

SPECIFIC RICHNESS OF BENTHIC MARINE CYANOPROKARYOTES NOSTOCALES (CYANOBACTERIA) FROM CAMPECHE, MEXICO

ERNESTO CABRERA-BECERRIL^{1,2*}, ANNIE MAY EK GARCÍA-GARCÍA^{1,2},
 MARÍA LUISA NÚÑEZ RESENDIZ², KURT M. DRECKMANN², ABEL SENTÍES²

¹ Doctorado en Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana, Mexico City, Mexico.

² Departamento de Hidrobiología, Universidad Autónoma Metropolitana-Iztapalapa, Mexico City, Mexico.

*Corresponding Author: votzila@gmail.com

Abstract

Background: Nostocales is one of the most diverse orders of cyanobacteria with 1,905 species currently recognised. Particularly, in Campeche only seven benthic marine species have been recorded.

Questions and/or Hypotheses: This study represents a first approach to the knowledge of the benthic marine diversity of Nostocales from Campeche, which, given its environmental heterogeneity, will be composed previously unrecorded species. Our aim is to expand the richness of this group, as well as provide detailed descriptions and illustrations for each species.

Site and years of study: Cyanobacteria collections were carried out during 2024, along three locations on the Campeche coast.

Methods: Semi-permanent preparations were made from fresh samples, microphotographs were taken, and morphometric measurements were recorded to determine taxonomic identification, comparing with specialized literature.

Results: A total of 17 species of Nostocales were obtained, of which nine correspond with new records from Campeche, representing 52.96 % of its diversity. Taxonomic notes were added to highlight morphological differences that do not match between our specimens and descriptions of species identified from specialised literature. Rivulariaceae is the most represented family.

Conclusions: The current study has allowed a greater appreciation of the state of knowledge of marine benthic Nostocales in the area, however, the diversity and specific richness of the group is currently widely underestimated, so more research focused on cyanoprokaryotes is needed.

Keywords: Prokaryote, littoral species, taxonomy, Gulf of Mexico.

Resumen

Antecedentes: Nostocales es uno de los órdenes de cianobacterias más diversos, con 1,905 especies reconocidas actualmente. Particularmente, en Campeche solo se han registrado siete especies marinas bentónicas.

Preguntas y/o Hipótesis: Este estudio representa un primer acercamiento al conocimiento de la diversidad marina bentónica de Nostocales de Campeche, la cual, dada su heterogeneidad ambiental, estará compuesta por especies no registradas previamente. Nuestro objetivo es ampliar la riqueza de este grupo, así como proporcionar descripciones e ilustraciones detalladas para cada especie.

Sitio y años de estudio: Las colecciones de cianobacterias se realizaron durante 2024, en tres ubicaciones a lo largo de la costa de Campeche.

Métodos: Se prepararon preparaciones semipermanentes a partir de muestras frescas, se tomaron microfotografías y se registraron mediciones morfométricas para determinar la identificación taxonómica, comparando con literatura especializada.

Resultados: Se obtuvieron un total de 17 especies de Nostocales, de las cuales nueve corresponden a nuevos registros para Campeche, representando el 52.96 % de su diversidad. Se añadieron notas taxonómicas para destacar las diferencias morfológicas que no coinciden entre nuestros especímenes y las descripciones de especies identificadas a partir de literatura especializada. Rivulariaceae es la familia más representada.

Conclusiones: El presente estudio ha permitido una mayor apreciación del estado del conocimiento de las Nostocales bentónicas marinas en la zona; sin embargo, la diversidad y riqueza específica del grupo se subestiman ampliamente en la actualidad, por lo que se necesita más investigación centrada en los cianoprocariontes.

Palabras clave: Procarionte, especies litorales, taxonomía, Golfo de México.

Nostocales is one of the most diverse orders of cyanobacteria, encompassing 43 families, 128 genera, and 1,905 currently taxonomic accepted species (Guiry & Guiry 2026), as well as fossil diversity comprising 18 families, 147 genera and 409 species (Hauer & Komárek 2026). Morphologically, all they are characterised by the presence of heterocytes, specialised cells responsible for nitrogen fixation, and akinetes (resistance structures). Also, they are recognised as the main primary producers in the aquatic environments such as rivers, lakes, oceans or coastal lagoons, even in extreme conditions (geysers, high sulphur content or hypersaline), or directly associated with other organisms (epizoic and epiphytic) (Whitton & Potts 2012). It is important to highlight that Nostocales includes several species that form harmful algal blooms (HABs), many of them potentially toxic (Komárek 2010a, Lind *et al.* 2016, Poot-Delgado *et al.* 2017, Bondarenko *et al.* 2021).

Over recent decades, they have been widely studied morphologically worldwide (Saker & Neilan 2001, Berrendero *et al.* 2008, Komárek 2010b, Werner *et al.* 2012, Galhano *et al.* 2011, Mishra *et al.* 2015, Radkova *et al.* 2020), leading to the description of new species (Chonudomkul *et al.* 2004, Rajaniemi *et al.* 2005, Vaccarino & Johansen 2011, 2012, Bohunická *et al.* 2015, 2024, Shalygin *et al.* 2018, Mesfin *et al.* 2020, Barbosa *et al.* 2021, Pecundo *et al.* 2021, Cai *et al.* 2022, Maltseva *et al.* 2022, Carmona-Jiménez *et al.* 2023, 2024, Saraf *et al.* 2024) or taxonomic arrangements at all hierarchical levels (Komárek 2010a, 2013, Komárek *et al.* 2014, 2016, Palinska & Surosz 2014, Strunecký *et al.* 2023, Hauer & Komárek 2026). Likewise, other important aspects of this group have been describe, such as phylogenetic relationships (Thomazeau *et al.* 2010, Galhano *et al.* 2011, Singh *et al.* 2015, Duval *et al.* 2018), ecological interactions (Saker & Neilan 2001, Sukenik *et al.* 2012, Cirés & Ballot 2016, Yema *et al.* 2016, Duval *et al.* 2018) or biotechnological approaches (Saker & Neilan 2001, Galhano *et al.* 2011, Nowruzi & Porzani 2021) including their toxic potential (Wang *et al.* 2015, Cirés & Ballot 2016, Capelli *et al.* 2017, Bondarenko *et al.* 2021, Nowruzi & Porzani 2021). However, the available studies pertain to species with a temperate distribution in the European region (Komárek 2013), whereas in tropical marine environments they remain unknown, partly due to the limited collection efforts targeting this group (Aguar-Caires *et al.* 2019, Cabrera-Becerril *et al.* 2024). In Mexico, particularly in the Gulf of Mexico and the Mexican Caribbean, the study of cyanobacteria remains underexplored, with merely 164 reports across the entire Mexican coastline (León-Tejera *et al.* 2019). The most recent review for these regions identifies 45 species of Nostocales (Cabrera-Becerril *et al.* 2025). Furthermore, the increase in the number of previously documented species, reported by Cabrera-Becerril *et al.* (2024) supports the hypothesis that species richness, particularly in marine ecosystems, remains underestimated. The above could be mainly due to the fact that in most cases, cyanobacteria species have been recorded as secondary components in phycofloristic studies (Ortega *et al.* 2001, Mateo-Cid *et al.* 2013b, Poot-Delgado *et al.* 2015, 2017, Mendoza-González *et al.* 2016), in which microphotographs or descriptions that facilitate comparison with other regions of the country are not provided (Mendoza-González *et al.* 2017, Cabrera-Becerril *et al.* 2024).

Campeche has been thoroughly analysed from a phycological perspective (Ortega *et al.* 2001, García-García *et al.* 2020, 2021), highlighting the heterogeneity of marine environments and their potential for the presence of both, algae and cyanoprokaryotes. However, only seven species of Nostocales have been previously recorded, belonging to five genera and five families along the entire coastline. In relation to marine environments, there are only seven studies that record benthic marine cyanoprokaryotes on the coasts of Campeche (Ortega *et al.* 2001, Tunnell Jr. *et al.* 2007, Mateo-Cid *et al.* 2013a, b, Poot-Delgado *et al.* 2015, 2017, Mendoza-González *et al.* 2016), of which none specifically focuses on the group.

Additionally, studies of Poot-Delgado *et al.* (2015, 2017) deal with lagoon towns that, although they present salinity values of 34 parts per thousand (ppt) - 39.7 ppt (Ponce-Vélez & Botello 1992, Ayala-Pérez *et al.* 2003), are coastal lagoons. However, given the salinity ranges (29.7 - 38 ppt) provided by Ortega (1995) in lagoons, close to seawater (Ortega *et al.* 2001), those records have been maintained here as marine environments. It is noteworthy that limited research exists on the phylogeny of Nostocales, in this sense, only González-Resendiz *et al.* (2018a, b) and Johansen *et al.* (2021) provide molecular data to the species from the Gulf of Mexico.

