Botanical Sciences 102 (2): 561-585. 2024
DOI: 10.17129/botsci.3391

Received: August 18, 2023, Accepted: January 17, 2024
On line first: March 15, 2024

Taxonomy and Floristics / Taxonomía y Florística

Diversity of marine benthic species of Nostocales (Cyanobacteria) in Veracruz, Mexico

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Abstract

Background: Nostocales is a widely distributed, monophyletic order of cyanobacteria, whose species are mainly characterized by the presence of specialized structures such as heterocytes and akinetes. Despite being the most diverse group in marine environments, little is known about coastal species in Mexico. Particularly in Veracruz, only 17 species have been recorded, without photographic, morphological references, or ecological data; these records are only mentioned in floristic lists.

Questions and / or Hypotheses: The present study aimed to contribute to the knowledge of the diversity of benthic marine Nostocales species in Veracruz, Mexico, as well as to provide detailed descriptions and illustrations of the species found, which can serve as a reference in subsequent studies.

Study site and dates: Collect of cyanobacterial growths were made in three locations throughout Veracruz in 2020.

Methods: The organisms were isolated from the field material. With the use of specialized taxonomic keys, they were morphologically identified, described and photographed.

Results: A total of 20 Nostocales species were obtained, of which 17 were additions to the phycoflora of Veracruz, constituting an increase of 55 %. Taxonomic notes are added highlighting their differences with the literature. One of the species was identified as cf. and seven as sp., because their characteristics fully coincided with the generic morphology, but did not completely concur with the literature.

Conclusions: These suggest that several records could correspond to new taxon not yet described that must be confirmed with different molecular markers.

Key words: flora, littoral species, morphology, taxonomy

Resumen:

Antecedentes: Nostocales es un orden monofilético de cianobacterias, ampliamente distribuido, cuyas especies se caracterizan principalmente por la presencia de estructuras especializadas como heterocitos y acinetos. A pesar de ser el grupo más diverso en ambientes marinos, en México se conoce poco sobre las especies litorales. Particularmente en Veracruz solo se han registrado 17 especies, sin referencias fotográficas, morfológicas, ni datos ecológicos; estos registros solo se mencionan en listas florísticas.

Preguntas y / o Hipótesis: El presente estudio tuvo como objetivo contribuir al conocimiento de la diversidad de especies Nostocales marinos bentónicos en Veracruz, México, así como brindar descripciones e ilustraciones detalladas de las especies encontradas, que puedan servir como referencia en estudios posteriores.

Sitio y años de estudio: Se realizaron recolectas de crecimientos de cianobacterias en tres localidades de Veracruz en 2020.

Métodos: A partir del material de campo se aislaron los organismos. Con el uso de claves taxonómicas especializadas se identificaron morfológicamente, describieron y fotografiaron.

Resultados: Se obtuvo un total de 20 especies de Nostocales, de las cuales 17 fueron adiciones a la ficoflora de Veracruz, constituyendo un incremento del 55 %. Se agregan notas taxonómicas destacando las diferencias de estas con la literatura. Una de las especies fue identificada como cf. y siete como sp., debido a que sus características coincidían plenamente con la morfología genérica, pero no lo hacían completamente con la literatura.

Conclusiones: Estos sugieren que varios registros podrían corresponder a nuevo taxón aún no descrita que deben ser confirmados con diferentes marcadores moleculares.

Palabras clave: especies litorales, flora, morfología, taxonomía

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Nostocales Borzì represents a monophyletic group currently made up of 1,531 living species taxonomically valid (Guiry & Guiry 2022 www.algaebase.org), distributed in 23 families and 128 genera (Hauer & Komárek 2022). They can be found throughout the world, in a wide range of environments, both terrestrial and aquatic, such as rivers, lakes, seas, coastal lagoons, extreme environments (such as geysers and waters with a high sulfur content), hypersaline, associated with rocks or other organisms (epizoic and epiphytic, mainly red algae), epibionts from the roots of mangroves, forming mats resistant to desiccation and tolerant to changes in salinity; particularly those species that are benthic in the littoral zone, form macroscopic growths from the supralittoral to the sublittoral zone (Hoffmann 1999, Whitton & Potts 2012, León-Tejera *et al*. 2016a). These species are distinguished from others mainly by the presence of specialized structures, both in nitrogen fixation (heterocytes) and in resistance to environmental stress (akinetes), in addition to a wide diversity of growth forms, types of branching (true and false) or trichome arrangements that can be isopolar or heteropolar (Komárek *et al*. 2014).

Although in other parts of the world the diversity of this group has been widely studied from morphological (Bolch *et al*. 1999, García-Pichel *et al.* 2001, Casamatta *et al*. 2005, Willame *et al*. 2006, Berrendero *et al*. 2008, Raabova *et al*. 2019, Conklin *et al*. 2020, Radkova *et al*. 2020), taxonomic (Skulberg *et al.* 1993, Hašler & Poulíčková 2010, Palinska & Surosz 2014, Komárek 2016, Mikhailyuk *et al*. 2016, Johansen *et al*. 2021), phylogenetic (Řeháková *et al*. 2007 Hrouzek *et al*. 2013, Genuario *et al*. 2015, Cai *et al*. 2019b, Jiang *et al*. 2020, Cai *et al.* 2020, 2022, Gaysina *et al*. 2022, Baldarelli *et al*. 2022), ecological (Stal 1995, Paerl & Millie 1996, Sellner 1997, Whitton & Potts 2012, Cohen & Gurevitz 2006, Paerl & Fulton 2006), or even the toxic potential of species (Falconer 1996, Baker *et al*. 2002, Lagos 2003, Paerl & Fulton 2006, Moreira *et al*. 2014, Kubickova *et al.* 2019), in Mexico they are practically unknown. Currently, there are 1,123 species recorded (Novelo & Tavera 2022) of which only 164 corresponds to marine environments (León-Tejera *et al*. 2019).

Particularly, in the Gulf of Mexico and the Mexican Caribbean, which represents one of the sites with great environmental heterogeneity in the country (García-García *et al.* 2021), conducive to the establishment of different biological groups, only 148 species have been recorded (León-Tejera *et al*. 2016b). Even though in these environments where the cyanoprokaryotes, mainly Nostocales, constitute one of the most conspicuous groups due to their diversity and abundance, they have gone almost unnoticed. In the few studies where they are included, are only mentioned indirectly as part of the macroalgae collections (Ortega *et al*. 2001) or in the best of cases, part of a general floristic lists that do not contain information on the criteria used for their identification, such as illustrations or diagnosis (Humm & Hildebrand 1962, Huerta *et al*. 1977(*Memorias del Congreso Nacional de Oceanografía)*, Sánchez-Rodríguez 1980, Mendoza-González & Mateo-Cid 1985, Ramírez-Rodríguez *et al*. 2011, Nava-Olvera *et al*. 2017), and even, most of them are identified only at generic level (Ortega *et al*. 2001, Varona-Cordero & Gutiérrez-Mendieta 2003).

Veracruz is one of the states of the Gulf of Mexico in which seaweeds have been well studied but cyanobacteria, and mainly marine Nostocales, are practically unknown, so the diversity currently known for this group is made up of only 12 species, distributed in eight genera and six families (Ortega *et al.* 2001, Ramírez-Rodríguez *et al.* 2011, González-Reséndiz *et al*. 2018a, b, Johansen *et al*. 2021). It is important to note that, in the entire region (Mexican Atlantic), there are currently no works that study the diversity or phylogeny of the group under molecular approaches. Although in the studies of González-Reséndiz *et al*. (2018a, b) and Johansen *et al*. (2021) records of species in Veracruz are mentioned, these were not verified molecularly, since these studies focus on the knowledge of the diversity of species with distribution in the Mexican tropical Pacific.

Therefore, our objective was to contribute to the knowledge of the diversity of benthic marine Nostocales species in Veracruz, Mexico, as well as to provide detailed descriptions and illustrations of the species found, which can serve as a reference in subsequent studies whether with molecular or biogeographic or ecological approaches.

Materials and Methods

Thirty-two samples were collected in the intertidal (0.5-1 m) and supratidal zones, in three locations throughout the state of Veracruz (Figure 1), during the month of March 2020 (Table 1). Playa Muñecos (rocky coast, on the rocks of

an island close to the coast), Morro de la Mancha (rocky coastal area, on the coast of the morro), and Costa de Oro (on cement structures). These collections were made with prior knowledge of the possible presence of Nostocales species according to the floristic records contained in Ortega *et al*. (2001) and González-Reséndiz *et al*. (2018a, b).

Samples were detached manually, using a spatula on soft substrates and a chisel and hammer on rocky substrates, in these cases they were detached with part of the rock on which they grew. For preservation, the detached samples were wrapped in blotting paper with silica gel; additionally, some fragments were also preserved in 4 % marine formalin. For morphological observations, semi-permanent preparations were made using hydrated glycerinated marine gelatin, in a 2:1 ratio. Photomicrographs of the diagnostic morphological characters were taken with a Quasar digital camera (Quasar TM., China) adapted to a Quasar Qm70 Infinity optical microscope (Quasar TM., China). Subsequently, from the photographs, measurements were taken with the Top View 3.7.8481 program (ToupTek Photonics Co., Ltd) and Fiji J. (Schindelin *et al*. 2012) to integrate the morphological descriptions. For taxonomic identification, the characters and measurements obtained were contrasted with those referred by Komárek (2013).

