



***Neogoniolithon* (Corallinales, Rhodophyta) on the Atlantic coast of Mexico, including *N. siankanensis* sp. nov.**

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Abstract

This is the first revision of *Neogoniolithon* species on the east coast of Mexico based on both DNA sequences (*psbA*) and morpho-anatomical characters. Nine species names are provisionally applied based on morpho-anatomical comparisons with type specimens or with species descriptions: *N. accretum*, *N. acropetum*, *N. erosum*, *N. mamillare*, *N. propinquum*, *N. rhizophorae*, *N. solubile*, *N. spectabile* and *N. strictum*. For none of these species was type or topotype material sequenced, but all have their type localities in the subtropical or tropical western Atlantic Ocean. *Neogoniolithon siankanensis* is described on the basis of a distinctive branched thallus, apical tetrasporangial conceptacles and DNA sequence. Another four species are present, each characterized by DNA sequence, but insufficient reproductive material was available to adequately describe these species. A suite of vegetative and reproductive characters can adequately segregate the currently named Mexican east coast *Neogoniolithon* species, including 1) branched versus unbranched thalli, 2) monomerous versus dimerous construction, 3) disposition of trichocytes, 4) interior dimensions of mature tetrasporangial conceptacles, 5) number of cell layers comprising tetrasporangial conceptacle roof and 6) shape of cells that line tetrasporangial pore canal. Morpho-anatomical descriptions and distributions are provided for all named species.

Key words: Caribbean Sea, Gulf of Mexico, Neogoniolithoideae, *psbA* sequences

Introduction

The use of DNA sequence data has profoundly altered our understanding of the phylogenetic relationships among families, subfamilies and genera of the Corallinales (Bailey & Chapman 1996, Gabrielson *et al.* 2011, Kato *et al.* 2013, Hind & Saunders 2012, Martone *et al.* 2012). Kato *et al.* (2013) segregated three new subfamilies from the Mastophoroideae based on DNA sequence data and supported by morpho-anatomical characters, including the Neogoniolithoideae, with the single genus, *Neogoniolithon*. The following suite of morpho-anatomical features characterize this genus: 1) lack of genicula, 2) cells of adjacent filaments linked by cell-fusions (secondary pit-connections absent), 3) palisade cells absent, 4) uniporate gametangial and sporangial conceptacles, 5) tetrasporangial conceptacles formed by filaments peripheral to the fertile area (type 1), 6) gonimoblast filaments derived from the entire dorsal surface of a fusion cell, and 7) spermatangia formed on both the floor and roof of male conceptacle chambers.

The best represented non-geniculate corallines on the Mexican Gulf of Mexico and Caribbean Sea coasts are *Neogoniolithon* and *Hydrolithon* Foslie (subfamily Hydrolithoideae). *Neogoniolithon* is the most important component of Mexican Caribbean coral reefs (Huerta-Múzquiz *et al.* 1987, Mendoza-González & Mateo-Cid 1992, Ortega *et al.* 2001, Mateo-Cid & Pedroche 2004) and is also very common on most of the rocky shores. However, despite *Neogoniolithon*'s abundance, representatives of this genus from Mexico have not been critically studied. This paper is the first account of Mexican Gulf of Mexico and Caribbean Sea *Neogoniolithon* species and their local distributions as well as a re-evaluation of morphological and reproductive characteristics of the genus.