As a result, this study provides the first approach to investigating benthic marine species of Nostocales from Campeche, with the intention of obtaining a more integrated study of specific richness in marine environments

from Campeche, Mexico. Additionally, we provide microphotographs and detailed descriptions of the species recorded, thereby facilitating future research on this group.

Materials and methods

During September 2024, two samplings were made in from the intertidal zone of the Champotón, Sabancuy and Bahía Tortugas beaches of Campeche, México (Figure 1), chosen based on literature (Ortega *et al.* 2001, Poot-Delgado *et al.* 2015, Poot-Delgado 2016). Champotón a rocky beach, with calm waves, pebbles, loose rocks, and rock masses on the shore 19° 20' 29" N; 90° 44' 00" W (Figure 2A, B), Sabancuy a rocky-sandy beach, with various medium-sized rocks on the shore 18° 59' 29" N; 91° 11' 20" W (Figure 2C) and Bahía Tortugas or Playa Chenkan a sandy beach, with few protruding rocks along the shoreline 19° 06' 30" N; 91° 00' 43" W (Figure 2D).

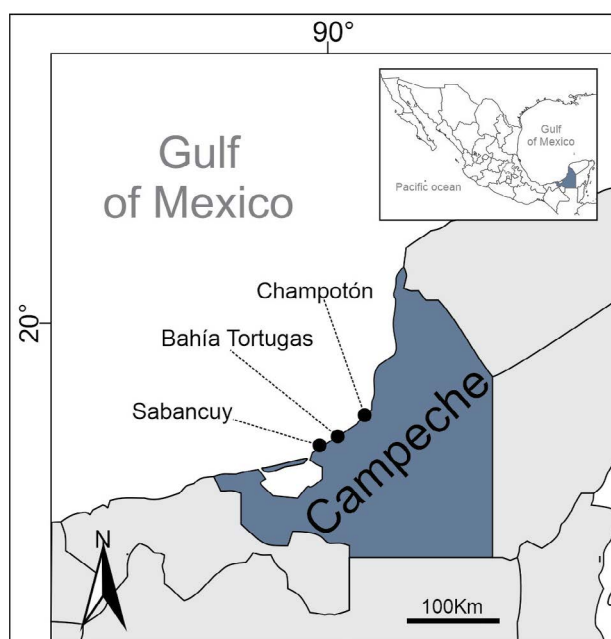


Figure 1. Map of the sampling sites on the coast of Campeche, Mexico. Champotón 19° 20' 29" N; 90° 44' 00" W. Sabancuy 18° 59' 29" N; 91° 11' 20" W. Bahía Tortugas or Playa Chenkan 19° 06' 30" N; 91° 00' 43" W.

Samples were collected manually using a chisel and hammer. Biofilms or mats were obtained from rock fragments of varying sizes, depending on the rock type, the ease of fragment extraction, and the characteristics of the colony or biofilm. The samples were preserved by drying the entire rock fragment with paper towels and silica to ensure proper conservation. Morphological descriptions were conducted using semi-permanent preparations, at least five preparations per sample were made, depending on the specific richness observed and the type of growth, whether it is mats, cushion-like, or spots, rehydrating material and mounted with 4 % glycerine gelatine. Furthermore, microphotographs were taken using a Quasar digital camera (Quasar TM, China), adapted to a Quasar Qm70 Infinity optical microscope (Quasar TM, China); characters of interest (general shape of the colony, length and width of cells, filament, shape of the tips, presence of branching, among others) were measured using the Top View 3.7.8481 program (ToupTek Photonics Co., Ltd). For taxonomic identification, the images and measurements were compared with the species referred in Komárek (2013) and recent publications (Bohunická *et al.* 2015, 2024, González-Resendiz 2018a, 2018b, Mesfin *et al.* 2020, Johansen *et al.* 2021, Cai *et al.* 2019, 2022, Carmona-Jiménez *et al.* 2023). Additionally, literature documenting Nostocales species in Campeche was consulted to obtain a potential list. The validity of the species name and synonymy were reviewed in the AlgaeBase (Guiry & Guiry 2026) and Ciano DB2 (Hauer & Komárek 2026) databases.



Figure 2. Images of the sampling sites. A-B) Champotón. C) Sabancuy. D) Bahía tortugas.

Results

The updated list of benthic marine species of Nostocales from Campeche is presented, consisting of 17 species distributed in 12 genera and seven families. The most represented families were: Rivulariaceae (5 spp), followed by Calotrichaceae (4 spp), Scytonemataceae (3 spp), Nostocaceae (2 spp); Aphanizomenonaceae, Hapalosiphonaceae, Stigonemataceae with a single species ([Table 1](#), [Figure 3](#)). one. Likewise, detailed descriptions, microphotographs, and taxonomic comments for each taxon are included.

Morphological Descriptions. Calotrichaceae Bennet & Murray.

Calothrix C. Agardh ex Bornet & Flahault

Calothrix clausa Setchell & N. L. Gardner ([Figure 4A-D](#))

Description. Mats in macroscopic mats, 870-1,131 μm long, black or dark green in colour. Heteropolar trichomes, bright to dark green in colour, up to 1 mm long, with a wavy to straight appearance, with a tapered conical apex, without terminal hair; the last cells can change shape, from wider than long to circular. Cells wider than long, the basal and middle ones (13.5)16-22.5(23.8) μm wide $\times$ (3.4)4-9(10.7) μm long, the apical cells (8.3)9.42-16.06(18.06) μm width $\times$ (3.5)4.61-8.62 μm long. Thick sheath colourless in the newer areas and light brown in the mature ones,

Cyanoprokaryotes from Campeche, Mexico

Table 1. Species of Nostocales from Campeche. 1. Ortega *et al.* 2001, 2. Tunnell Jr. *et al.* 2007, 3. Mateo-Cid *et al.* 2013b, 4. Poot-Delgado *et al.* 2015, 5. Mendoza-González *et al.* 2016, 6. Poot-Delgado 2016, 7. Cabrera-Becerril *et al.* 2024, 8. Setchell & Gardner 1924, X = in this work and bold. Environment: M = marine; E = estuary

Family	Taxonomically valid name	Reported Species	Environment	References
Aphanizomenonaceae	<i>Raphidiopsis cuspis</i> (Komárek & Kling) Aguilera, Berrendero Gómez, Kastovsky, Echenique & Salerno	as <i>Cylindrospermopsis cuspis</i> Komárek & Kling	E	6, 4
Calotrichaceae	<i>Calothrix clausa</i> Setchell & N.L. Gardner		M	X
	<i>Calothrix fusca</i> Bornet & Flahault		M	X
	<i>Calothrix longifila</i> W. R. Taylor		E	1
	<i>Calothrix nidulans</i> Setchell & N. L. Gardner		M	X
Hapalosiphonaceae	<i>Chlorogloeopsis fritschii</i> (A. K. Mitra) A. K. Mitra & D. C. Pandey		M	X
Nostocaceae	<i>Anabaena</i> sp.		E	6,4
	<i>Nostoc</i> sp.		E	6
Rivulariaceae	<i>Dichothrix fucicola</i> Bornet & Flahault		M	1
	<i>Dichothrix orsiniana</i> Bornet & Flahault		M	X
	<i>Dichothrix seriata</i> Setchell & N. L. Gardner		M	X
	<i>Kyrtuthrix</i> sp.		M	X
	<i>Nunduva</i> sp.		M	X
	<i>Brachytrichia quoyi</i> Bornet & Flahault		M	3
Scytonemataceae	<i>Scytonema hoffmannii</i> C. Agardh ex Bornet & Flahault	as <i>Calothrix crustacea</i> Thuret ex Bornet & Flahault (7, 12, 18); as <i>Scytonematopsis crus- tacea</i> (Thuret ex Bornet & Flahault) Kováčik & Komárek (7, 9)	M	3, 1, 2, 5
	<i>Scytonematopsis pilosa</i> (Bornet & Flahault) Umezaki & M. Watanabe		M	7, X
Stigonemataceae	<i>Stigonema tomentosum</i> Hieronymus		M	X

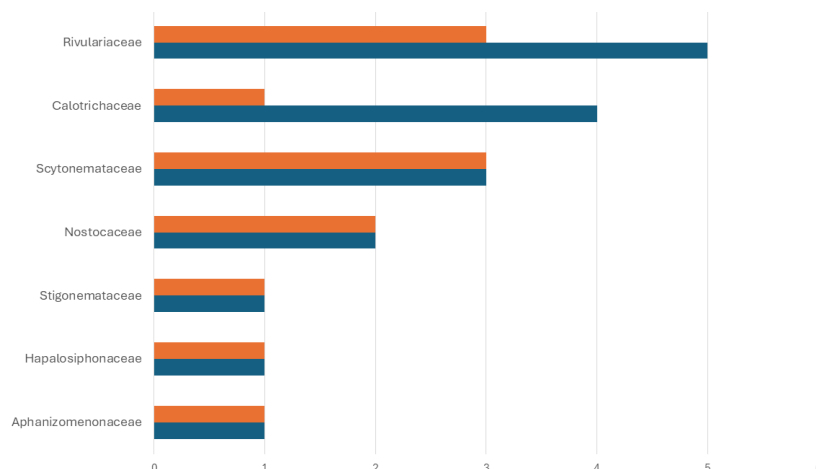


Figure 3. Species by family of benthic marine cyanoprokaryotes from Campeche. In orange, the number of genera per family and in blue, the present species.

lamellated, with several distinguishable layers, (29.6) 33-42.8 μm wide. Heterocytes numerous, up to 5 in the basal region of the trichome, with a crescent shape and several intercalary ones with a square shape, up to wider than long. The intercalary heterocytes can measure up to 23 μm in diameter.