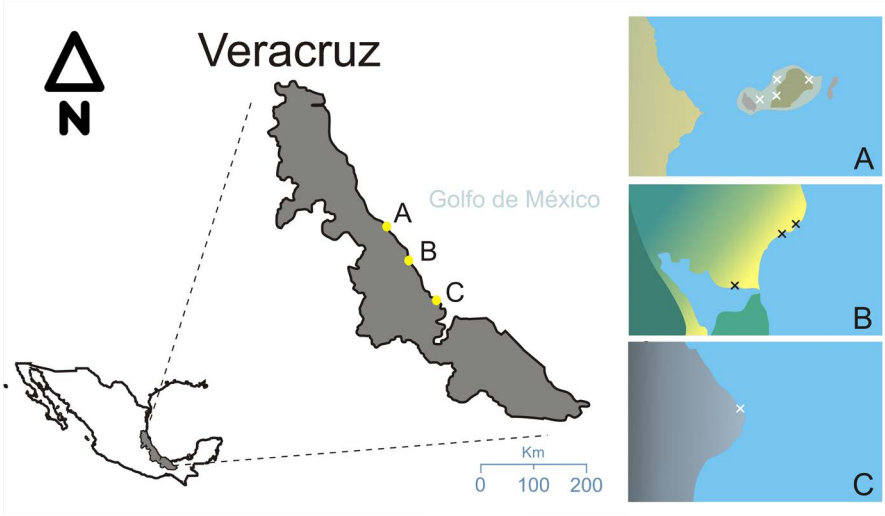

Figure 1. Map of Veracruz showing the collection sites in this work. A) Playa Muñecos. B) Morro de la Mancha. C) Costa de Oro.

Results

An updated floristic list of benthic marine cyanoprokaryotes of the order Nostocales from Veracruz, Mexico, is presented, which incorporates 30 species distributed in 12 genera and seven families (Table 2). Of the total of the species describing in this study, 15 correspond with additions to the flora and three were confirmed records, one species was identified as cf. and seven at the genus level, because they did not fully coincide with the information provided in the available specialized literature. The best represented families were Rivulariaceae (9), followed by Scytonemataceae (7) and Calotrichaceae (7); the lowest diversity corresponded to the families Nostocaceae (3), Aphanizomenonaceae (2) and Hapalosiphonaceae and Capsosiraceae with only one species each.

Morphological descriptions. Order Nostocales. Family Scytonemataceae. *Scytonematopsis* Kisseleva

Scytonematopsis crustacea (Thuret ex Bornet & Flahault) Kováčik & Komárek (Figure 2A, B, C)

Description.- Caespitose growth, yellow or green. Trichomes broad, olive green to ocher yellow, unconstrained, 16.9 µm wide, isopolar; apex attenuate rounded and sometimes with a terminal hair; not branched. Cells always longer than wide, (11)13-20(22) µm wide × 1-5.8 µm long, content not completely homogeneous; boundaries between

Table 1. Samples collected by each location in Veracruz, Mexico.

Sample number	Locality	Date	Salinity
54-63; 98	Costa de Oro	16/03/2020	31 ppt
64-83; 96, 97	Playa Muñecos	17/03/2020	30 ppt
95	Morro de La Mancha	17/03/2020	35 ppt

cells distinguishable by septa, with clusters of pigment granules. Distinct sheath, with irregular edges, mucilaginous, lamellar, yellow, or brown, 23-30(34) µm wide. Heterocytes intercalary, biporate, with a space between heterocyst and cells, 9-20 µm wide × 7.8(13)-18(21) µm long.

Field data.- Costa de Oro and Playa Muñecos; samples: 54-56, 58, 59, 62, 63, 64, 96.

Habitat.- Marine, on rocks and cement structures; splash surge.

Taxonomic comments.- Our specimens partially coincided with the morphology described by Komárek (2013), such as the measurement intervals for the width of the filament and the environment in which they grow (rocky marine or among algae); however, the range of measurements for the width of the cells was greater in our specimens, likewise, the trichomes are not constricted and, although they are attenuated, they do not end in a hair. Previously recorded in México as *Calothrix crustacea* in Tamaulipas (Ortega *et al*. 2001), Veracruz (Ortega *et al*. 2001, Tunnell Jr *et al.* 2007, Ramírez-Rodríguez *et al.* 2011), Campeche (Ortega *et al*. 2001, Tunnell Jr *et al.* 2007, Mateo-Cid *et al*. 2013a), Yucatán (Ortega *et al*. 2001, Tunnell Jr *et al.* 2007), Quintana Roo (Ortega *et al*. 2001, Mendoza-González *et al.* 2007, Tunnell Jr *et al.* 2007), along the Mexican Gulf León-Tejera *et al*. 2009). In the mexican Pacific reported for: Baja California (Javor & Castenholz 1981), Baja California Sur (Mateo-Cid & Mendoza-González 1994a, b), Sonora (Raimondi 1988), Jalisco (Mendoza-González *et al*. 2011), Guerrero (León-Tejera *et al*. 1993) Oaxaca (León-Tejera *et al.* 1993). As *Scytonematopsis crustacea* in Veracruz (Nava-Olvera *et al.* 2017), Tabasco (Mendoza-González *et al.* 2017), Campeche Bank (Mateo-Cid *et al.* 2013b), Campeche (Mendoza-González *et al.* 2016), Yucatán (Mendoza-González *et al.* 2016, Ortegón-Aznar & León-Tejera 2022), Quintana Roo (Mendoza-González *et al.* 2016). In the mexican Pacific reported for: Guerrero (Quiroz-González *et al*. 2020), Oaxaca (González-Reséndiz *et al.* 2015), Chiapas (Torres-Ariño *et al*. 2019).

Scytonematopsis fuliginosa (Tilden) J.J. Copeland (Figure 2G, H, I)

Description.- Growths shaped like mats or domes, green or yellow; macroscopically evident thalli. Trichomes bright green, 16.0 µm wide, constricted, with rounded tips, unbranched. Cells longer than wide, with purple or red pigment granules, 2.7 µm wide × 16.6 µm long. Sheath colorless, diffluent, mucilaginous, lamellar, 29.6 µm wide; the distance between the trichome and the sheath is 6 µm. Heterocytes intercalary, trapezoidal to square, wider than long, 16.8 µm wide × 11.7 µm long.

Field data.- Costa de Oro; samples: 54, 55.

Habitat.- marine, on substrate such as cement structures; splash and flood waves.

Taxonomic comments.- our specimens morphologically correspond with the reference figure shown in Komárek (2013), they grow in the same environment and presented calyptra; however, the measurements reported for the width of the filament, as well as the measurements of the width and length of the trichome, were greater in our specimens. Currently, this species has only been reported for the Hawaiian Islands and has not been reported again (Copeland 1936, Komárek 2013).

Scytonematopsis pilosa (Harvey ex Bornet & Flahault) Umezaki & M. Watanabe. (Figure 3F)

Description.- Caespitose growths forming large patches together with other mixed species of cyanobacteria, filamentous, with different shades of orange and green, several centimeters in length. Trichomes dark orange; apices attenuate with a short apical hair, not branched. Cells broader than long, 6.5-20.9 µm wide × 1.5-4.3(5.2-7.4) µm

Table. 2. Taxonomic list of the marine species of Nostocales from Veracruz. Ortega *et al*. 2001 (1); Tunnell Jr *et al.* 2007 (2), Ramírez-Rodríguez *et al*. 2011 (3), Nava-Olvera e*t al*. 2017 (4), González-Reséndiz *et al*. 2018b (5), González-Reséndiz *et al*. 2018a (6), Johansen e*t al*. 2021 (7), X = In this work.

Family	Genus	Species	Synonym	Reference
Nodularia	*Nodularia harveyana*Thur. ex Bornet et Flahault	.-	1	
Aphanizomenonaceae		*Nodularia spumigena* Mertens ex Bornet & Flahault	*Nostoc spumigena (*Mertens) Drouet	3
Calothricaceae	*Calothrix*	*Calothrix aeruginea* Thur. ex Bornet & Flahault	-	1, 2 X
		Calothrix confervicola C. Agardh ex Bornet & Flahault	.	1, 4
		Calothrix contarenii Bornet & Flahault		X
		Calothrix prolifera Flahault in Bornet & Flahault		X
		Calothrix fonticola Brabez		X
		Calothrix sp.1		X
		Calothrix sp.2		X
Hapalosiphonaceae	*Mastigocoleus*	*Mastigocoleus testarum* Lagerheim ex Bornet & Flahault	.-	1
Nostocaceae	*Anabaena*	*Anabaena oscillarioides* Bory ex Bornet & Flahault	*Anabaena psudosscillatoria* Bory de Saint-Vicent	3
	Nostoc	*Nostoc caladarium* Wor nom. inval. 1868	invalid	2
		Nostoc sp. 1	-	X

