi.org/10.1073/pnas.1307701110>
- Friedlander, A. M., Ballesteros, E., Breedy, O., Naranjo-Elizondo, B., Hernández, N., Salinas-de-León, P., Sala, E., & Cortés, J. (2022). Nearshore marine biodiversity of Osa Peninsula, Costa Rica: Where the ocean meets the rainforest. *PLoS ONE*, 17(7), e0271731. <https://doi.org/10.1371/journal.pone.0271731>
- Guiry, M. D., & Guiry, G. M. (2024). *AlgaeBase* [Online database]. National University of Ireland. <https://www.algaebase.org>; searched on 19 April 2024.
- Gutiérrez-Rodríguez, A., Slack, G., Daniels, E. F., Selph, K. E., Palenik, B., & Landry, M. R. (2014). Fine spatial structure of genetically distinct picocyanobacterial populations across environmental gradients in the Costa Rica Dome. *Limnology and Oceanography*, 59(3), 705–723. <https://doi.org/10.4319/lo.2014.59.3.0705>
- Hallegraeff, G. M. (2010). Ocean climate change, phytoplankton community responses, and harmful algal blooms: A formidable predictive challenge. *Journal of Phycology*, 46(2), 220–235. <https://doi.org/10.1111/j.1529-8817.2010.00815.x>
- Hargraves, P. E., & Víquez, R. (1981). *Spirulina subsalsa* Oersted en Costa Rica. Estructura y posible importancia comercial. *Revista de Biología Tropical*, 29(2), 304–308.
- Hauer, T., & Komárek, J. (2022). *CyanoDB 2.0 - On-line database of cyanobacterial genera* [Online database]. Univ. of South Bohemia & Inst. of Botany AS CR. <http://www.cyanodb.cz>
- Hoffman, L. (1999). Marine cyanobacteria in tropical regions: Diversity and ecology. *European Journal of Phycology*, 34(4), 371–379. <https://doi.org/10.1080/09670269910001736432>
- Komárek, J. (2007). Phenotype diversity of the cyanobacterial genus *Leptolyngbya* in the maritime Antarctic. *Polish Polar Research*, 3, 211–231.
- Konstantinou, D., Gerovasileiou, V., Voultsiadou, E., & Gkelis, S. (2018). Sponges-Cyanobacteria associations: Global diversity overview and new data from the Eastern Mediterranean. *PLoS ONE*, 13(3), e0195001. <https://doi.org/10.1371/journal.pone.0195001>
- Li, Y. Y., Chen, X. H., Xue, C., Zhang, H., Sun, G., Xie, Z. X., Lin, L., & Wang, D. Z. (2019). Proteomic response to rising temperature in the marine cyanobacterium *Synechococcus* grown in different nitrogen sources. *Frontiers in Microbiology*, 10, 1976. <https://doi.org/10.3389/fmicb.2019.01976>
- Linington, R. G., González, J., Ureña, L.-D., Romero, L. I., Ortega-Barriá, E., & Gerwick, W. H. (2007). Venturamides A and B: antimarial constituents of the panamanian marine Cyanobacterium *Oscillatoria* sp. *Journal of Natural Products*, 70(3), 397–401. <https://doi.org/10.1021/np0605790>
- Loza-Álvarez, S., Benavides-Morera, R., Brenes-Rodríguez, C. L., & Ballester-Saxon, D. (2018). Estructura del fitoplancton en las épocas seca y lluviosa en el golfo de Papagayo, Costa Rica. *Revista de Ciencias Marinas y Costeras*, 10(2), 9–30. <https://doi.org/10.15359/revmar.10-2.1>
- McPhail, K. L., Correa, J., Linington, R. G., González, J., Ortega-Barriá, E., Capson, T. L., & Gerwick, W. H. (2007). Antimalarial linear lipopeptides from a Panamanian strain of the marine cyanobacterium *Lyngbya majuscula*. *Journal of Natural Products*, 70(6), 984–988. <https://doi.org/10.1021/np0700772>