Materials & Methods

Specimens of *Neogoniolithon* were borrowed from ENCB (Department of Botany, National School at Biological Sciences, Mexico, D.F.) and IZTA (Faculty of Graduate Studies, National Autonomous University of Mexico, Mexico, D.F.). We compared our material of *Neogoniolithon cf. erosum*, with the type description of *Hydrolithon improcerum* (Foslie & M. Howe) Foslie provided by Maneveldt (2005). Lectotype specimens of *Neogoniolithon fosliei* (Heydrich) Setchell & L.R. Mason, *N. propinquum* (Foslie) Me. Lemoine and *N. solubile* (Foslie & M. Howe) Setchell & L.R. Mason were borrowed from TRH; herbarium acronyms follow Thiers (2014). Additional specimens of *Neogoniolithon* were collected by reef-walking or snorkeling. Samples were preserved in 5% formalin/seawater for anatomical observations; duplicate samples of some specimens were preserved in silica gel for molecular analyses. Formalin preserved specimens were decalcified with 0.6M HNO₃ and dehydrated with ethyl alcohol at different concentrations (10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90% and absolute ethyl alcohol). Small fragments were embedded in paraffin and sectioned 9-12 µm thick with a manual microtome, fixed on slides with Riuter's adhesive (Martoja & Martoja-Pierson 1970), and stained with aniline blue and hematoxylin-eosine for anatomical observations and measurements. Procedures for morphological observations followed Kato *et al.* (2006); thallus terminology followed Chamberlain (1993) and Peña *et al.* (2011). Diameters and lengths of epithallial cells, dorsal region (cortex), basal layers (medulla) and trichocytes were measured as were conceptacle height (greatest distance from top to bottom of chamber) and inside diameter (greatest distance across conceptacle chamber) and conceptacle canal diameter and height. Formalin preserved specimens were deposited in ENCB; specimens for molecular analyses were deposited in NCU with duplicates in ENCB.

Silica gel-dried samples for DNA extraction were examined under high magnification with a dissecting microscope to check for red algal epiphytes. Clean fragments about 3 mm³ total volume were placed in heavy paper packets and crushed and ground to a fine powder before being extracted following the protocol in Hughey *et al.* (2001) and the recommendations in Hughey & Gabrielson (2012). The *psbA* gene was amplified using the primer combination *psbAF1* and *psbAR2* of Yoon *et al.* (2002). Amplification and sequencing protocols were those of Hughey *et al.* (2001), and sequences were trimmed to a length of 849 base pairs (bp). Sequences were obtained from an ABI 3100 Genetic Analyzer (DNA Analysis Core Facility, Center for Marine Sciences, University of North Carolina, Wilmington), and were manually aligned and compiled using Sequencer (Gene Codes Corp., Ann Arbor, MI, USA), and Sequence Alignment Editor available at <http://evolve.zoo.ox.ac.uk/Se-AI/Se-AI.html>. A Maximum Likelihood (ML) analysis was performed using the default parameters of RaxML BlackBox (Stamatakis *et al.* 2008) until 500 bootstrap (BS) replications were amassed. *Ahnfeltia* was used as the outgroup as it provided the best segregation of orders and subfamilies.

Results

DNA Sequences

A Maximum Likelihood analysis of our dataset (Table 1) of Mexican Gulf of Mexico and Caribbean Sea specimens identified as belonging to *Neogoniolithon* occurred in a strongly supported, monophyletic clade (98% BS) with other worldwide specimens also identified as belonging to this genus (Fig. 1). Thirteen Gulf of Mexico and Caribbean Sea species were found, eight of which could be associated by morpho-anatomical characters to pre-existing species of *Neogoniolithon* whose type localities occurred in the tropical western Atlantic or Caribbean Sea, one which is described as a new species, and four which appear to be undescribed but were represented by too few specimens (one or two for each species) to adequately provide species descriptions. Sequence divergence values of Mexican east coast *Neogoniolithon* species vary from 1.6% to 19% (Table 2).

TABLE 1. List of specimens sequenced, including herbarium number, collection data and GenBank Accession number (*psbA*). Taxa are listed in alphabetical order.