Family	Genus	Species	Synonym	Reference
Rivulariaceae	*Nunduva*	*Nunduva kania* González-Resendiz, León-Tejera & J.R.Johansen	.-	6
		Nunduva komarkovae González-Resendiz, León-Tejera & J.R. Johansen	-	7
	Phylonema	*Phyllonema ansata* González -Resendiz, León -Tejera & Johansen	.-	X, 5
	Rivularia	*Rivularia nitida* C. Agardh ex Bornet & Flahault	-	X
		Rivularia litorea G.S. An	-	X
	Kyrtuthrix	*Kyrtuthrix munecosensis* J.R.Johansen, González-Reséndiz & León-Tejera	-	7
		Kyrtuthrix totonaca J.R. Johansen, González-Reséndiz & León-Tejera	-	7
		Kyrtuthrix huatulcensis León-Tejera, González-Reséndiz & Johansen		X
		Kyrtuthrix sp1.		X
Scytonemataceae	*Scytonematopsis*	*Scytonematopsis crustacea* (Thuret ex Bornet & Flahault) Koválik & Komárek	*Calothrix crustacea* Thur. ex Bornet & Flahault	1, 3, 4 X
		Scytonematopsis fuliginosa (Tilden) J.J.Copeland	-	X
		Scytonematopsis sp 1.	-	X
		Scytonematopsis sp 2.	-	X
		Scytonematopsis sp 3.	-	X
		Scytonematopsis pilosa (Bornet & Flahault) Umezaki & M. Watanabe	*Calothrix pilosa* Harvey ex Bornet & Flahault	X
	Scytonema	*Scytonema crispum* C Bornet ex De Toni.	*Scytonema cincinnatum* Thuret ex Bornet & Flahault	X
Capsosiraceae	*Desmosiphon*	*Desmosiphon* cf. *neocaledonicus* Bourrelly		X

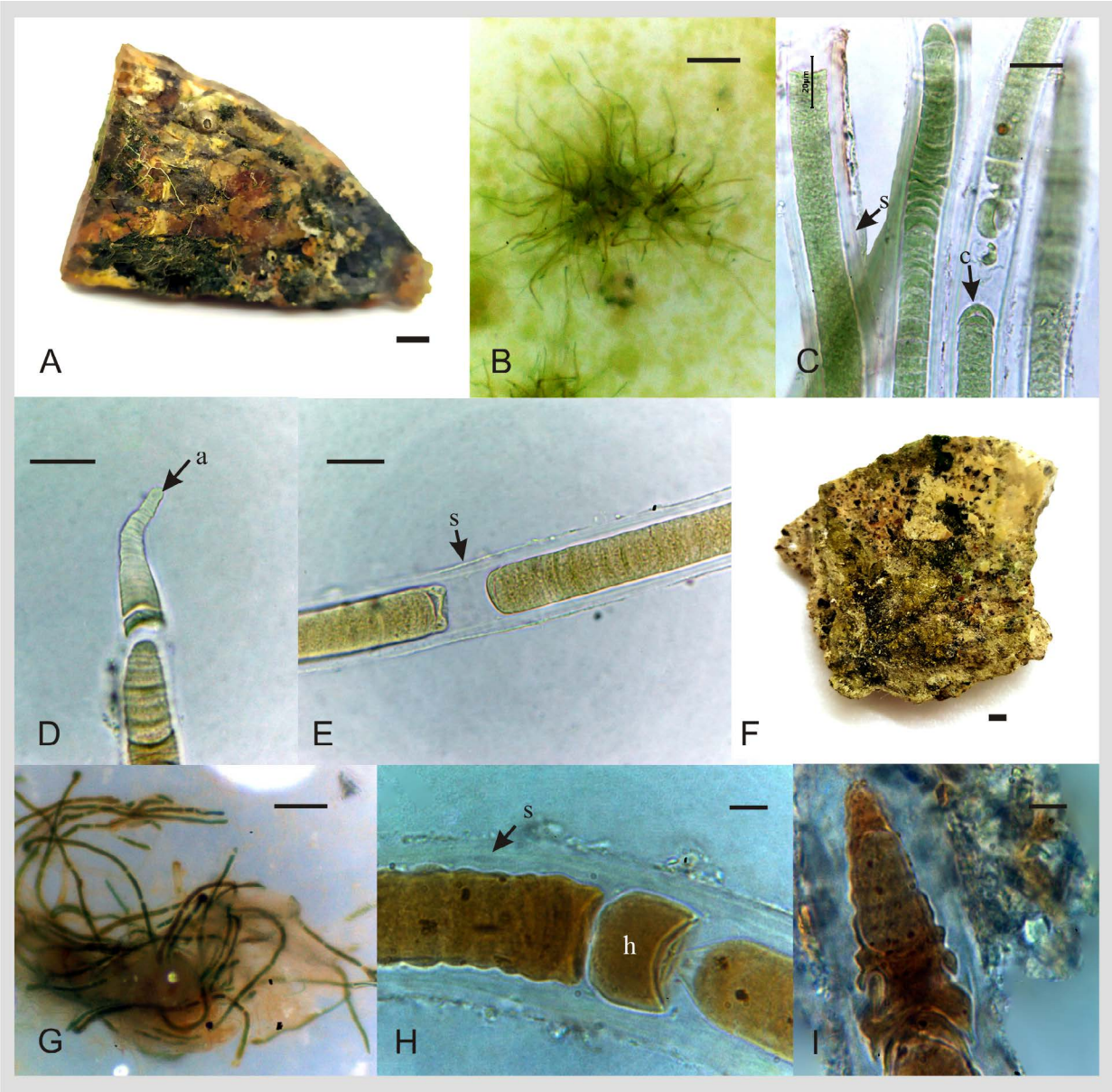

Figure 2. Micrographs of Nostocales species of Veracruz. *Scytonematopsis crustacea* (A, B, C). A) Field sample. B) Trichomes forming mats. C) Apex with calyptra (arrow c), thick hyaline sheath (arrow s). *Scytonema crispum* (D, E, F). D) Detail of attenuated trichome apex without apical hair formation (arrow a). E) Ocher yellow trichome, thick hyaline sheath (arrow s). F) Field sample. *Scytonematopsis fuliginosa* (G, H, I). G) Trichomes forming mats with other bacteria. H) Intercalary heterocyte (h), thick lamellated sheath (arrow s). I) Detail of the attenuated apex without apical hair formation. Scale bar: A, F = 1 cm; B= 210 µm; G = 300 µm; C-E = 20 µm; H, I = 6 µm; h = heterocyte.

long, becoming quadrangular towards apex; a chromoplast (more concentrated region of pigment) is observed in the cytoplasm, this can also show dark red pigment granules in the external region of the cells. Hyaline sheath, with poorly defined borders, markedly mucilaginous surface, lamellar appearance, 13.4-30 µm wide. Heterocytes intercalary, quadrangular to rectangular, 10.4-18.8 µm wide × (7.1) 8.4-11.3(23.1) µm long, may have more than one heterocyst per trichome.

Field data.- Playa Muñecos; samples: 65, 68.

Habitat.- marine, on rocks; splash and flood waves.

Taxonomic comments.- our specimens concur morphologically with what was described by Komárek (2013) for *Sytonematopsis crustacea* in the range of measurements for the width of the cells. However, the reference image differs considerably, as well as the range of measurements for the length of the cells and the sheath, which is not open at the apex, nor does it show projections. On the other hand, our specimens were more similar to the description of *S. pilosa* in Komárek (2013), mainly in the measurements for the width of the cells, the width and length of the heterocyst, the marine environment, rocky, sandy or epiphytic substrate. According to Komárek (2013), the taxonomic position of this record is uncertain, reported only for Central America, although the location was not specified. The species *Calothrix pilosa* Harvey ex Bornet & Flahault is synonymous with *S. pilosa*. This species has been recorded for Mexico as *Calothrix pilosa* in Yucatán (Ortega *et al*. 2001), Mexican Gulf northeast and southeast (León-Tejera *et al*. 2009).

Scytonemaptosis sp. 1 (Figure 3H)

Description.- Grass-like growths, lime green. Isopolar trichomes, 6.8-13.5 µm wide, pale yellow to ocher yellow, with attenuate tips without apical hair formation; false branch formed by the clash of two trichomes, when growing in the same direction, sometimes the trichomes detach from a main branch, forming new trichomes with a heteropolar appearance. Cells ocher yellow to pale yellow, square to rectangular, with striations towards the apex, those closest to the heterocytes are wider than long becoming longer than wide as they approach the apex of the branches, 2-8.9 µm wide × 1.8-14.4 µm long. Diffluent and colorless hyaline sheath. Heterocytes intercalary, 5.1-10.3 µm wide × 1.3-6.2 µm long.

Field data.- Morro de la Mancha; sample: 95.

Habitat.- marine, on sandy rocks; splash surge.

Taxonomic comments.- Our specimens partially accord with the morphological description of Komárek (2013) for *Scytonematopsis contorta* M.A. Vaccarino & J.R. Johansen, mainly in the reference images, the attenuated apices, the basal heterocyst, and the false branching. However, the measurements reported for the width and length of the cells were smaller in our specimens, as well as the environment in which it grows (subaerial in the splash zone of the falls in Oahu, Hawaiian Islands, USA) was different. Regarding *S. crustacea*, the measurement intervals for the width of the trichome were higher in our specimens and lower compared to *S. starmachii* Kovácik & Komárek (Komárek 2013).