Habitat. Rocks at the edge of the coast, with light splashing waves and tides, exposed to the sun.

Samples. Champotón and Sabancuy. Collection date: September 5th and 7th 2024.

Taxonomic notes. Our specimens partially match morphologically and the reference image with *Calothrix clausa* (Komárek 2013), as well as with the length of the trichomes and the environment described as marine. However, the sheath is not stratified nor does it present solitary heterocytes, as well as the reported cell wide (24-28 μm wide), above our specimens. It also partially agrees with the general morphology described for the genus *Nunduva* (González-Resendiz *et al.* 2018), due to the type of heteropolar trichome and the intercalary heterocytes, although it does not match the morphology described for the species of the genus. Previously reported for Mexico, Isla Guadalupe, Baja California (Setchell & Gardner 1930).

Calothrix fusca Bornet & Flahault ([Figure 4E-F](#))

Description. Black mats, 50-100 millimeters in diameter. Short filaments, 130-192 μm long. Olive to bright green trichomes, heteropolar; cells slightly attenuated towards the ends, without apical hair formation, slightly constricted, unbranched. Cells wider than long, with homogeneous content, 6-10.2 (12.9) μm wide $\times$ 2-4.5 (5.4) μm long, apical cells (4.07) 4.62-6.91 (7.07) μm wide $\times$ (1.83) 2.29-3.01 (3.89) μm long. Sheath thick, colourless, distinguishable, open towards the apex, 12.7-20.8 (23.2) μm wide. Basal heterocytes, semicircular or horn-shaped, one to two per trichome, 6.8-13 (14.6) μm wide $\times$ 4.6-10.3 μm long.

Habitat. Rocks at the edge of the coast, with gentle splashes from the waves and changes in tides, exposed to the sun.

Samples. Champotón. Collection date: September 7th, 2024.

Taxonomic notes. Our description matches with *Calothrix fusca* and the reference image by Komárek (2013), the cell wide match, although the interval is larger in our material (7-8 μm wide) (Komárek 2013). However, it does not

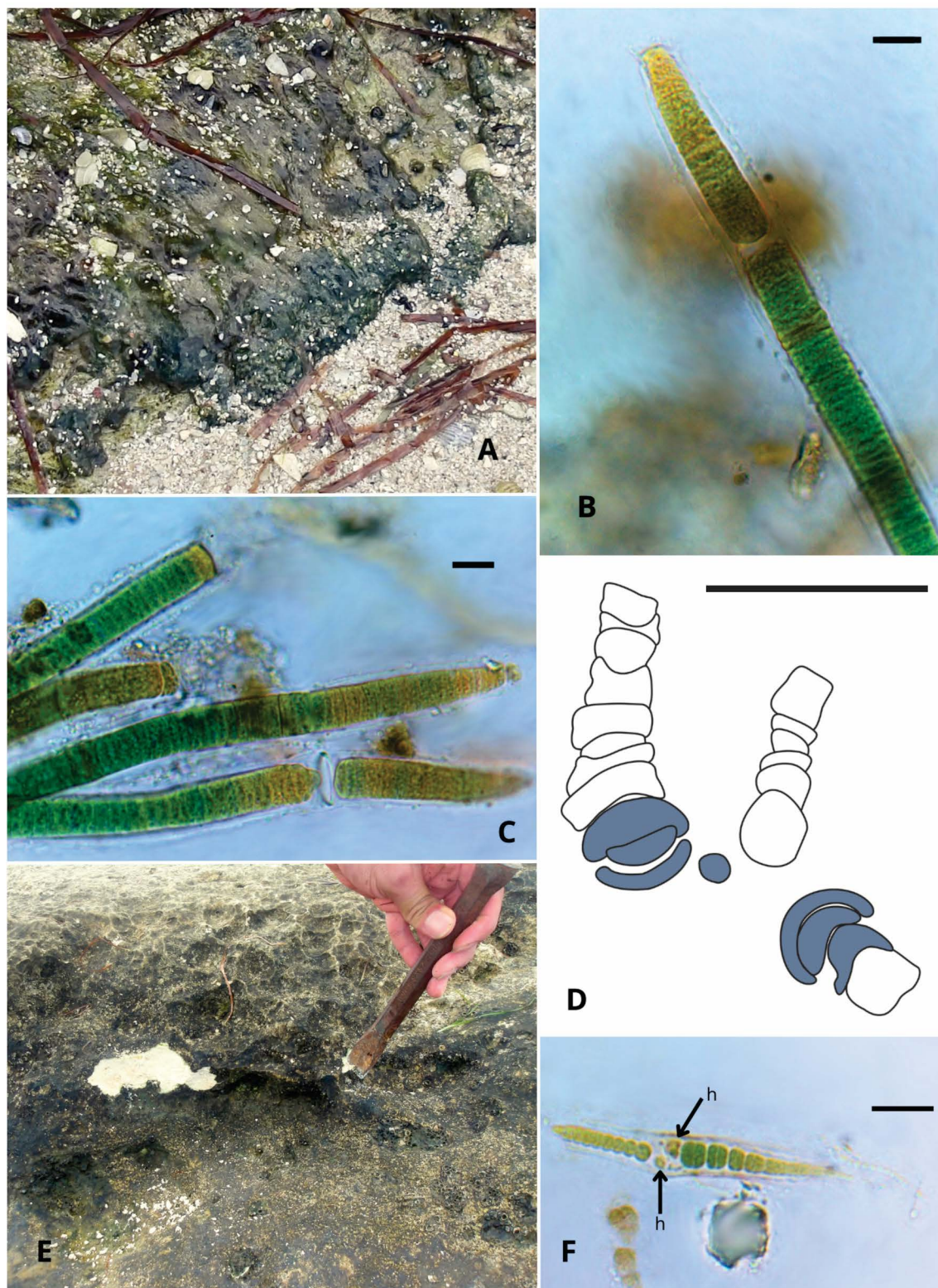


Figure 4 *Calothrix clausa* (A-D). A) Field sample, black mats. B) Thick sheath, lamellated, detail of the attenuated apex (B-C). D) The diagram shows basal heterocytes, up to 5 (blue). *Calothrix fusca* (E-F). E) Field sample Mats black, several millimetres in diameter. F) Small filament, bright green cells are noticeable, within the sheath open at the apex, basal heterocytes. Scale 20 μm.

match the wideness of the filament base or the environment, described as cosmopolitan and subaerophytic in temperate soils. Komárek (2013) describes this species with some varieties, including *C. fusca* var. *marina* Ercegović (not recognised by Guiry & Guiry (2026) classification system, without further morphological data for comparison; however, he also suggests that the species requires a more in-depth review. Furthermore, our specimens exhibit partial congruence with *C. aeuriginosa* Woronichin; nevertheless, according to Komárek (2013), only the filament length matches the description, but it doesn't match in wide interval, while the reference image, habitat, and intercalary heterocytes. It partially matches *C. violacea* Jaag in growth form, but the reference image does not correspond to the widening at the base or the intervals of cell measurements (3-6 µm in width). In contrast, it matches the reference image of *C. fonticola* Brabez, although it does not align with the measurements for the wide and long of the filament and cells.

Calothrix nidulans Setchell & N. L. Gardner ([Figure 5A-D](#))

Description. Thallus postrate or mats on rocks, resembling grass like mats black spots. Filament 73-250 µm long, colourless sheath, (12) 13.6-29.5 (32) µm wide, yellowish in mature filaments, open at the apex, occasionally showing a widening near the apex. Trichome bright green, heteropolar, attenuated, with apical hair formation, slightly constricted, straight or curved, cytoplasm with pigment granules. Basal cells 16.56-20.7(26.15) µm wide × (6.17)6.7-8.63(12.15) µm long, in the middle part (10.77)10.98-15.65(16.28) µm wide × (3.72)3.91-5.52(5.86) µm long, apical cells (4.66)5.64-9.51(10.06) µm wide × (1.79)2.68-3.41 µm long; always wider than long to slightly square. Basal heterocytes, rounded to semicircular, one to five per trichome, 13.6-14.5 µm wide width × 2.5-8.5 (10.4) µm long.