Species	Herbarium Number	Collection Data	GenBank Accession #
<i>Heydrichia woelkerlingii</i>	NCU 597127	South Africa, Cape Province, Oudekraal (-33.9871, 18.3497), 2.ix.2011, bedrock, low intertidal, <i>leg.</i> M. Rothman & C. Boothroyd	JQ917415
<i>Porolithon</i> sp.	NCU 627394	USA, Florida, reef near Pickle Reef (25.00139, -80.41528), 4.i.2012, 5-6 m deep on dead coral, <i>leg.</i> E. Broderick	KJ637690
<i>Neogoniolithon accretum</i>	NCU 624405	Mexico, Quintana Roo, Playa Bonita (19.94389, -87.46528), 22.i.2011, epilithic intertidal, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ637660
<i>Neogoniolithon accretum</i>	NCU 624411	Mexico, Quintana Roo, Playa Hualapich (19.87889, -87.46111), 18.xii.2011, 0 m deep on coral skeleton, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & D.Y. Garcia Lopez	KJ637659
<i>Neogoniolithon acropetum</i>	NCU 631649	Mexico, Quintana Roo, Playa Pelicanos (19.99389, -87.46528) 19.vi.2010, 2 m deep, <i>leg.</i> L.E. Mateo Cid & A.C. Mendoza Gonzalez	KJ637662
<i>Neogoniolithon acropetum</i>	NCU 624410 Neo1.21iv11	Mexico, Quintana Roo, 2 km southeast of Boca Paila (20.00833, -87.56428), 9.v.2010, 1 m deep, <i>leg.</i> L.E. Mateo Cid & A.C. Mendoza Gonzalez & J.A. Acosta Calderon	KJ637663
<i>Neogoniolithon acropetum</i>	NCU 624401	Mexico, Quintana Roo, Playa Xoquem (19.82722, -87.45833), 21.xii.2011, 0 m deep, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez & J.A. Acosta Calderon	KJ637661
<i>Neogoniolithon mamillare</i>	NCU 624389	Mexico, Quintana Roo, Puerto Morelos, (20.8500, -86.86667), 15.iii.2013, on mangrove roots, <i>leg.</i> D. Gonzalez-Nieto	KJ667664
<i>Neogoniolithon propinquum</i>	NCU 624387	Mexico, Veracruz, Playa Los Muñecos, (19.74389, -96.40750), 3.iv.2013, epilithic intertidal, <i>leg.</i> L.E. Mateo Cid & A.C. Mendoza Gonzalez	KJ667665
<i>Neogoniolithon propinquum</i>	NCU 624430	Mexico, Quintana Roo, Pulticub (19.00806, -87.55083) 16.xii.2011, epilithic intertidal, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & D.Y. Garcia Lopez	KJ667667
<i>Neogoniolithon propinquum</i>	NCU 624397	Mexico, Quintana Roo, Isla Cozumel, (20.40222, -87.10028), 25.xii.2011, epilithic intertidal pools, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & D.Y. Garcia Lopez	KJ667668
<i>Neogoniolithon propinquum</i>	NCU 624377	Mexico, Quintana Roo, Playa Bonita (19.94389, -87.46528), 22.vi.2010, epilithic intertidal, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ667666
<i>Neogoniolithon rhizophorae</i>	NCU 624437	Mexico, Quintana Roo, Pulticub (19.00806, -87.55083), 16.xii.2011, 1 m deep on Gorgonian coral <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ667669
<i>Neogoniolithon rhizophorae</i>	NCU 624381	Mexico, Veracruz, Bajos de Tuxpan, (21.02917, -97.19972), 17.viii.2013, 1 m deep on coral skeleton, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, D.Y. Garcia Lopez, & J.A. Acosta Calderon	KJ667670
<i>Neogoniolithon rhizophorae</i>	NCU 624375	Mexico, Quintana Roo, Rio Indio (18.81722, -87.66278), 6.xi.2013, 1 m deep on Gorgonian coral, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, J. Acosta, & D. Garcia	KJ667671
<i>Neogoniolithon rhizophorae</i>	NCU 624420	Mexico, Quintana Roo, Hualastoc, B. Ascension (19.66472, -87.44750), 19.xii.2011, 0 m deep on coral skeleton, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ667672
<i>Neogoniolithon siakanensis</i>	NCU 624415 holotype	Mexico, Quintana Roo, Playa Hualapich (19.87889, -87.46111), 18.xii.2011, 0 m deep, <i>leg.</i> L.E. Mateo Cid & A.C. Mendoza Gonzalez	KJ667673