Scytonematopsis sp. 2 (Figure 3G)

Description.- Caespitose growths, different shades of green, forming small patches of a few millimeters on the rock. Heteropolar trichomes, constricted, with slightly attenuated apices, no apical hair formation, false branching. Cells pale yellow to green, wider than long 3.3-9.8 µm wide × (1.19)1.8-5 µm long, except near apex, becoming slightly longer than wide; cytoplasmic content with granulations of homogeneous distribution in the cytoplasm, giving a granulated appearance to the cells. Sheath wide, colorless, hyaline, distinguishable, lamellar, (8.5)9.9 × 15.9(25) µm wide and 5 µm thick. Heterocytes intercalary, when the sheath breaks trichomes are formed with basal heterocytes, hyaline in appearance, 5.8-11.8 µm wide × 1.6-4.5(7.4) µm long.

Field data.- Morro de la Mancha; sample: 95.

Habitat.- marine, on sandy rocks, splash waves.

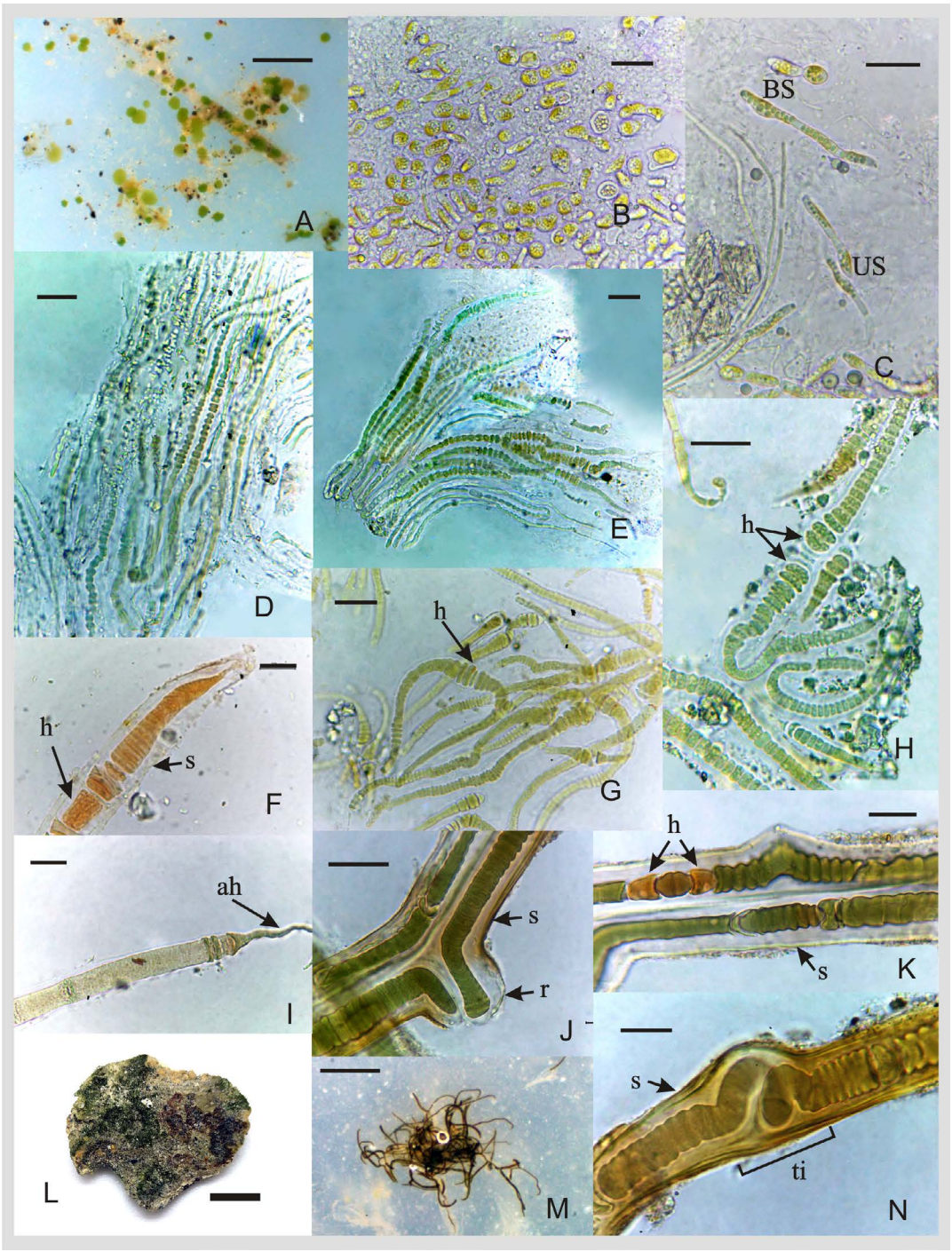

Figure 3. Micrographs of Nostocales species of Veracruz. *Nostoc* sp. 1 (A, B, C). A) Colonies with defined circular edges. B) Spherical to hemispherical colonies. C) Formation of uni (US) and biseriate (BS) pseudotrichomes. *Kyrtuthrix* sp1. (D). Long attenuated trichomes with "U" shape and parallel arrangement. *Kyrtuthrix huatulcensis* (E) Long attenuated "U"-shaped trichomes, parallel arrangement, intercalary heterocytes. *Scytonematopsis pilosa* (F) F) Non lamellated hyaline sheath (arrow s), intercalary heterocyte (h). *Scytonematopsis* sp. 1 (G) Isopolar trichomes, heterocyte intercalary(h), slightly attenuated apices. *Scytonematopsis* sp.2 (H) Isopolar trichomes with intercalary heterocytes(h) and false branches. *Scytonematopsis* sp 3 (I). Attenuated apex with formation of apical hair (arrow ah). *Phylonema ansata* (J, K, L, M, N) J) False branching (arrow r), thick lamellated sheath (arrow s). K) Intercalary heterocyte (h), more than one can be found. L) Field sample. M) Trichomes forming tufts. N) Trichomes intertwined within the general (square bracket "ti"), thick, lamellated sheath (arrow "s"). Scale bar: A = 600 µm; M = 380 µm B-K, N = 20 µm; L = 1 cm.

Taxonomic comments.- The morphological characteristics of our specimens coincided with the generic description of Komárek (2013), such as attenuated apices, firm or diffluent sheath, false branching and constricted trichome; however, for the two species described, only *Scytonematopsis crustacea* is marine. The measurement intervals for the width of the trichome reported for this species were greater than those presented by our specimens, which were more similar to that described by Komárek (2013) for *S. woronichinii* Kiseleva, with which it differs only in the measurements of the width of the trichome, which were greater than that reported for this species, and also has an uncertain taxonomic status in the work of Komárek (2013). On the other hand, this species has been recorded only for soil environments in El Salvador and rice fields in India.

Scytonematopsis sp. 3 (Figure 3I)

Description.- Cespitose growths, forming dense patches together with other species of cyanobacteria. Isopolar trichomes, olive green to orange, attenuated tips with formation of apical hair, unbranched. Cells clearly wider than long, (3.3)9-18.5 µm wide × 1-3.9(5) µm long, those closest to the apex are small, becoming attenuated as they approach the apical zone. Granulated cytoplasmic content. Diffluent sheath, hyaline, poorly distinguishable, lamellar in appearance, 18.5-22.1(27.6) µm wide. Heterocytes intercalary, quadrangular to trapezoidal, 13.4 µm wide × 5.1-10.3 µm long.

Field data.- Costa de Oro and Playa Muñecos; samples: 54, 55, 66, 68, 78.

Habitat.- marine, brackish rocks and cement structures, splash zone and flood waves.

Taxonomic comments.- Although our specimens concur morphologically with the generic description of Komárek (2013), the most similar species was *Scytonematopsis crustacea*, with which it shares the measurements of the width of the cells, attenuated apices and described environment. However, the reference image did not coincide with our specimens, as well as the sheath, which is not open at the apex and does not have projections. In the unclear species section of Komárek (2013), *Calothrix vivipara* Harvey ex Bornet & Flahault is described; with which they coincide with the reference image and the width of the cells; but, they differ in a much larger interval of the width of the cells in our specimens.

Scytonema C. Agardh ex E. Bornet & C. Flahault
Scytonema crispum Bornet ex De Toni (Figure 2D, E, F)

Description.- Cespitose growths, forming small dark green spots. Dark green to shiny green trichomes, not constricted, with rounded, not attenuated tips, not branched. Cells always wider than long, (6.9)10-19.6 µm wide × 1.2-7.9(10.4) µm long. Diffluent sheath, hyaline, lamellar, thick, (23.5)25-35.5(38.2) µm wide, very evident. Heterocytes intercalary, 15.2-19.9 µm wide × 3.1-17.3 µm long.

Field data.- Costa de Oro and Playa Muñecos; samples: 54, 55, 57, 58, 63, 69, 70, 82, 96.

Habitat.- marine, on cement and rock structures, waves due to splashing and flooding.

Taxonomic comments.- Our specimens coincided morphologically with the reference image shown in Komárek (2013) for *Scytonema cincinnatum* Thuret ex Bornet & Flahault species, as well as in the range of measurements for the cells, which are wider than long, maintain their shape along the trichome and the shape of the apex. However, the interval of measurements of the width of the cells was greater in our specimens than that reported, likewise, the environment is described only as aquatic, Komárek (2013) refers that if they are reports in tropical environments,

they require revision. *Scytonema cincinnatum* is a synonym of *Scytonema crispum*, reported for Mexico in the states of Jalisco (Pedroche & González-González, 1981), Hidalgo terrestrial biocrusts (Becerra-Absalón *et al*. 2019) and Puebla terrestrial biocrusts (Becerra-Absalón *et al*. 2019).