Habitat. On rocks by the shore, with splashing waves, exposed to the sun.

Samples. Champotón. Collection date: September 7th, 2024.

Taxonomic notes. Our findings correspond with the genus description provided by Komárek (2013). The characterization of *C. nidulans* corresponds to the marine environment, whereas the reference image fails to align with the specified parameters for filament and cell wide. This species is found in a subsection of the genus, where species without akinetes, with and without apical hairs are found. According to the dichotomous key of the genus in Komárek (2013), it corresponds with *C. aeruginea*; however, neither the reference image nor the measurement intervals in general match our material. Previously recorded for the Gulf of California, Mexico, by Setchell & Gardner (1924).

Rivulariaceae Bornet & Flahault

Nunduva González-Reséndiz, León-Tejera & J. R. Johansen

Nunduva sp.1. ([Figure 6A-D](#))

Description. Mats in dark clumps, forming dark patches of several millimeters in diameter on rocks. Trichomes bright blue-green to yellow color, with false branching, heteropolar, slightly constricted, with rounded to slightly tapered apices, without apical hair formation. Cells wider than long, occasionally isodiametric, (18.92)20.3-27.7(29.0) µm wide × 3.4-10.8(16.2) µm long. Evident sheath, lamellated, colourless to brownish tones in mature filaments, 36.5 × 42.5 µm wide. Intercalary heterocytes, trapezoidal to semicircular in shape, 24.8-35 µm wide × (8.7)10-23.7 µm long.

Habitat. Rocks at the edge of the coast, with gentle waves splashing and tides, exposed to the sun.

Samples. Champotón. Collection date: September 7th, 2024.

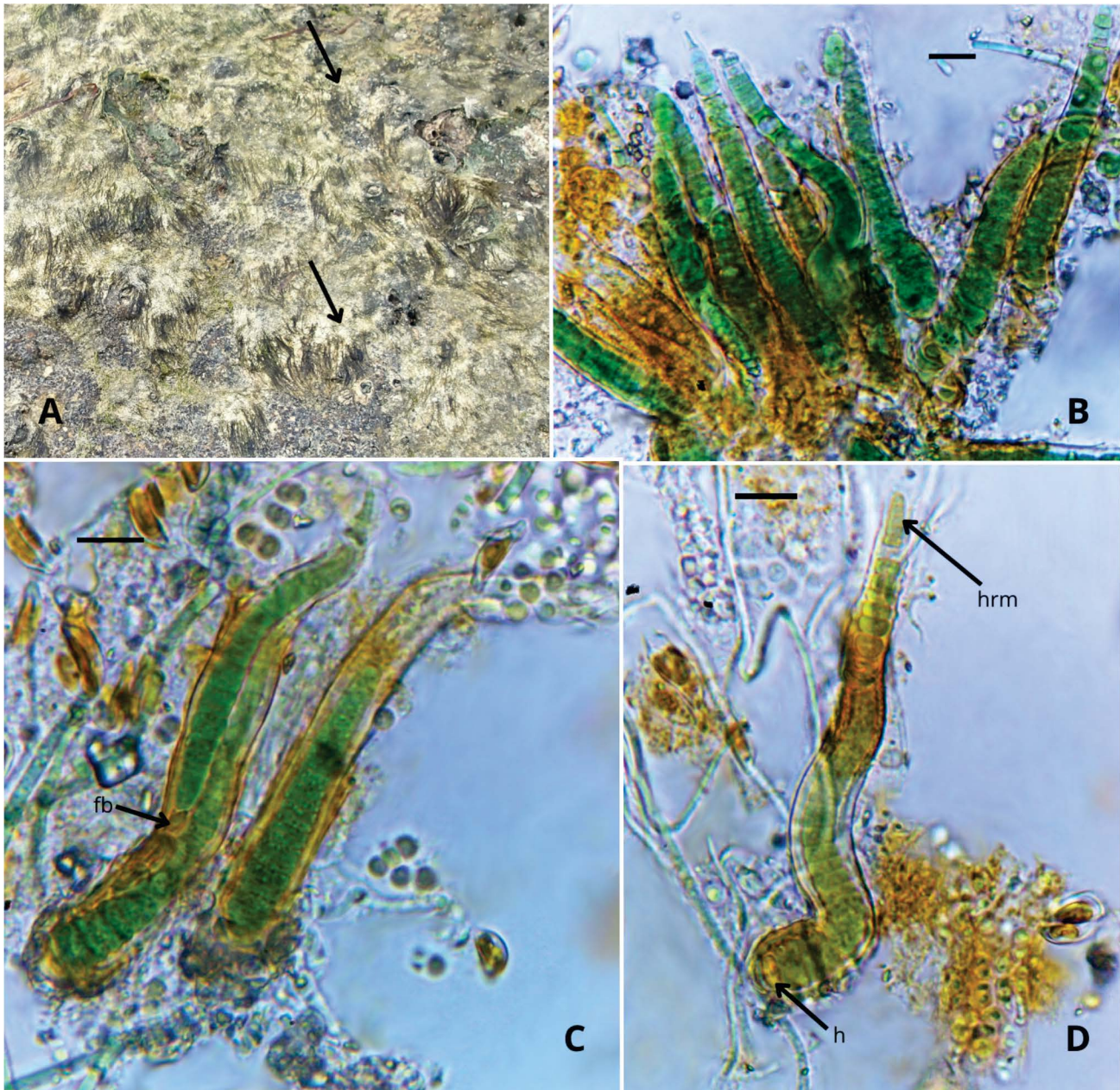


Figure 5. *Calothrix nidulans* (A-D). A) Field sample prostrate thallus or mats on rocks. B) Growth of the species, heteropolar filaments, attached at the base to the substrate. C) False branching (fb), rarely observed. D) Basal heterocytes (h) formation of a hormogonium (hrm) at the apex. Scale 20 μ m.

Taxonomic notes. Our observations do not align with species and genera outlined in Komárek (2013). While there are shared characteristics with *Scytonematopsis* Kisseleva, including the positioning of heterocytes and the attenuated apex, discrepancies exist in the false branching pattern, sheath opening, and cell measurements. Our specimens might match the description of the genus *Nunduva*, as they exhibit heteropolar trichomes, attenuated at the apex, as well as intercalary and basal heterocytes; however, they do not match the description or reference images of any of the seven species recorded so far (Johansen *et al.* 2021).