- Medeanic, S., Zamora, N., & Corrêa, I. C. (2008). Non-pollen palynomorphs as environmental indicators in the surface samples from mangrove in Costa Rica. *Revista Geológica de América Central*, 39, 27–51. <https://doi.org/10.15517/rgac.v0i39.12246>
- Medina, R. A., Goeger, D. E., Hills, P., Mooberry, S. L., Huang, N., Romero, L. I., Ortega-Barriá, E., Gerwick, W. H., & McPhail, K. L. (2008). Coibamide A, a potent antiproliferative cyclic depsipeptide from the Panamanian marine cyanobacterium *Leptolyngbya* sp. *Journal of the American Chemical Society*, 130(20), 6324–6325. <https://doi.org/10.1021/ja801383f>
- Muñoz-Simon, N. (2012). Cianobacterias bentónicas marinadas en el Caribe central y sur de Costa Rica. *Revista*



- de Ciencias Marinas y Costeras, 4, 13–32. <https://doi.org/10.15359/revmar.4.1>
- Muñoz-Simon, N., Piedra-Castro, L. M., Jiménez-Montealegre, R., Pereira-Chaves, J., Guevara-Mora, M., & Piedra-Marín, G. (2020). Efecto de las descargas del emisario submarino de aguas residuales de la ciudad de Limón sobre la calidad del agua, abundancia y diversidad del fitoplanton en los alrededores de isla Uvita, Costa Rica. *Revista de Ciencias Marinas y Costeras*, 12(2), 115–141. <https://doi.org/10.15359/revmar.12-2.6>
- Mutalipassi, M., Riccio, G., Mazzella, V., Galasso, C., Somma, E., Chiarore, A., de Pascale, D., & Zupo, V. (2021). Symbioses of cyanobacteria in marine environments: Ecological insights and biotechnological perspectives. *Marine Drugs*, 19(4), 227. <https://doi.org/10.3390/md19040227>
- Niemann, H., Linke, P., Knittel, K., MacPherson, E., Boetius, A., Brueckmann, W., Larvik, G., Wallmann, K., Schacht, U., & Omorogie, E. (2013). Methane-carbon flow into the benthic food web at cold seeps—a case study from the Costa Rica subduction zone. *PLoS ONE*, 8(10), e74894. <https://doi.org/10.1371/journal.pone.0074894>
- Nübel, U., Garcia-Pichel, F., & Muyzer, G. (1997). PCR primers to amplify 16S rRNA genes from cyanobacteria. *Applied and Environmental Microbiology*, 63(8), 3327–3332. <https://doi.org/10.1128/aem.63.8.3327-3332.1997>
- Rastogi, R. P., Sinha, R. P., Moh, S. H., Lee, T. K., Kottuparambil, S., Kim, Y.-J., Rhee, J.-S., Choi, E.-M., Brown, M. T., & Häder, D.-P. (2014). Ultraviolet radiation and cyanobacteria. *Journal of Photochemistry and Photobiology B: Biology*, 141, 154–169. <https://doi.org/10.1016/j.jphotobiol.2014.09.020>
- Reignier, O., Bormans, M., Marchand, L., Sinquin, C., Amzil, Z., Zykwinska, A., & Briand, E. (2023). Production and composition of extracellular polymeric substances by a unicellular strain and natural colonies of *Microcystis*: Impact of salinity and nutrient stress. *Environmental Microbiology Reports*, 15(6), 783–796. <https://doi.org/10.1111/1758-2229.13200>
- Rippka, R., Deruelles, J., Waterbury, J. B., Herdman, M., & Stanier, R. Y. (1979). Generic assignments, strain histories and properties of pure cultures of cyanobacteria. *Microbiology*, 111(1), 1–61. <https://doi.org/10.1099/00221287-111-1-1>