Family Rivulariaceae
Kyrtuthrix Ercegovic
Kyrtuthrix huatulcensis León-Tejera, González-Reséndiz & Johansen (Figure 3E)

Description.- Trichomes short, attenuated, olive green to bright green, isopolar, constricted, forming a "U", with the two apices pointing towards the direction of growth and arranged parallel, apices with an apical hair, not branched. Cells broader than long, 2-6 µm wide × 2-6(7) µm long, barrel-shaped, polygonal, or nearly spherical; those closest to the apex can be longer than wide as they taper, triangular or conical, arranged in a rosary. Non-heterogeneous cytoplasmic content. Sheath colorless, diffluent. Heterocytes intercalary, trapezoidal, or crescent-shaped to hemispherical, 4-8 µm wide × 2-5 µm long.

Field data.- Playa Muñecos; samples: 64, 69, 78.

Habitat.- marine, on rocks; splash and flood waves.

Taxonomic comments.- The morphological characteristics of our specimens be consisten with those reported by León-Tejera *et al*. (2016a). However, this species has only been recorded for the Mexican Tropical Pacific, in Oaxaca (León-Tejera *et al*. 2016a, Torres-Ariño *et al*. 2019).

Kyrtuthrix sp. 1 (Figure 3D)

Description.- Growths like mats or small domes. Trichomes short, isopolar, yellow or light orange to light brown, 4.6 µm wide, forming a very distinctive "U" shaped turn or arrangement, both apices attenuated, pyramidal or conical in shape with an apical hair, pointing in the direction of the growth of the trichome "outwards". Cells 3-6(7) µm wide × 1-6(10) µm long, very close to each other with a slight space between them, polygonal to almost spherical, can become elongated, obtaining a barrel shape, always wider than long. Sheath very diffluent, hyaline, colorless, difficult to observe. Heterocytes intercalary, square to hemispherical, 4-5 µm wide × 3-5 µm long.

Field data.- Costa de Oro and Playa Muñecos; samples: 56, 58, 69.

Habitat.- marine, on rocks and cement structures, exposed to waves, splashing.

Taxonomic comments.- Although the morphological characteristics of our specimens matched the generic description, they did not match the characters or reference images of the only two species described by Komárek (2013), *Kyrtuthrix dalmatica* Ercegovic recorded in Europe and *K. maculans* (Gomont) I. Umezaki for the rest of the world. The species here recorded did not agree with the morphology of the species described by Johansen *et al*. (2021) (*K. huatulcensis*, *K. totonaca* J.R. Johansen, González-Reséndiz & León-Tejera and *K. muneconsensis* J.R. Johansen, González-Reséndiz & León-Tejera), previously reported for Mexico (Johansen *et al.* 2021).

Phylonema D.O. Alvarenga, J. Rigonato, L.H.Z. Branco, I.S. Melo & M.F. Fiore
Phyllonema ansata González-Reséndiz, León-Tejera & J.R. Johansen (Figure 3J-N)

Description.- Dark to yellowish pom-pom-like growths, circular to irregular, several millimeters in length. Trichomes forming fascicles that are usually coiled, forming turns or twists within the sheath, two per sheath, olive green to

dark brown in color, evidently constricted throughout, false branching, with branches perpendicular to the main axis that do not separate, giving the appearance of being other trichomes inside the sheath, which does not open. Cells barrel-shaped, (8)10-21(24) µm wide × 2-7(10) µm long, always wider than long, with well-defined borders. Cytoplasmic content with evident chromoplast, defined by a darker shade in the center of each cell. Sheath lamellar, 27 -43µm wide, mucilaginous, dark brown to ocher, to yellowish or transparent, thick, smooth the innermost part of the trichome, the distance between the trichome and the sheath is 9.4 µm. Heterocytes intercalary, sometimes at base of ramifications, trapezoidal to round, biporate, 13-21(23) µm wide × 5(7)-12(14) µm long.

Field data.- Paya Muñecos and Costa de Oro; samples: 55, 66, 69, 70.

Habitat.- marine, on cement structures and rocks exposed to waves due to splashing and flooding.

Taxonomic comments.- Our specimens concur with most of the morphological characteristics described by González-Reséndiz *et al.* (2018b). However, they differed in the color of the trichomes and the range of measurements for the width and length of the cells and the heterocytes, greater in our samples. Reported previosly for Mexico in Oaxaca (González-Reséndiz *et al*. 2018a, Torres-Ariño *et al.* 2019) and Veracruz (González-Reséndiz *et al*. 2018b).

Rivularia C. Agardh ex Bornet & Flahault
Rivularia litorea G.S. An (Figure 4A, B, C)

Description.- Macroscopic thalli like mats, green or yellow. Short trichomes, 4.3 µm wide, colorless or light green, fan-shaped, forming small patches, heteropolar, constricted, attenuated apices without forming an apical hair. Cells 2-6(8) µm wide × 2-8(16) µm long, with varied shapes along the trichome, from wider than long and isodiametric to longer than wide reaching the apex, as they move away of the heterocyst the ratio between width and length increases. Diffluent mucilage, colorless, surrounding the trichomes and shaping the contours of the fan. Heterocytes, basal trapezoidal or pyramidal or hemispherical, 4-8(11) µm wide × (4)6-9 µm long.

Field data.- Playa Muñecos; samples: 72, 74.

Habitat.- marine, on rocks, exposed; strong waves and splash zone.

Taxonomic comments.- Our specimens morphologically be concurred with the description of Komárek (2013) in the yellow coloration on the edge of the sheath. However, the range of measurements for the width of the cells was greater in our specimens, while the measurements for the width and length of the heterocytes were less than described, nor did they coincide with the reference image and the distribution described for the species in North Korea (Komárek 2013).

Rivularia nitida C. Agardh ex Bornet & Flahault. (Figure 4D, E)

Description.- Macroscopic thalli forming mats, light brown or yellow to ocher, mucilaginous. Ocher to light brown trichomes, arranged in a fan shape forming small patches, heteropolar, constricted, 4.3 µm wide, attenuated apices without forming apical hair. Cells 2-6(8) µm wide × 2-8(16) µm long, with varied shapes along the trichome, from wider than long and isodiametric to longer than wide near the apex, as measured move away from the heterocyst the ratio between width and length increases. Diffluent mucilage, colorless, surrounding the trichomes and shaping the contours of the fan. Heterocytes basal, trapezoidal, pyramidal, or hemispherical, 4-8(11) µm wide × (4)6-9 µm long.