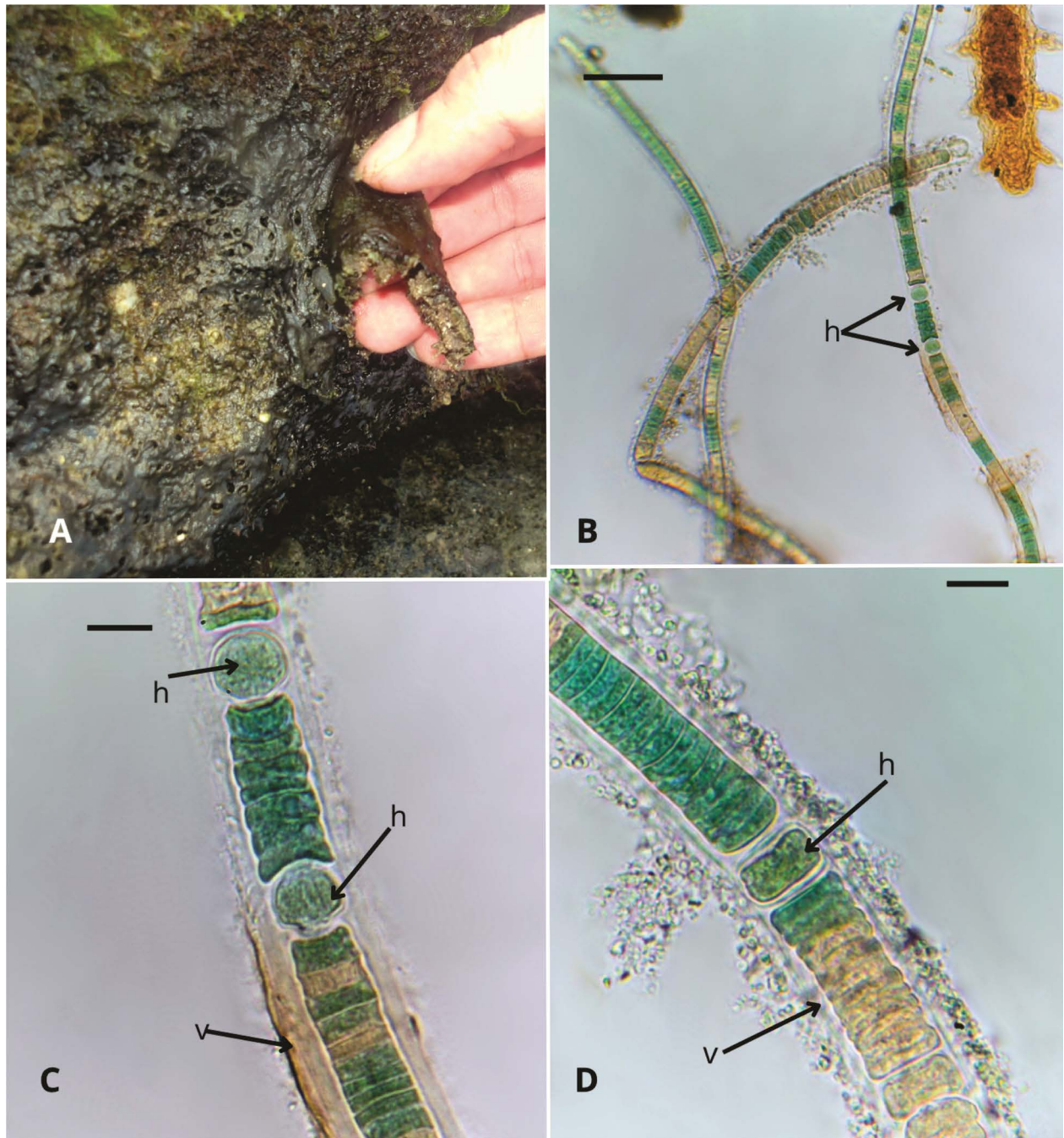


Figure 6. *Nunduva* sp. (A-D). A) Mats in dark clumps, forming dark patches. B) Detail of growth at lower magnification, heterocytes (h). C-D) Hyaline sheath (v), thick with indistinguishable edges, intercalary heterocytes (h), cells wider than long. Scale 20 µm.

Dichothrix Zanardini ex Bornet y Flahault

Dichothrix orsiniana Bornet & Flahault ([Figure 7A-B](#))

Description. Mats in small, circular packages, like hemispheric, or lobate mats, dark, black, or dark green. Filaments of (20)50-180(249.6) µm long. Heteropolar trichomes, dark to bright green, attenuated, gradually narrowed tower ends, without apical hair formation; the apical parts are less coloured, becoming yellowish. Cells wider than long,

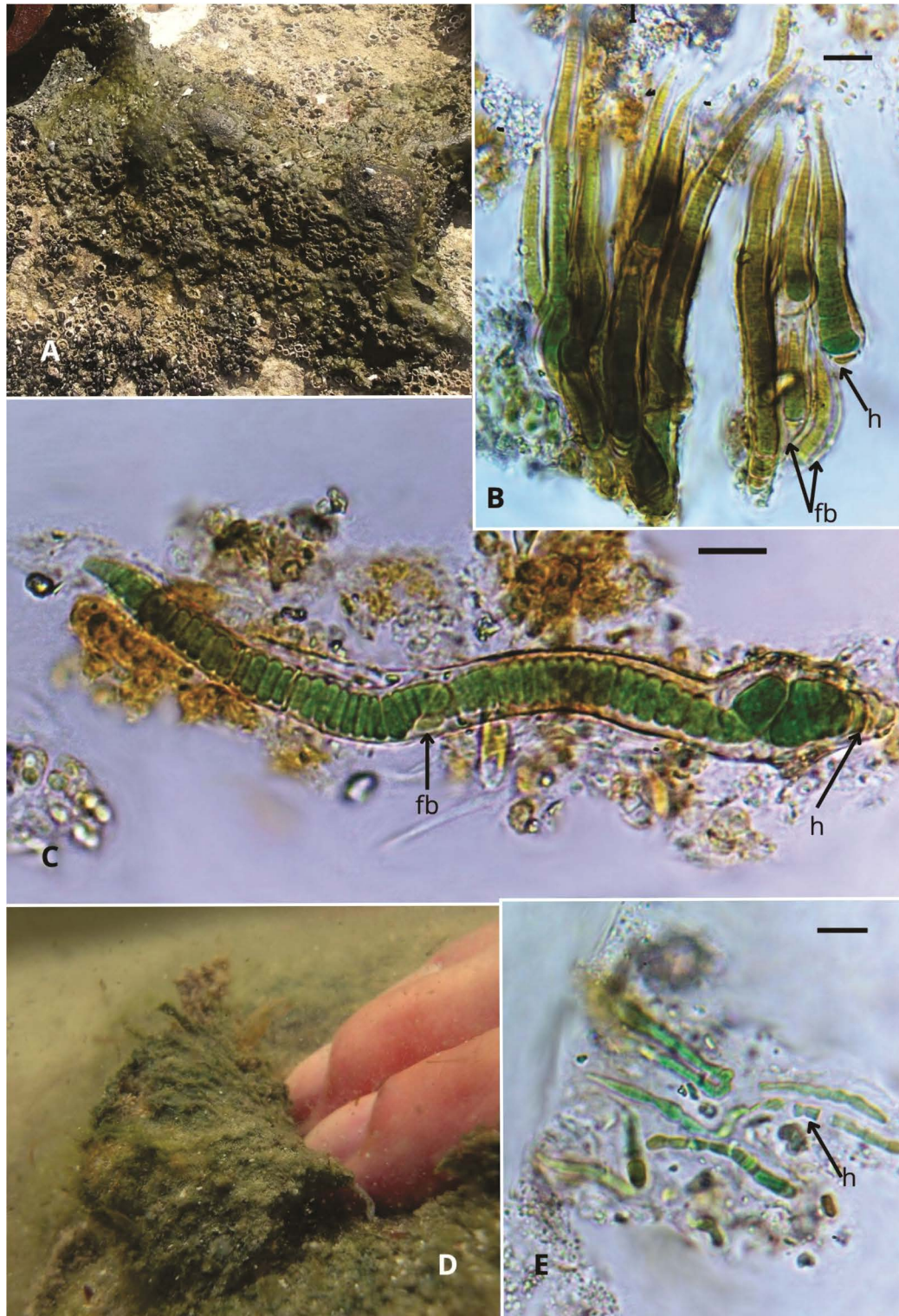


Figure 7. *Dichothrix orsiniana* (A-B). A) Mats in small, circular packages, like pom-poms. B) Forming false branches (fb), basal heterocysts are observed (h), yellow in color, sheath brown; the filaments show a swelling in the basal areas. *Dichothrix seriata* (C)., filament with false branching (fb) (arrow), the new filament growing over the original trichome, both within the same sheath (fasciculated) typical of *Dichothrix*, heterocysts (h). *Kyrthothrix* sp. (D-E). D) Cluster of mats, dark green. E) Branching in “V” or “U”, olive green filaments with intercalary heterocysts (h). Scale 20µm.

almost isodiametric, becoming less wide as they move away from the basal apex; cells in the middle part (6.5)8.72-15.7(19.3) μm wide $5 \times$ (4.03)4.92-6.7(11.8) μm long, apical cells (2.63)2.93-6.95(8.72) μm wide $\times$ (2.68)2.93-3.36(3.53) μm long. Thick sheath, distinguishable, non-lamellated, colourless to dark brown, (8.8)13.8-15.5(21) μm wide. Basal heterocytes, one or two per trichome, yellow in colour, trapezoidal to semicircular, 5.3-13.5 μm wide $\times$ 2.6-8 μm long.

Habitat. Rocks at the edge of the coast, with light splashing waves and tides, exposed to the sun.

Samples. Champotón. Collection date: September 7th, 2024. Bahía Tortugas or Playa Chenkan. Collection date: September 6th, 2024.

Taxonomic notes. The characteristics of our specimens partially match with the description, reference image, and the long and wide measurements of the filament of *Dichothrix orsiniana* in Komárek (2013). However, our material does not match the shape of crescent heterocytes in terms of the cell wide, which presents a smaller interval (6-8 μm), nor with the reported environment (rocks in rivers, streams, and waterfalls).

Dichothrix seriata Setchell & N.L. Gardner ([Figure 7C](#))

Description. Mats in the shape of dark green hemispheric or clusters. Filaments up to 165.3 μm long. Heteropolar trichomes, constricted, with false branching, slightly attenuated in the apical region, without apical hair formation; the basal cells are thicker. Cells of (9.5)10.4-19.7 μm wide $\times$ (2.4)2.9-6.4(9.2) μm long, bright green, with homogeneous content. Thick, colourless sheath with defined edges, (16.1)20.5-24.9(33.3) μm wide. Basal heterocytes, 2 to 5, 8.4-13.6 μm wide $\times$ 3.5-6 μm long.

Habitat. Growing on rocks, exposed to the sun and splashed by the waves.

Samples. Champotón, Campeche. Collection date: September 7th, 2024.