- Saito, M. A., Rocap, G., & Moffett, J. W. (2005). Production of cobalt binding ligands in a *Synechococcus* feature at the Costa Rica upwelling dome. *Limnology and Oceanography*, 50(1), 279–290. <https://doi.org/10.4319/lo.2005.50.1.0279>
- Simmons, T. L., McPhail, K. L., Ortega-Barría, E., Mooberry, S. L., & Gerwick, W. H. (2006). Belamide A, a new antimitotic tetrapeptide from a Panamanian marine cyanobacterium. *Tetrahedron Letters*, 47(20), 3387–3390. <https://doi.org/10.1016/j.tetlet.2006.03.082>
- Steinsdóttir, H. G., Gómez-Ramírez, E., Mhatre, S., Schauberger, C., Bertagnoli, A. D., Pratte, Z. A., Stewart, F. J., Thamdrup, B., & Bristow, L. A. (2022). Anaerobic methane oxidation in a coastal oxygen minimum zone: Spatial and temporal dynamics. *Environmental Microbiology*, 24(5), 2361–2379. <https://doi.org/10.1111/1462-2920.16003>
- Taylor, W. R. (1945). Pacific marine algae of the Allan Hancock Expeditions to the Galapagos Islands. *Allan Hancock Pacific Expeditions*, 12, 1–528.
- Vargas, A., Hentschke, G. S., Leão, P., & Vasconcelos, V. (2023). Marine cyanobacteria diversity and biotechnological potential in Caribbean waters. *Cryptogamie, Algologie*, 44(8), 143–156. <https://doi.org/10.5252/cryptogamie-algologie2023v44a8>
- Vargas-Montero, M. (2004). *Floraciones algales en Costa Rica, su relación con algunos factores meteorológicos y consideraciones sobre sus efectos socioeconómicos* [Tesis de maestría], Universidad de Costa Rica, Costa Rica.
- Vargas-Montero, M., & Freer, E. (2004). Proliferaciones algales nocivas de cianobacterias (Oscillatoriaceae) y dinoflagelados (Gymnodiniaceae) en el Golfo de Nicoya, Costa Rica. *Revista de Biología Tropical*, 52(Suppl. 1), 121–125.
- Vining, O. B., Medina, R. A., Mitchell, E. A., Videau, P., Li, D., Serrill, J. D., Kelly, J. X., Gerwick, W. H., Proteau, P. J., & Ishmael, J. E. (2015). Depsiipeptides companionamides from a panamanian marine cyanobacterium associated with the coibamide producer. *Journal of Natural Products*, 78(3), 413–420. <https://doi.org/10.1021/np5007907>
- Williamson, S. J., Rusch, D. B., Yoosoph, S., Halpern, A. L., Heidelberg, K. B., Glass, J. I., Andrews-Pfannkoch, C., Fadrosh, D., Miller, C. S., Sutton, G., Frazier, M., & Venter, J. C. (2008). The Sorcerer II Global Ocean Sampling Expedition: Metagenomic characterization of viruses within aquatic microbial samples. *PLoS ONE*, 3(1), e1456. <https://doi.org/10.1371/journal.pone.0001456>
- Zehr, J. P., Bench, S. R., Mondragon, E. A., McCaren, J., & DeLong, E. F. (2007). Low genomic diversity in tropical oceanic N<sub>2</sub>-fixing cyanobacteria. *Proceedings of the National Academy of Sciences*, 104(45), 17807–17812. <https://doi.org/10.1073/pnas.0701017104>
- Zhong, C., Yamanouchi, S., Li, Y., Chen, J., Wei, T., Wang, R., Zhou, K., Cheng, A., Hao, W., Liu, H., Konhauser, K. O., Iwasaki, W., & Qian, P. (2024). Marine biofilms: cyanobacteria factories for the global oceans. *mSystems*, 9, e00317-24. <https://doi.org/10.1128/msystems.00317-24>