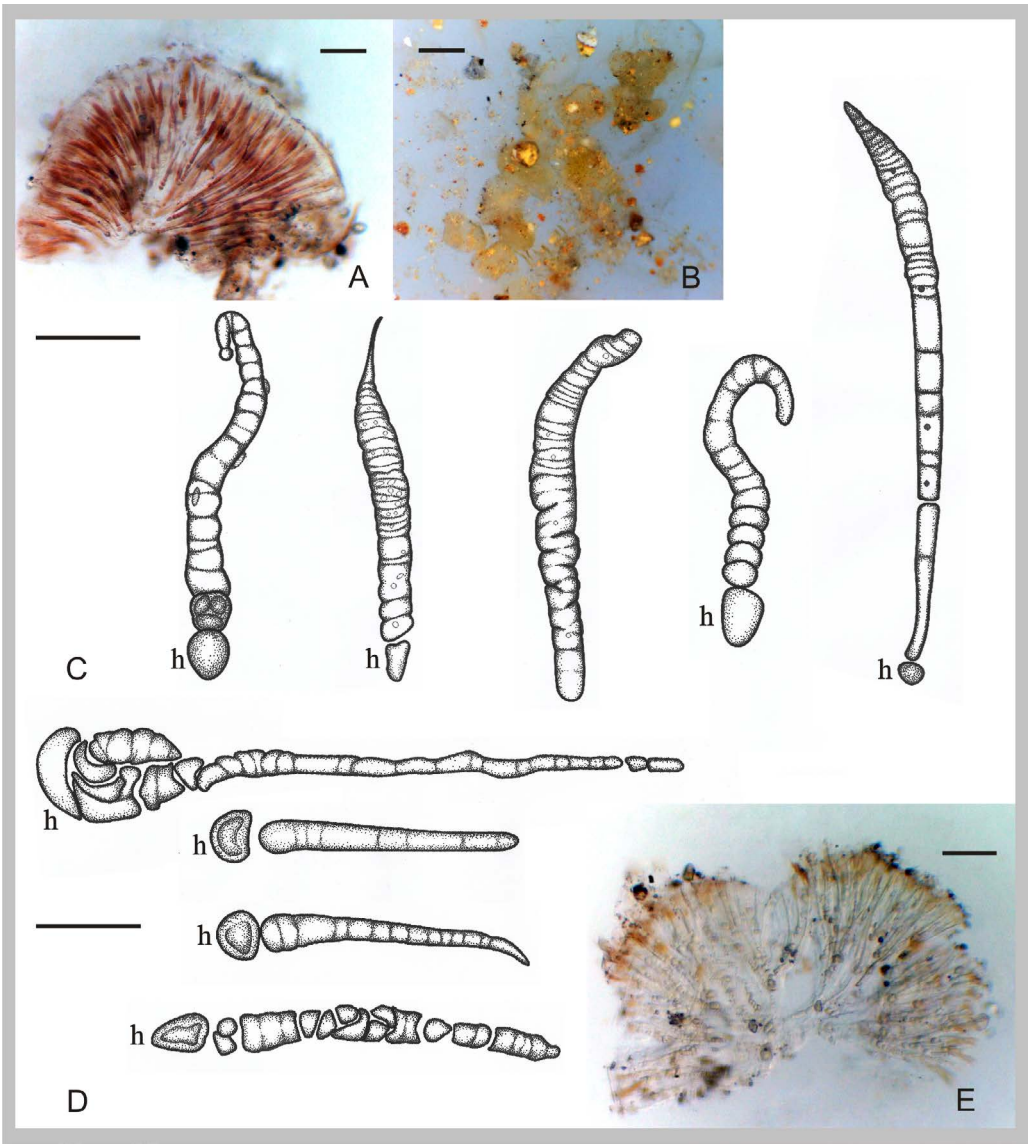

Figure 4. Micrographs of Nostocales species of Veracruz. *Rivularia litorea* (A, B, C) A) Hemispherical fan-shaped colony, trichomes with radial arrangement, the outer edge of the colony has a reddish color. B) Colonies in culture. C) Different shapes of heteropolar trichomes, cellular shapes and basal heterocytes (h). *Rivularia nitida* (D, E). D) Different shapes of heteropolar trichomes, cellular shapes and basal heterocytes (h). E) Hemispherical fan-shaped colony, trichomes have a radial arrangement, the outer edge of the colony has yellow coloration. Scale bar A, E = 60 µm; B = 160 µm; C, D = 20 µm.

Field data.- Playa Muñecos; sample: 67.

Habitat.- marine, on rock; splash and flood waves.

Taxonomic comments.- Our specimens concur with the morphological description of Komárek (2013) in the range of measurements for the width and length of the cells. However, the reference image, the measures of width and length of the heterocyst, the color of the sheath, and the distribution of the cells in the meristematic zone described did not coincide with our specimens. Although this species has been reported for marine environments, it is suggested that records from tropical areas require revision (Komárek 2013).

Family Calothricaceae
Calothrix C. Agardh ex Bornet & Flahault
Calothrix aeuriginea Thuret ex Bornet & Flahault (Figure 5A, B, C)

Description.- Caespitose growths, orange, associated with *Scytonematopsis* and *Petalonema* species, forming patches of filaments. Heteropolar trichomes of different shades of orange, constricted, attenuated apices, possible formation of apical hair. Cells 5.6-11.9(12.5) µm wide × 1.4-4.8(7.5) µm long, wider than long, those closest to the apex being larger, quadrangular, orange, sometimes with granules of lighter shades. Sheath (8.5)10.2-15.7(16.3) µm wide, colorless, hyaline, with well-defined edges, clearly distinguishable. Heterocytes, basal, crescent-shaped, hyaline, 6.7-10.3(12) µm wide × 2.4-4.4(8.6) µm long.

Field data.- Costa de Oro; samples: 56, 59.

Habitat.- marine, on cement structures; splash surge.

Taxonomic comments.- The morphological characteristics of our specimens agree with that reported by Komárek (2013). Previously recorded in Veracruz (Ortega *et al*. 2001), Quintana Roo (Ortega *et al*. 2001), Yucatán (Ortegón-Aznar & León-Tejera 2022), and Mexican Gulf southwest and southeast (León-Tejera *et al*. 2009).

Calothrix contarenii Bornet & Flahault (Figure 5D, E)

Description.- Growths like domes or mats, bright green. Trichomes short, heteropolar, bright green, 5.6 µm wide in the middle and wider at the base, slightly twisted, crescent-shaped, constricted, attenuate, with a coarse apical hair. Cells 4-8 µm wide × 1-3(5) µm long, always wider than long, except for the apical ones which are longer than wide, barrel- or rod-shaped, light green to bright green. Cytoplasm with pigment granules without a particular arrangement. Sheath thick, 7-10(15) µm wide, hyaline, colorless, smooth inside, open at the end near the apex, where the layers or lamellae open giving it a feathery appearance.

Field data.- Playa Muñecos; samples: 62, 64.

Habitat.- marine, on rocks; splash and flood waves.

Taxonomic comments.- The morphological characteristics of our specimens correspond with the description of Komárek (2013) in the measurements for the width of the cells, non-lamellar and colorless sheath, and the environment. However, the range of measurements for filament width and the feathery appearance of the sheath near the apex did not match in the reference image. Species with uncertain taxonomic position according to Komárek (2013). Although it coincides with the type of environment described, its distribution range must be reevaluated, since it has previously been recorded in the Mexican Pacific in Baja California Sur (López-Cortez 1999), Baja California (López-Cortez *et al*. 2001) and tropical environments in Oaxaca (León-Tejera *et al*. 1993) and in the Mexican Atlantic in Quintana Roo (Nava-Olvera *et al.* 2017).

Calothrix fonticola Brabez (Figure 5G, H, I)

Description.- Brown to ocher growths, like pom-poms. Trichomes long, to 2 mm long x 5.7 µm wide, attenuated, heteropolar, not constrained or slightly constrained, light brown to ocher, sometimes united at the base, false branching. Cells (3)4.0-5.1(6) µm wide × (1.31)1.5-2.7(3.4) µm long, longer than wide near apex, barrel-shaped or square. Sheath 6.9-10(11.5) µm wide, lamellar, distinguishable, open at the apical end. Heterocytes, basal and intercalary, trapezoidal, pyramidal or rectangular, (3.7)5-6. 1(8) µm wide × (2.4)3-4.6(6) µm long.

Field data.- Costa de Oro; sample: 56, 59.

Habitat.- marine, on cement structures, splash waves.

Taxonomic comments.- Although the morphology of our specimens be consistent with the description of Komárek (2013) in the range of measurements for the width of the filament and the trichome, neither the reference image nor the heterocytes coincided, which may be intercalary, not only basal; neither did the environment coincide with the reported environment (mineral sources). According to Komárek (2013), the description of the species requires revision.

Calothrix prolifera Flahault (Figure 5F)

Description.- Yellowish growths, large, forming creams and pompoms. Trichomes long, to 250 µm in length, slightly constricted, olive green to dark yellow, heteropolar, sometimes attached to each other at the base, 7.1 µm wide in middle region but always wider at base, false branching. Cells 5-13 µm wide × 1-4.5 µm long, wider than long, up to almost square, closer to the apex they become almost rectangular, longer than wide, homogeneous content. Sheath thick, 9-16 µm wide, hyaline, colorless, open at the apices, lamellate, near the apex the layers separate giving a feathery appearance. Heterocytes, basal, from 1 to 4, and intercalated in the longest trichomes, 7-10(12) µm wide × 2-7(11) µm long.

Field data.- Costa de Oro; sample: 56.

Habitat.- marine, on cement structures, splash waves.

Taxonomic comments.- our specimens correspond morphologically with the description of Komárek (2013) in the measurements of the width of the filaments, the sheath, and the type of environment. However, both the reference image and the interval measured for the width and length of the cells, greater in our specimens, did not coincide with what was described, as well as the presence of intercalated heterocytes.

Calothrix sp. 1 (Figure 5J, K)

Description.- Growth in patches, orange to light brown. Trichomes many times individual, short, 6.70 µm wide, being wider at the base, orange to ocher or olive green, heteropolar, slightly attenuated, with apical hair formation, false branching. Cells (2)4-13(16) µm wide × 1-5(7) µm long, barrel- or rod-shaped, wider than long, those closest to the apex being longer than wide, as attenuate Sheath thick, (4.8)6-12(30) µm wide, hyaline, colorless, open at the end, not lamellar. Heterocytes basal, trapezoidal or hemispherical, 4-9(15) µm wide × 2-8(10) µm long.

Field data.- Playa Muñecos and Costa de Oro; samples: 56, 64, 66.

Habitat.- marine, on rocks and cement structures, exposed, splash waves and flooding.

Taxonomic comments.- Our specimens agreed morphologically with the general shape and generic characteristics described in Komárek (2013), they did not agree in most diagnostic characteristics with the two most similar species, *Calothrix brevissima* G.S. West and *C. marchica* Lemmermann, neither with the reference images, nor in the environments reported for both species (plant epiphytes and *Nostoc* endogloic, respectively).

Calothrix sp. 2 (Figure 5L)

Description.- Caespitose growths, mixed with filaments of other species of cyanoprokaryotes, green and orange. Heteropolar trichomes, olive green, slightly constricted, attenuated apices with formation of apical hair. Cells 0.9-5.7(7.9) µm wide × 0.9-2.2(5.3) µm long, always longer than wide, quadrangular near the apices. Sheath 8.2-9.9(11.4) µm wide, hyaline, colorless. Heterocytes basal, crescent-shaped, 3.4-4.9 µm wide × 1.9-3.6 µm long.

Field data.- Costa de Oro; sample: 56.

Habitat.- marine, on cement structures, exposed to waves due to splashing and flooding.