Taxonomic notes. Our specimens match with those described for the genus *Dichothrix* in Komárek (2013); the type of branching resembles that described for the genus, distinct from the false branching configuration present in *Calothrix*. Our material matches the description of the species *D. seriata* in the reference image, the measurements of the wide of the trichomes and cells, and the environment described as marine; however, it does not match the wide of the filament, as our material presents a smaller interval than that described for the species (25-35 μm wide). In Komárek (2013), they are described in the section of species outside Europe, for the Pacific coast of North America. Komárek (2013) mentions the need for a more thorough review of these species.

Kyrtuthrix Ercegović

Kyrtuthrix sp.1. ([Figure 7D-E](#))

Description. Clusters of mats, dark green. Filaments of (18.15) 29.5-87 (143) μm in length. Thin trichomes, bright green to yellow, isopolar, constricted, attenuated, without forming apical hairs, forming “U” turns or “V” branches. Cells wider than long to longer than wide, (2.4)3.5-6.7(7.2) μm wide $\times$ (2.9)3.7-12.5(16.3) μm long. Hyaline sheath, firm, with indistinct edges, colourless, (11.5)18-30.4(31.6) μm wide. Intercalary heterocytes, trapezoidal to semi-spherical, 6.4-8.6 μm wide $\times$ 4.8-7.61(10.9) μm long.

Habitat. Rocks at the edge of the coast, with gentle splashes from the waves and changes in tides, exposed to the sun.

Samples. Champotón, Campeche Collection date: September 7th, 2024.

Taxonomic notes. The characteristics of our specimens match with description of the genus by Komárek (2013), in the U or V branching pattern, growth forms, the general shape of the trichomes, and the presence of a sheath. However, it does not match either of the two species reported in this book: *K. maculans* (Gomont) I. Umezaki and *K. dalmatica* Ercegovic. It also does not match the descriptions and reference images described for *Kyrtuthrix huatulcensis* León-Tejera, González-Resendiz & Johansen, *K. totonaca* León-Tejera, González-Resendiz & J. R. Johansen, or *K. munecosensis* J. R. Johansen, González-Resendiz & León-Tejera 2021 (León-Tejera *et al.* 2016, Johansen *et al.* 2021). More analyses are required to determine its identity.

Scytonemataceae Rabenhorst ex Bornet & Flahault

Scytonematopsis Kiseleva

Scytonematopsis pilosa (Bornet y Flahault) Umezaki y M. Watanabe ([Figure 8A-D](#))

Description. Thallus dark green, in the form of clumps and mats. Filaments Bright to olive green. Trichome heteropolar, constricted; rounded, slightly tapered, conical tips, with or without calyptra, the calyptra measures 29.6 µm in width × 3.4 µm in length. Cells wider than long, (18.8)19.5-26.5(30.7) µm wide × (3.61)4.5-15.6(18.7) µm long. Thick, diffuse, colourless, lamellated sheath, 36.5-45.8 µm wide. Heterocytes present, basal, waning moon, one or two per trichome, intercalary, conical to isodiametric, more than one per filament, 22.4-29.6 µm wide × 9.9-24.7(26.3) µm long.

Habitat. Rocks at the edge of the coast, with light splashing waves and tidal changes, exposed to the sun.

Samples. Champotón, Campeche. Collection date: September 7th, 2024; and Sabancuy. Collection date: September 5th, 2024.

Taxonomic notes. Our observations partially correspond with the description of *S. pilosa* in Komárek (2013), in the reference image. The presence of calyptra, the measurements and shape of the heterocytes, the wide of the filament (19.5-43.7 µm wide) and the cells (6.9-20.7 µm wide), which is greater in ours, the coiling of the trichome within the sheath, and the presence of CaCO₃ incrustations do not match. According to Komárek (2013), this species requires review, as it likely contains several genotypes. Cabrera-Becerril *et al.* (2024) provides a description that aligns well with the original one; however, it exhibits certain distinguishing traits, particularly in the coloration of the trichomes and the sheath, which differ from our sample. This also partially aligns with *Calothrix nodulosa* Setchell & N. L. Gardner, as described in Komárek (2013). Setchell & Gardner (1924) previously reported this for Mexico; however, the reference image and cell measurements differ. The measurements of the filaments and trichomes match those of *C. consociata* Bornet & Flahault (as “unclear species” in Komárek (2013), for the genus *Calothrix*), which does not contain a reference image; with *Isactis plana* Thuret ex Bornet & Flahault, it also matches in the reference image, the environment, and the image in Golubic *et al.* (1999); however, the descriptions lack measurements for comparison. The species *Calothrix pilosa* Harvey ex Bornet & Flahault is a synonym of *S. pilosa*, both have been previously reported for Mexico as *Calothrix pilosa* in Yucatán (Ortega *et al.* 2001), the northeastern and southeastern Gulf of Mexico (León-Tejera *et al.* 2009), and as *S. pilosa* for Veracruz (Cabrera-Becerril *et al.* 2024).

Chlorogloeopsidaceae Mitra & Pandey

Chlorogloeopsis A.K. Mitra & D.C. Pandey

Chlorogloeopsis fritschii (A. K. Mitra) A. K. Mitra & D. C. Pandey ([Figure 8E-F](#))

Description. Colonies growing on rocks, with a cushion-like shape, dark green. It forms packages of cells or clusters, irregular or semicircular with smooth edges. Filaments or pseudofilaments, 152-264 µm long, widened towards the base. Uniseriate to biseriate trichomes, isopolar, space between cells of the same trichome. Circular to semicircu-

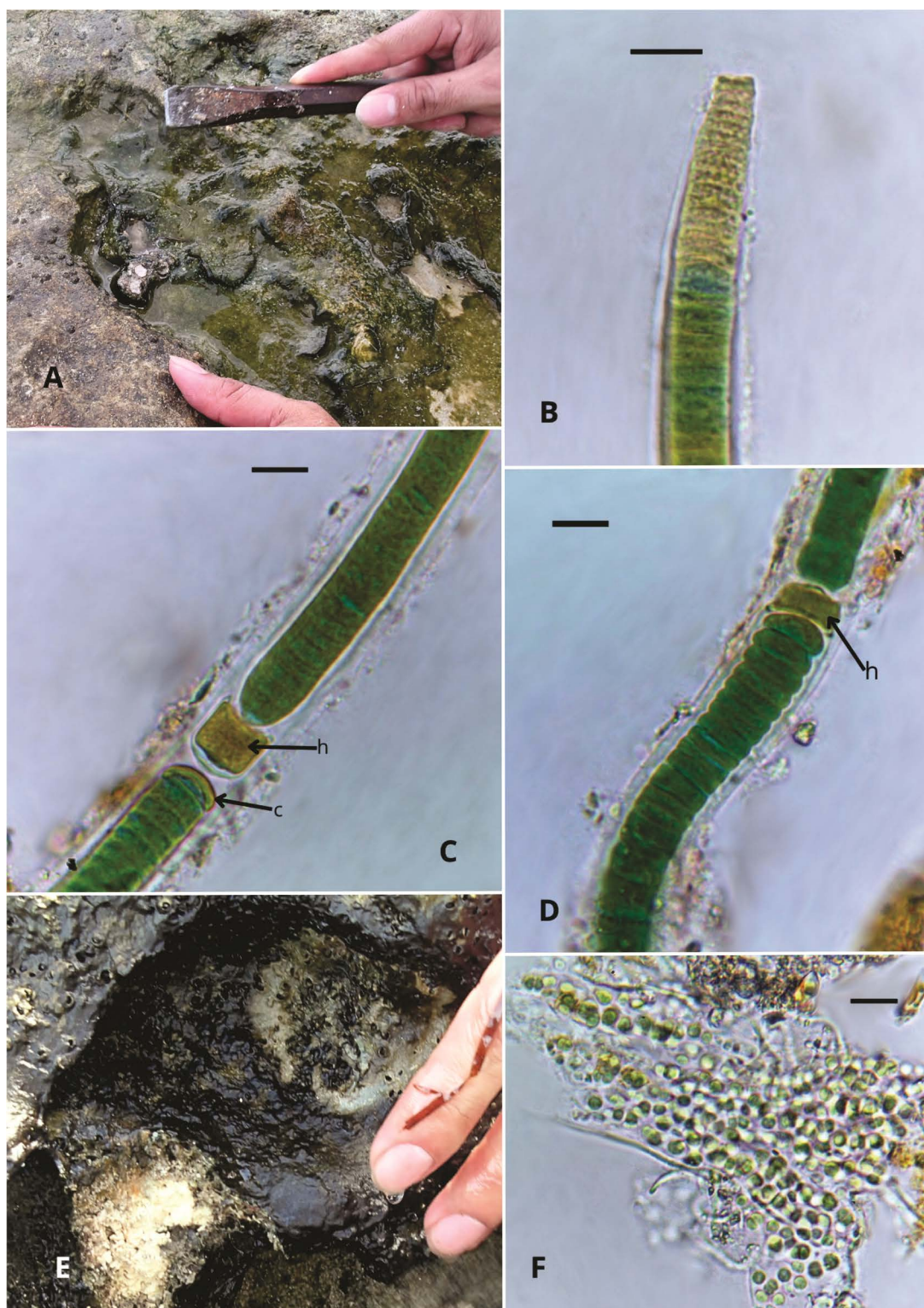


Figure 8. *Scytonematopsis pilosa* (A-D). A) Thallus dark green, in the form of clumps. B) Rounded apices, C) Trichome with calyptra (c), heterocytes (h). D) Lamellated sheath and intercalary heterocytes (h). *Chlorogloeopsis fritschii* (E-F). E) Colonies growing on rocks, with a cushion-like shape. F) Smooth edges of the colonies, *Pleurocapsa*-like filaments, range from 1 to 3 or more rows of cells without an independent sheath for each cell. Scale 20 μ m.