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TABLE 1 (Continued)

Species	Herbarium Number	Collection Data	GenBank Accession #
<i>Neogoniolithon siankanensis</i>	NCU 631648	Mexico, Quintana Roo, Playa Bonita (19.94389, -87.46528), 18.xii.2011, 0 m deep, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez & J.A. Acosta Calderon	KJ667674
<i>Neogoniolithon siankanensis</i>	NCU 624398	Mexico, Quintana Roo, Playa Hualapich (19.87889, -87.46111), 18.xii.2011, 0 m deep, <i>leg.</i> L.E. Mateo-Cid, A.C. Mendoza Gonzalez, & D.Y. Garcia Lopez	KJ667675
<i>Neogoniolithon solubile</i>	NCU 624396 Neo.fos.Baj.1 9xii13	Mexico, Veracruz, Bajos de Tuxpan (21.02917, -97.19972), 17.viii.2013, 1 m deep on coral skeleton, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ637677
<i>Neogoniolithon solubile</i>	NCU 624976 Neo3.17xii13	Mexico, Quintana Roo, Punta Majahual (18.72917, -87.70000), 9.xi.2013, 1 m deep on coral skeleton, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ667679
<i>Neogoniolithon solubile</i>	NCU 624380 Neo13.2v11	Mexico, Quintana Roo, Playa Bonita (19.94389, -87.46528), 21.i.2010, 1 m deep on Gorgonian coral, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ667676
<i>Neogoniolithon solubile</i>	NCU 624974	Mexico, Quintana Roo, Punta Majahual (18.72917, -87.70000), 8.xi.2013, 1 m deep on coral skeleton, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ667678
<i>Neogoniolithon spectabile</i>	NCU 624418	Mexico, Quintana Roo, Playa Hualapich (19.87889, -87.46111), 18.xii.2011, 0 m deep, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ667680
<i>Neogoniolithon spectabile</i>	NCU 624407 Neo7.19iv11	Mexico, Quintana Roo, Bahía de Espiritu Santo (19.48333, -87.56861), 9.i.2011, 1 m deep, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & D.Y. Garcia Lopez	KJ637681
<i>Neogoniolithon spectabile</i>	NCU 624986 M19.9iv12	Mexico, Quintana Roo, Hualastoc, B. Ascension (19.66472, -87.44750), 19.xii.2011, 1 m deep, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ637682
<i>Neogoniolithon strictum</i>	NCU 624429	Mexico, Quintana Roo, Pulticub (19.00806, -87.55083), 16.xii.2011, 2 m deep <i>leg.</i> L.E. MateoCid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ667683
<i>Neogoniolithon strictum</i>	NCU 624376	Mexico, Quintana Roo, Pulticub (19.00806, -87.55083), 19.vi.2010, 2 m deep, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, & J.A. Acosta Calderon	KJ667684
<i>Neogoniolithon</i> sp. 1	NCU 627724	Mexico, Quintana Roo, Rio Indio (18.81722, -87.66278), 6.xi.2013, 1 m deep on coral skeleton, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, J. Acosta, & D. Garcia	KJ667685
<i>Neogoniolithon</i> sp. 1	NCU 627722	Mexico, Veracruz, Bajos de Tuxpan (21.02917, -97.19972), 17.viii.2013, on coral skeleton, <i>leg.</i> L.E. Mateo-Cid, A.C. Mendoza Gonzalez, D.Y. Garcia Lopez, & J.A. Acosta Calderon	KJ667686
<i>Neogoniolithon</i> sp. 2	NCU 624386	Mexico, Veracruz, Bajos de Tuxpan (21.02917, -97.19972), 17.viii.2013, on coral rubble, <i>leg.</i> L.E. Mateo Cid, A.C. Mendoza Gonzalez, D. Y. Garcia Lopez & J.A. Acosta Calderon	KJ667687
<i>Neogoniolithon</i> sp. 3	NCU 624426	Mexico, Quintana Roo, Pulticub (19.00806, -87.55083), 16.xii.2011, 1 m deep on coral rubble, <i>leg.</i> L.E. MateoCid, A.C. Mendoza Gonzalez, & D.Y. Garcia Lopez	KJ667688
<i>Neogoniolithon</i> sp. 4	NCU 624403	Mexico, Quintana Roo, Punta Xoquem (19.82722, -87.45222), 21.xii.2011, 0 m deep, <i>leg.</i> L.E. Mateo Cid, D.Y. Garcia Lopez, & J.A. Acosta Calderon	KJ667689
<i>Spongites decipiens</i>	NCU 593921	USA, California, Del Norte Co., Crescent City, 2.viii.2008, on cobble, mid-intertidal, <i>leg.</i> W. Wood	KJ667691