Taxonomic comments.- Although our specimens meet the characteristics of the genus described in Komárek (2013), they do not match the species described for it. *Calothrix brevissima* and *C. marchica*, slightly coincide with our description. However, they do not coincide in the measurement intervals of the width of the cells (greater in our material), constricted trichomes, the barrel shape, the coloration, the presence false branching and the environments described for both species (plant epiphyte and endogloicum in Nostoc, respectively).

Family Nostocaceae
Nostoc Vaucher ex Bornet & Flahault
Nostoc sp. 1 (Figure 3A, B, C)

Description.- Growths in the form of small domes, with a caespitose appearance, mixed with other species of *Chroococcidiopsis* Geitler forming small colonies microscopic that vary from spherical to hemispherical in shape in one stage of the life cycle, until they form wide or elongated and thin trichomes. Spherical colonies 7.7-11.7 µm in diameter. Trichomes 3-5.8 µm wide × (3.2)9.3-30(35.7) µm long. Cells of 1.3-3.7 µm in diameter, completely spherical, colorless, or blue green, randomly distributed in the sheath, as the shape of the colony changes, they are arranged along the trichome. Sheath general, 4.8-6.8 µm wide, hyaline, colorless to slightly greyish or ocher yellow. Heterocytes apical, presents only in pseudotrichomes.

Field data.- Playa Muñecos and Costa de Oro; sample: 59, 67.

Habitat.- marine, on rocks and cement structures, waves due to splashing and flooding.

Taxonomic comments.- The morphology of our specimens coincided with characteristics of some *Nostoc* species described by Komárek (2013), although not fully enough to relate it to any of them. With *N. verrucosum* Vaucher ex Bornet & Flahault it coincides in the shape of the colony and the filaments, but it differs in the measurements of the cells and the environment. With *N. edaphicum* N.V. Kondrateva it coincides with the reference image but not with the measurements of the diameter, shape of the cells and the environment. On the other hand, with the genus *Halotia* D.B. Genuario *et al.* concur in environments and some forms and stages of the life cycle, such as the presence of biseriate trichomes (Genuario *et al*. 2015). However, not all forms of the life cycle coincide, nor the range of cell diameter measurements reported by Genuario *et al*. (2015).

Family Capsosiraceae
Desmosiphon Borzì
Desmosiphon cfneocaledonicus Bourrelly (Figure 5I)

Description.- Epiphytic thalli, growing on the sheath of caespitose species of the genus Scytonematopsis and Scytonema. Heteropolar trichomes, attached to the basibiont sheath at the basal end. Cells 2.5-7.3 µm wide × 2-9.3(14.9) µm long, square, trapezoidal or rectangular, bright olive green or blue green, with orange to red pigment granules; basal cells elongated, towards the point of union with the sheaths of the basibiont. Sheath 5.1-10.5(13.8) µm wide,

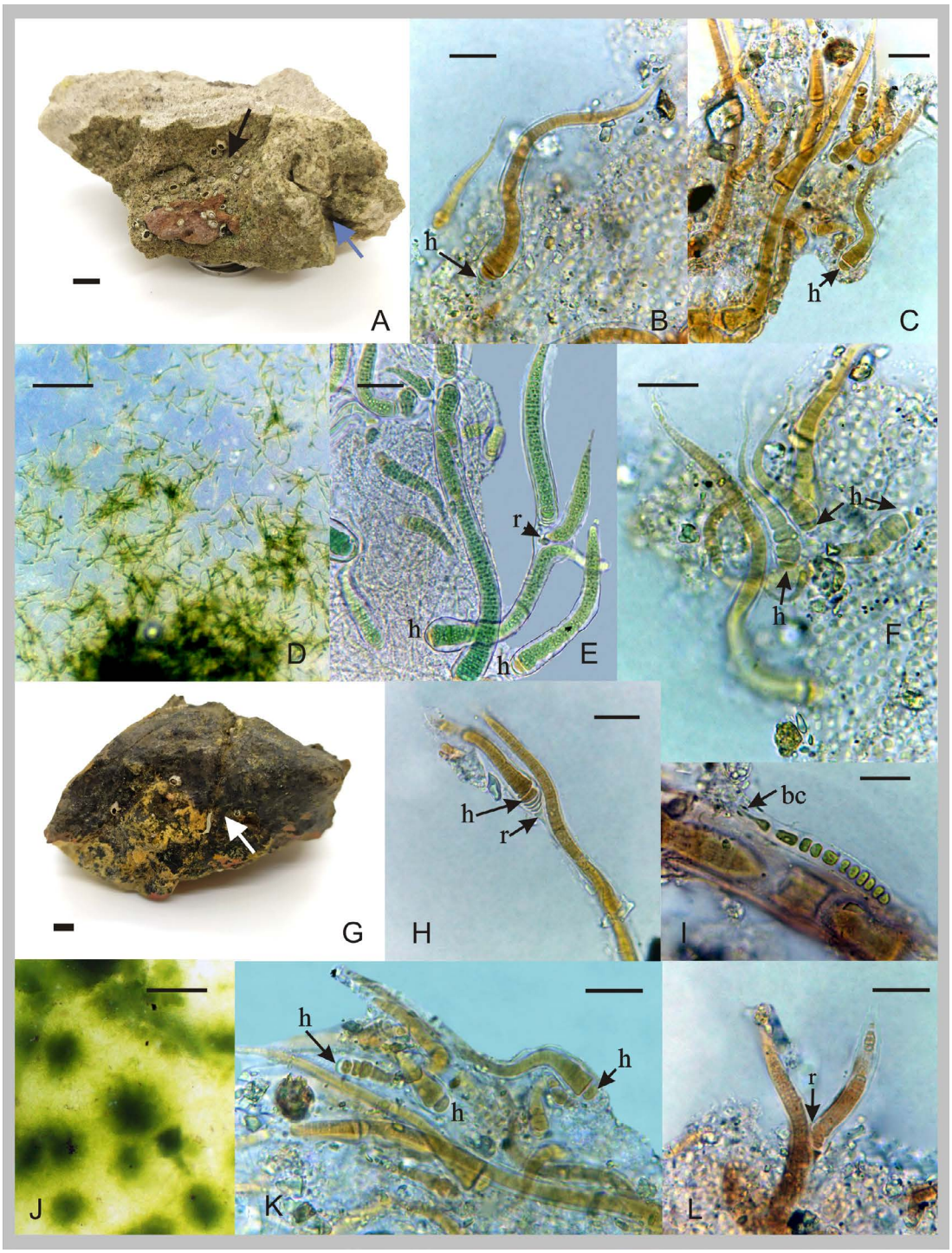

Figure 5. Micrographs of Nostocales species of Veracruz. *Calothrix aeruginea* (A, B, C) A) Field sample (scale bar 1cm). B, C) Heteropolar trichomes with basal heterocytes(h). *Calothrix contarenii* (D, E) D) Growth in culture forming green clump. E) Heteropolar trichomes, false branching (arrows r). *Calothrix prolifera* (F) Heteropolar trichomes, basal heterocytes (h). *Calothrix fonticola* (G, H, I) G) Field sample. H) Heteropolar trichomes, multiple basal heterocytes (arrow h), false branching (arrow r). *Desmosiphon* cf. *neocaledonicus* (I). I) Epibiont trichome of other cyanobacteria, the basal cell elongated towards the base (arrow bc). *Calothrix* sp. 1 (J, K), J) Growth in culture, forming green patches. K) Heteropolar trichomes, basal heterocytes (h). *Calothrix* sp. 2 L) Heteropolar trichomes with attenuated apex, false branching (arrow r). Scale bar A, G= 1 cm; B, C, E, F, H, I, K, L = 20 µm; D = 210 µm; J = 223 µm.

hyaline, colorless, diffluent.

Field data.- Costa de Oro; samples: 54, 57.

Habitat.- marine, epiphytes of turfgrass species, which grow in cement structures, exposed to waves due to splashing and flooding. Taxonomic comments: our specimens be consistent with the generic description of Komárek (2013). However, they did not fully coincide with the diagnosis of any of the known species. With *Desmosiphon viveri* Bourrelly they correspond with the range of measurements for the width of the filament, but not with the reference image, the environment, and the measurements of the width of the cells. With *D. neocaledonicus* Bourrelly coincided in the reference image, the basal cell of the trichomes and the measurement interval for the filament, but not with the environment described as freshwater species, **(**Komárek 2013, Guiry & Guiry 2022 www.algaebase.org**)** and the measurement intervals for the width of the cell and the sheath, which is larger than in our specimens. Additionally, since its original description, this species has not been reported again (Guiry & Guiry 2022 www.algaebase.org). The genus and species require an in-depth review, although in the main classification systems it is recognized as an accepted genus and species, there are no works that have reported it again.

Discussion

The 20 species described in the present study represented an increase of 57 % to the previously known diversity of marine benthic Nostocales (17 species) for the coasts of Veracruz. Likewise, these records represented a 10 % increase in the diversity of this group in the Mexican Atlantic, compared to previous records of 148 species. Of the total species, six constituted new records for Mexico *Desmosiphon* cf. *neocaledonicus*, *Calothrix fonticola*, *Calothrix prolifera*, *Rivularia nitida*, *Rivularia litorea* and *Scytonematopsis fuliginosa*. Furthermore, four had already been previously registered for Veracruz: *Phyllonema ansata*, *Scytonematopsis crustacea*, *Calothrix aeruginea*, and *Scytonematopsis pilosa* in other studies (Ortega *et al.* 2001, León-Tejera *et al*. 2009, Nava-Olvera *et al*. 2017, González-Reséndiz *et al*. 2018b).