lar cells, olive green, 4-8.6(9) μm in diameter, 12.8-58.4(65) μm in area, 12.7-26.8(28.6) μm in perimeter, exhibit a binary fission pattern, change the growth pattern to form branches. Evident sheath, with smooth edges, hyaline, (14.5)23-38(42.3) μm wide. Heterocytes and akinetes are not observed.

Habitat. On rocks, together with other cyanobacteria, exposed to wave action due to tidal changes and splashing, exposed to sunlight.

Samples. Champotón, in front of the Hotel Lua. Collection date: September 7th, 2024.

Taxonomic notes. Our specimens match those described in Komárek (2013) for this species, both in general shape and reference image, as well as in the number of cell rows in the pseudofilaments similar to those present in *Pleurocapsa*. However, it does not match the presence of apical heterocytes or the previously described environment of soils or hot springs in India, USA, and Europe. The genus has been poorly studied in a natural environment; most reports and descriptions of the genus and species come from cultures, so a more thorough review is required. It is likely that the similarity with coccal-type species causes confusion when recognizing it from field or even cultivation material.

Stigonemaceae (Bornet & Flahault) Borzi

Stigonema Agardh ex Bornet & Flahault

Stigonema tomentosum Hieronymus ([Figure 9A-F](#))

Description. Black, spot-shaped mats on a rock. Filaments up to 40 μm long, violet to dark brown, uni- or biseriate, with “T” branching. Uniseriate and biseriate trichomes, violet to black, the branches are not entirely distinguishable from a central filament, erect and folded towards it. Cells of (2.4)3-6(6.7) μm in width $\times$ (2.3)3-5.8(6), trapezoidal to semicircular, two planes of division, violet pigment granules present. Hyaline sheath, colourless or yellowish in mature filaments, distinguishable, (5.6)6-9.33 μm wide. Heterocytes were not observed.

Habitat. On sandy rocks, at the edge of the beach, exposed to the waves by splashes and tidal changes, exposed to the light.

Samples. Sabancuy. Collection date: September 5th, 2024.

Taxonomic notes. Our specimens match with the genus description by Komárek (2013). For *S. tomentosum*, it matches the reference image, the colour of the macroscopic thalli, and the characteristics of the sheath; it does not match the filament wide measurements (12-17 μm wide) and the cell measurements (10-12 μm wide); our material has smaller measurement intervals. The environment is generally described as aerophilic, on moist rocks and wood; it is suggested that tropical populations require thorough review, as they may be several different species.

Discussion

Of the 17 species recorded in the present study, nine constitute new reports for Campeche, representing a 52.96 % increase of the state species richness, with respect to the previously reported species. Likewise, for the Mexican Atlantic, whose specific richness currently consists of 167 species, it represents a 4 % increase. On the other hand, of the nine seven are also new records for Mexico: *Calothrix clausa*, *C. fusca*, *C. nidulans*, *Chlorogloeopsis fritschii*, *Dichothrix orsiniana*, *D. seriata* and *Stigonema tomentosum*; being only *Scytonema pilosa* and *Calothrix nidulans* previously documented for the country (Setchell & Gardner 1924, Ortega *et al.* 2001, León-Tejera *et al.* 2009, Cabrera-Becerril *et al.* 2024).

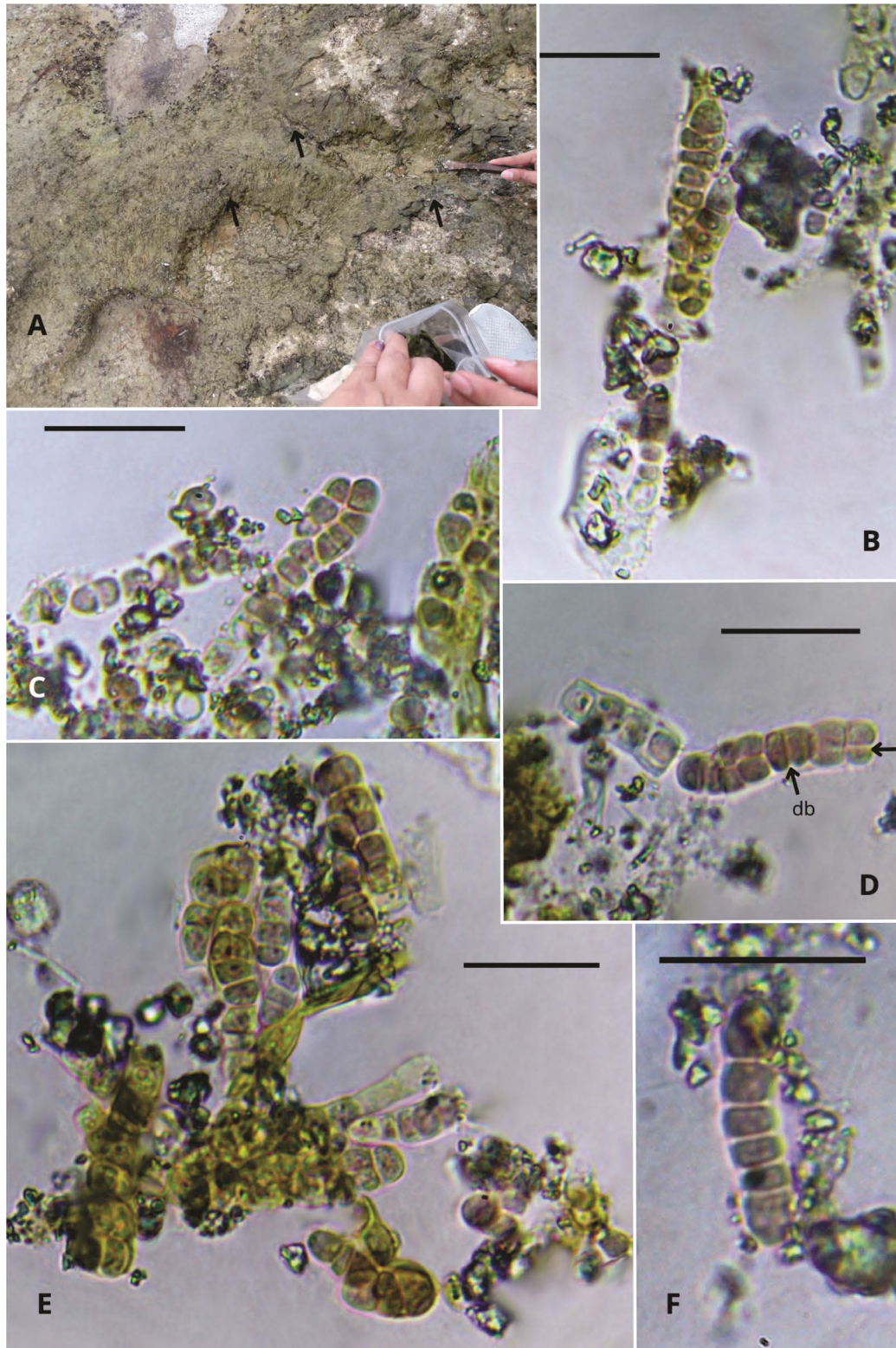


Figure 9. *Stigonema tomentosum* (A-F). A) Mats in the form of spots, on rock, black. B-C) Multiseriate violet-colored fragmented trichomes. D) Change in division pattern (dp) forming true branches. E) Colony: the growth turns yellow in older cultures, and true branching is observed. F) uniseriate fragmented trichomes. Scale 20 µm.

The families with the highest specific richness were: Rivulariaceae (5 spp.), representing 29 % of the total and being the family with the highest richness, Calotrichaceae (4 spp. - 23 %), Scytonemataceae (3 spp. - 18 %), Nostocaceae (2 spp. - 12 %), and Aphanizomenonaceae (1), Hapalosiphonaceae (1), and Stigonemataceae (1), each representing 6 %. It is noteworthy that the family Calotrichaceae constituted 23 % of the specific richness, comprising only one genus (*Calothrix*), despite its high species count, whereas Rivulariaceae demonstrated greater genetic diversity with three genera, representing the family with the highest richness (Figure 5; Table 1).