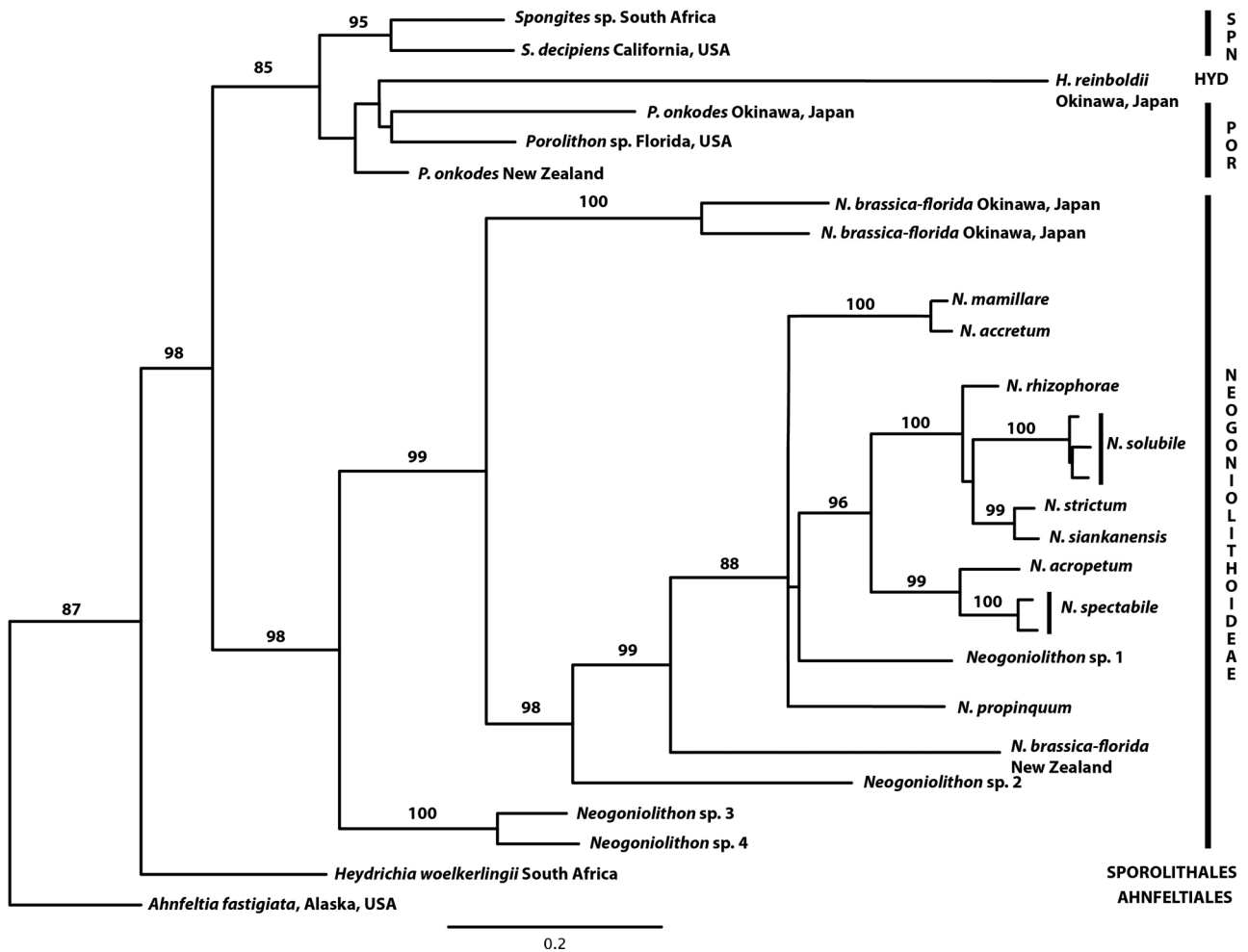


FIGURE 1. Consensus maximum likelihood tree inferred from *psbA* sequences. Numbers above nodes are bootstrap values. All *Neogoniolithon* sequences without locality data are from the east coast of Mexico (see Table 1). Abbreviations: HYD = Hydrolithoideae; POR = Porolithoideae SPN = *Spongites*.

TABLE 2. *psbA* sequence divergence values (in %) among Mexican east coast species of *Neogoniolithon*. *acc* = *N. accretum*, *acr* = *N. acropetum*, *mam* = *N. mamillare*, *pro* = *N. propinquum*, *rhi* = *N. rhizophorae*, *sia* = *N. siankanensis*, *sol* = *N. solubile*, *spe* = *N. spectabile*, *str* = *N. strictum*.

	<i>acc</i>	<i>acr</i>	<i>mam</i>	<i>pro</i>	<i>rhi</i>	<i>sia</i>	<i>sol</i>	<i>spe</i>	<i>str</i>	sp1	sp2	sp3
<i>acr</i>	10.1											
<i>mam</i>	2.0	9.9										
<i>pro</i>	10.5	10.4	10.4									