Regarding the diversity by family, Rivulariaceae with nine species distributed in six genera, was the most diverse (30 % of the species), followed by Calotrichaceae with seven species, contained in a single genus (23 % of the species), and Scytonemataceae with seven species, contained in two genera (23 % of the species). However, in Rivulariaceae, the genera *Kyrtuthrix* and *Scytonematopsis* grouped the largest number of species, while in Calotrichaceae, we only identified the genus *Calothrix*. Of the two species we identified as *Kyrtuthrix*, one specimen did not match the descriptions for any of the known species, so it was identified only to the genus level. With certainty, this record will correspond to a new species, although its confirmation requires molecular analysis. In general, the species of *Kyrtuthrix* are poorly known due to the absence of identified species in different environments of the world. Even the two species described by Komárek (2013), *K. Dalmatica* and *K. maculans*, require evaluation since they could be the same species; therefore, a full evaluation of the taxonomic status of the genus is needed. Of the five species identified three were recognized as *Scytonematopsis* sp., because our specimens presented the morphological characteristics of the genus, but they did not fully coincide with what was described for the known species. It should be noted that our species did not agree with other genera such as *Brasilonema* and *Petalonema*, previously reported for the Mexican Tropical Pacific (González-Reséndiz *et al.* 2015). With those genera they share Scytonematopsis-like morphology but are distinguished by the width and length of the cells and the morphology of the apical cells and the sheath.

The same happened with *Calothrix* in which two of the seven registered species were also identified as *Calothrix* sp. Among the main differences were the measurement ranges for the cells, the trichome, heterocytes, thickness of the sheaths, and shape of the tips. Although in some cases there were partial coincidences, as in the case of *Calothrix* sp.2 and *C. brevissima* or *C. marchica*, the reference images or the environments described did not match, as we referred to in the taxonomic comments for these cases. As mentioned by Komárek (2013) and Berrendero *et al.* (2008) many species of *Calothrix* could belong to other genera. This observation is supported by the notable differ-

ences observed in characteristics such as cell measurements, trichomes, branching patterns and presence of akinetes in tropical populations, like those presented by our specimens. At this time, several of the species of the genus *Calothrix* have been transferred to other genera, some of which were recently created as: *Nunduva* González-Resendiz, León-Tejera & J.R. Johansen and *Macrochaete* Berrendero, J.R. Johansen & Kastovsky (Berrendero-Gómez *et al.* 2016, González-Reséndiz 2018a,b), in which, although the Calothrix-type morphology is shared, differences can be found. Although morphologically we can suggest that our specimens correspond to new species, further analyses are still required to confirm this.

The least diverse families were Nostocaceae with two species and Capsosiraceae and Hapalosiphonaceae with one species each. Regarding the genus *Nostoc*, a morphospecies was recorded that, like in the previous cases, did not fully fit the descriptions of the species in Komárek (2013). However, this author mentions that many species are described as *Nostoc* sp. in the literature due to the complexity and number of morphs and genotypes included in the genus (Řeháková *et al*. 2007, Hrouzek *et al*. 2013, Cai *et al*. 2019a). Based on the use of molecular tools, new genera such as *Mojavia* Řeháková & Johansen (Řeháková *et al*. 2007), *Desmonostoc* (Bornet & Flahault) Hrouzek & Ventura (Hrouzek *et al*. 2013), *Halotia* (Genuario *et al*. 2015), and *Compactonostoc* F.Cai & R.Li (Cai *et al*. 2019b) have been described. It should be noted that morphological studies with descriptions are important, since by describing diagnostic characters, they facilitate the delimitation of species and can serve as the starting point for evolutionary and phylogenetic studies. In cases of cyanoprokaryotes, with complex life cycles, like *Halotia* and *Nostoc*, studies in culture and the morphology of the species are useful to be able to properly direct more complex studies (Berthold *et al.* 2022). However, identifying the species through traditional morphology has been complicated, so, as in the cases that we described above, these specimens must also be treated molecularly to confirm their taxonomic status. In addition, studies are required with a polyphasic approach that considers morphology, ecology, ultrastructure, and molecular analysis, so that the morphological, genetic and ecological information of the species in different environments is grouped (Komárek 2016), from these, could be developed works of an ecological (including richness, diversity, and physicochemical parameters), biogeographic and phylogeographic approach, which require the integration of the information obtained through the polyphasic approach.

Given that knowledge of the benthic marine cyanoprokaryotes of Mexico in general is scarce, one of the main problems for most of our specimens was to identify them at the species level, only reaching genus in several cases. The descriptions at the species level do not fully coincide with the non-European specimens, thus in the present study one species remains to be confirmed and seven specimens were identified as sp. Only 3 works in the Mexican Atlantic treat the group individually (González-Reséndiz *et al*. 2018a, b, Johansen *et al*. 2021), which has resulted in the underestimation of the richness and diversity of the group. Particularly in Mexico, the knowledge of the group comes from the floristic lists for marine macroalgae, in which the cianoprocariota are included or briefly mentioned, since they share substrates and environments (Pedroche & González-González 1981, Dreckmann *et al.* 1990, Mateo-Cid & Mendoza-González 1991, 1994a,b, León-Tejera *et al*. 1993, Mendoza-González *et al* 1994, 2011, Núñez-López *et al*. 1998) Although these records have provided an important starting point for the study of these organisms, they do not constitute works focused on the study of cyanoprokaryotes, but rather an enumeration of the species present in a certain site, without any reference for their identification, much less associated morphological or ecological information (diversity, abundances, abiotic and biotic interactions). Another problem is the use of European identification manuals such as that of Komárek (2013), which is the only work that deals with the detailed systematics and morphology of these organisms. One of the reasons why the above happens may be the lack of sampling effort in benthic marine environments in Mexico as suggested Caires *et al.* (2019). Some examples of the above have also occurred in other countries with tropical marine environments such as Brazil, where the identity of some species must be confirmed using molecular tools since the specialized literature is not entirely compatible with the tropical populations (da Silva *et al*. 2020, Caires & Affe 2021, Berthold *et al.* 2022).

Another important aspect to highlight is the possible presence of amphioceanic species. *Kyrtuthrix huatulcensis, Scytonema crispum* and *Calothrix contarenii*, recorded in this study, have also been recorded for the Mexican Tropical Pacific (Pedroche & González-González 1981, León-Tejera *et al*. 1993, López-Cortez 1999, López-Cortez *et al*.

2001, González-Reséndiz *et al.* 2015, León-Tejera *et al*. 2016a, Torres-Ariño *et al*. 2019), which must be confirmed. The morphological characteristics of our specimens from Veracruz fully be consistent with those reported for the Pacific populations, although their identification has not been confirmed molecularly, so the possibility of cryptic diversity between these species cannot be ruled out.

On the other hand, of the sites sampled to carry out this study, Costa de Oro was the locality where the highest number of species was found (14), followed by Playa Muñecos (12) and Morro de la Mancha (2). This diversity, however, can be explained by the physiography of the first two sites, where limestone or sedimentary rocks predominate, exposed to intense waves and with mainly crusty growths, among which cyanoprokaryotes predominate. For this reason, the diversity of benthic marine macroalgae is considerably lower in these sites compared to that found in Morro de la Mancha, where large macroalgae predominate (García-García *et al*. 2020, 2021), which can obliterate the development of these organisms or at least make them less evident at the time of collection.

The most frequent species were *Scytonema crispum*, *Scytonematopsis crustacea*, *Scytonematopsis* sp.3, *Phyllonema ansata*, which present evident macroscopic growths, forming bushes with a thick sheath, generally lamellar. The lamellar sheath allows them to better resist solar radiation and drying caused by tidal changes, very marked on these beaches (Díez & Ininbergs 2013), It is also important to highlight that all Nostocales species recorded in this study were epilithic or epizoic (on the surface of shells).

It is also important to continue with future studies that integrate molecular characters to support taxa taxonomic position, generating more robust classifications, and resolving the problems highlighted here. The detailed morphological description of the recorded species and the photographic references of the main characters described constitute the first approach and an important contribution to the knowledge of the Mexican tropical marine Nostocales species.

Acknowledgements

We thank the anonymous reviewers for their valuable comments throughout the text.

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Associate editor: Antonio Zertuche González

Author contributions: ECB and AMEGG carried out sample collection, analysis and taxonomic identification, and writing of the text. MLNR contributed analysis of results, discussion of results, and writing. KMD with text writing, discussion analysis. AS with the writing of the text, the analysis of the discussion.

Supporting Agencies: Consejo Nacional de Humanidades Ciencia y Tecnologías (scholarship granted to ECB (CVU: 1080205) and AMEGG (CVU: 1256053). MLNR, KMD and AS thank for support the projects UAMI-CBS2023-2026 y UAMI-CA-117, Programa para el Desarrollo Profesional Docente de la Secretaría de Educación Pública (PRODEP-SEP).

Conflict of interest: The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data and results of this article.