A similar trend was previously described by Cabrera-Becerril *et al.* (2024) regarding the Nostocales species from Veracruz, where Rivulariaceae (with seven species and four genera) was also the most diverse, while Capsosiraceae and Hapalosiphonaceae (with one species and one genus each) were the least diverse (Cabrera-Becerril *et al.* 2024). However, because the article included Capsosiraceae species (*Desmosiphon* cf. *neocaledonicus*) that the present study did not, the recorded families were different. Similarly, species from the Stigonemataceae family (*Stigonema tomentosum*; Table 1) were not included in the present research (Cabrera-Becerril *et al.* 2024). Previous investigations indicate that the family Rivulariaceae is highly polyphyletic and exhibits significant morphological diversity, it can be inferred by examining the morphological diversity present in the genera of this family (Berrendero *et al.* 2008, León-Tejera *et al.* 2016, Saraf *et al.* 2019, Berthold *et al.* 2022). The morphological diversity of Rivulariaceae is reflected in our data, in which 29 % of the recorded species belong to this family, as well as in previous studies from other states, such as Veracruz, as has been previously discussed (Cabrera-Becerril *et al.* 2024). Comparing our findings with other research carried out in Mexico that demonstrate this (León-Tejera *et al.* 2016, González-Resendiz *et al.* 2018 a, b, Johansen *et al.* 2021, Cabrera-Becerril *et al.* 2024), it is evident that substantial potential exists in the description of new species within this group in tropical zones, given the percentage increase in species (53 % in Campeche and 57 % in Veracruz) compared to previous studies (Briggs 1996, Büdel 1999, Thajuddin & Subramanian 2005, Rigonato *et al.* 2017, Cabrera-Becerril *et al.* 2024). The genera *Calothrix*, *Kyrtuthrix*, and *Nunduva*, which are part of this family, gave compelling cases for discussion. The morphology of *Kyrtuthrix* sp., does not align with the other species documented within the genus, which includes three recently described Mexican species (León-Tejera *et al.* 2016, Johansen *et al.* 2021). While its morphology is consistent with the descriptions for the genus *Kyrtuthrix* as outlined by Komárek (2013) and Johansen *et al.* (2021), molecular analyses are necessary to ascertain its identity in relation to the other Mexican species of the genus *Kyrtuthrix*, despite the afore mentioned advancements, is insufficiently studied globally and needs comprehensive evaluations employing a polyphasic approach to ascertain its actual species richness. Although Johansen *et al.* (2021) mention the possibility that molecular analyses and the discovery of new species at the generic level, such as *Kyrtuthrix*, could lead to a saturation of cyanobacterial taxonomy, which would imply the need for a rearrangement of species to merge some or the fusion of genera for better rearrangement, we believe that this case does not yet apply to the particular case of tropical species, especially Mexican ones, in marine environments. As mentioned before and demonstrated in several investigations (Ortega *et al.* 2001, González-Resendiz *et al.* 2018 a, b, Cabrera-Becerril *et al.* 2024), this area remains inadequately investigated, and not all species now inhabiting the nation's tropical marine ecosystems are yet identified. On the other hand, the treatment that should be given to genera and species described as requiring review (Komárek 2013) to ascertain their validity, or even their existence, must be considered, as there are several examples of polyphyletic genera within Nostocales that have presented a considerable number of cryptic species. In this case, we find genera such as *Nostoc*, which has been divided into several genera using molecular tools (Rajaniemi *et al.* 2005, Komárek 2010a, Hrouzek *et al.* 2013, Mishra *et al.* 2015, 2021, Cai *et al.* 2019), or *Calothrix*, which presents a great morphological variety that could potentially involve new species (Berrendero-Gómez *et al.* 2016, Saraf *et al.* 2019, Villanueva *et al.* 2019) or phenotypic plasticity (Komárek 2013, Johansen *et al.* 2021, Cabrera-Becerril *et al.* 2024).

The *Nunduva* sp. described in this article displays a morphology akin to that of *Brasilonema*. (González-Resendiz *et al.* 2018a, Berthold *et al.* 2022), although it also shows resemblance to species of the genera *Scytonema* and *Calothrix*. In the specific instance of *Brasilonema*, these species are distinguished by their freshwater and subaerial habitats, whereas *Nunduva* has predominantly been documented in marine environments, particularly in rocky intertidal zones. Therefore, an analysis of the species of these genera is required to compare morphology and molecular

sequences to identify possible new species, possible new genera, reclassify species, or simply determine the taxonomic position of those previously described (Margheri *et al.* 2008, Brito *et al.* 2017, Carmona-Jiménez *et al.* 2023). Thanks to the use of molecular tools and phylogenetic analyses, with a polyphasic approach, the genus *Nunduva* was separated from *Scytonemataceae* and placed as a new genus within *Rivulariaceae* (González-Resendiz *et al.* 2018a).

The presence of these types of analogous morphology, (by example *Chlorogloeopsis fritschii*, *Stigonema tomentosum*, *Kyrtuthrix* sp., *Dichothrix orsiniana*, *Calothrix fusca*, which have been described for other environments, as mentioned in the taxonomic notes) in species from different environments suggests phenotypic plasticity or evolutionary convergence, where the characteristics of the observed phenotypes are the result of adaptation to various environments at different points in the evolutionary history of the species that do not maintain correlation with each other (Fusco & Minelli 2010, Pfennig *et al.* 2010, Koch *et al.* 2017). Furthermore, we will encounter cryptic species within several genera where these morphological features have been recognised (*Scytonema*, *Scytonematopsis*, *Calothrix*, and *Brasilonema*), as documented in other species and genera from different orders such as *Phormidium retzii* Kützing ex Gomont (*Oscillatoriales*) (Casamatta *et al.* 2003), *Oculatella* Zammit Billi & Albertano (*Pseudanabaenales*) (Osorio-Santos *et al.* 2014), *Nostoc indistinguendum* Řeháková & Johansen, and *Nostoc desertorum* Řeháková & Johansen (Řeháková *et al.* 2007).

Species within *Calothrix* requires further investigation alongside the previously described Mexican species, due to their morphological similarities with other genera, including *Tolypothrix* Kützing ex Bornet and Flahault, molecular techniques have been the sole means of delineating these species (Berrendero *et al.* 2011). *Calothrix* has recently undergone several taxonomic rearrangements linked to molecular work with the genes 16s and ITS 16S-23S (Berrendero *et al.* 2008, 2011, Saraf *et al.* 2019). However, the taxonomic position of the family remains uncertain until sequences of the type species is obtained (Strunecký *et al.* 2023). Although classification systems like Hauer & Komárek (2026) acknowledge their existence, supported by works such as Saraf *et al.* (2019), which, after analysing several species of the family, suggest their presence. Therefore, research on Mexican *Calothrix* species could be beneficial to gain greater certainty about the existence of the family, as well as to delineate the distinctive characteristics of Mexican, tropical, marine, and other environmental species.

In Campeche, although being coastal, the collecting sites, specifically Champotón and Sabancuy, exhibit distinct characteristics compared to other locations, such as Veracruz (Cabrera-Becerril *et al.* 2024). The environmental conditions, wave characteristics, geological composition, and current dynamics are distinct. In Veracruz, the waves are more vigorous, whereas the Campeche beaches feature milder waves. In both locations, the waves that submerge the growths are mostly influenced by the tide rather than the intensity of the waves themselves. The environment in both cases is rocky intertidal; yet, due to the characteristics, the populations are distributed differently. Furthermore, in Campeche the rock types appear to be sandy and less consolidated compared to the sedimentary and limonite rock found in Veracruz. In Campeche, numerous growth mats resembling pom-poms or semi-spherical mats are noted, generated by species of *Calothrix* and *Dichothrix*. Conversely, in Veracruz, the mat-forming species exhibit longer filaments from the families *Scytonemataceae*, *Calotrichaceae*, and *Rivulariaceae* (*Rivularia*). The different physiographic characteristics and wave action of the collection areas could affect the growth forms (Whitton & Potts 2012, Cabrera-Becerril *et al.* 2024).

The findings of the present study, together with the morphological discrepancies observed in previously described species lacking complete correspondence and the environmental and growth variability recorded, indicate that the diversity of benthic marine cyanobacteria remains insufficiently understood. These results highlight the need for further research along the Campeche coast, encompassing broader sampling areas and the application of a polyphasic approach integrating ecological and molecular tools. Such efforts would improve our understanding of the specific richness of *Nostocales* in the region and contribute to broader biological knowledge of this important group.

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