<i>rhi</i>	10.1	7.5	10.5	10.4								
<i>sia</i>	10.7	9.0	10.4	10.0	3.8							
<i>sol</i>	11.5	8.4	11.5	9.9	5.1	5.8						
<i>spe</i>	10.8	4.7	10.7	10.6	8.8	9.4	9.5					
<i>str</i>	11.1	9.0	10.7	10.1	3.8	1.6	5.5	9.3				
sp1	9.7	10.5	8.8	9.3	10.1	9.7	10.8	10.2	9.3			
sp2	15.2	15.7	15.9	13.5	14.3	14.5	15.0	16.4	14.3	14.0		
sp3	16.7	16.7	16.8	14.7	17.3	17.0	16.9	18.0	16.2	16.2	15.9	
sp4	16.9	18.1	17.0	15.9	17.4	17.4	17.4	19.0	16.7	16.3	16.4	5.2

Taxonomic Treatment

Neogoniolithon Setchell & L.R. Mason 1943: 89.

Type (Holotype): *Neogoniolithon fosliei* (Heydrich) Setchell & L.R. Mason 1943: 90

Species Descriptions. Morpho-anatomical characters useful in segregating the named *Neogoniolithon* species along the east coast of Mexico are in Tables 3 and 4.

TABLE 3. Morphological and reproductive characters of unbranched Mexican east coast species of *Neogoniolithon*.

Character	<i>N. accretum</i>	<i>N. erosum</i>	<i>N. mamillare</i>	<i>N. propinquum</i>	<i>N. solubile</i>
Growth form	Encrusting	Encrusting	Warty	Encrusting	Foliose
Thallus construction	Monomerous	Dimerous	Monomerous	Monomerous	Monomerous and strongly coaxial
Trichocytes	Single	Single	Single and in horizontal rows	In vertical and horizontal rows	Single, and in vertical or horizontal rows
Tetrasporangial conceptacles					
Chamber diameter	250–470 µm	170–180 µm	500–700 µm	500–900 µm	500–900 µm
Chamber high	210–310 µm	240–250 µm	300–380 µm	170–300 µm	200–340 µm
Number of cells in roof filaments	6–7	3–4	14–16	10–12	8–12
Length of the pore canal	200–350 µm	110–180 µm	200–300 µm	180–250 µm	500–700 µm
Shape of the pore canal cells	Truncate-spatulate	Spike	Elongated	Sigmoid	Papillae-like
Columella	Present	Absent	Present	Absent	Absent
Male conceptacles Chamber diameter	210–310 µm	230–250 µm	ND	350–400 µm	250–300 µm
Chamber high	80–110 µm	100–120 µm	ND	150–200 µm	130–150 µm
Female conceptacles Chamber diameter	200–380 µm	ND	ND	ND	ND
Chamber high	140–200	ND	ND	ND	ND

ND= Data not available.

TABLE 4. Morphological and reproductive characters of the branching or with excrescences Mexican east coast species of *Neogoniolithon*.

Character	<i>N. acropetum</i>	<i>N. rhizophorae</i>	<i>N. siankanensis</i>	<i>N. spectabile</i>	<i>N. strictum</i>
Thallus growth	Encrusting	Encrusting	Encrusting	Free form	Encrusting, rarely unattached
Primary crust	Conspicuous	Conspicuous	Conspicuous	Absent	Absent
Branching	Subdichotomous	Unbranched or once branched	Subdichotomous or trichotomous	Irregular to subdichotomous	Subdichotomous
Shape of the branches	Terete to strongly compressed	Terete	Terete	Terete	Subterete to compressed

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TABLE 4 (continued)

Character	<i>N. acropetum</i>	<i>N. rhizophorae</i>	<i>N. siakanensis</i>	<i>N. spectabile</i>	<i>N. strictum</i>
Thallus construction	Radial in branches	Monomerous in encrusting base and radial in branches	Monomerous in encrusting base and radial in branches	Radial in branches	Radial in branches
Trichocytes	Singly or in vertical rows	Singly or in horizontal rows	Singly	Singly or in vertical rows	Singly or in horizontal rows
Asexual conceptacles Position on the branches	Lateral	Terminal on excrescences	Terminal on excrescences	Lateral	Lateral
Chamber diameter	750–850 µm	600–700 µm	500–800 µm	500–800 µm	750–1000 µm
Chamber high	225–450 µm	250–320 µm	200–300 µm	250–370 µm	200–300 µm
Length of the canal	200–220 µm	280–300 µm	500–600 µm	700–750 µm	300–400 µm
Number of cells in roof filaments	10–14	15–18	10–12	16–20	10–14
Shape canal cells	Clavate	Arcuate	Lanceolate	Elliptical	Semilunated
Columella	Absent	Absent	Absent	Absent	Absent
Male conceptacles Chamber diameter	ND	350–450 µm	450–500 µm	ND	ND
Chamber high	ND	150–250 µm	250–300 µm	ND	ND

ND= Data not available.

Neogoniolithon accretum (Foslie & M. Howe) Setchell & L.R. Mason 1943: 90.

Basionym: *Goniolithon accretum* Foslie & M. Howe, 1906a: 131–132; Pl. 85, Fig. 2; Pl. 91.

Holotype: NY, Howe no. 2920a.

Isotype: TRH, Howe no. 2920a. Include one slide also numbered 2920a.

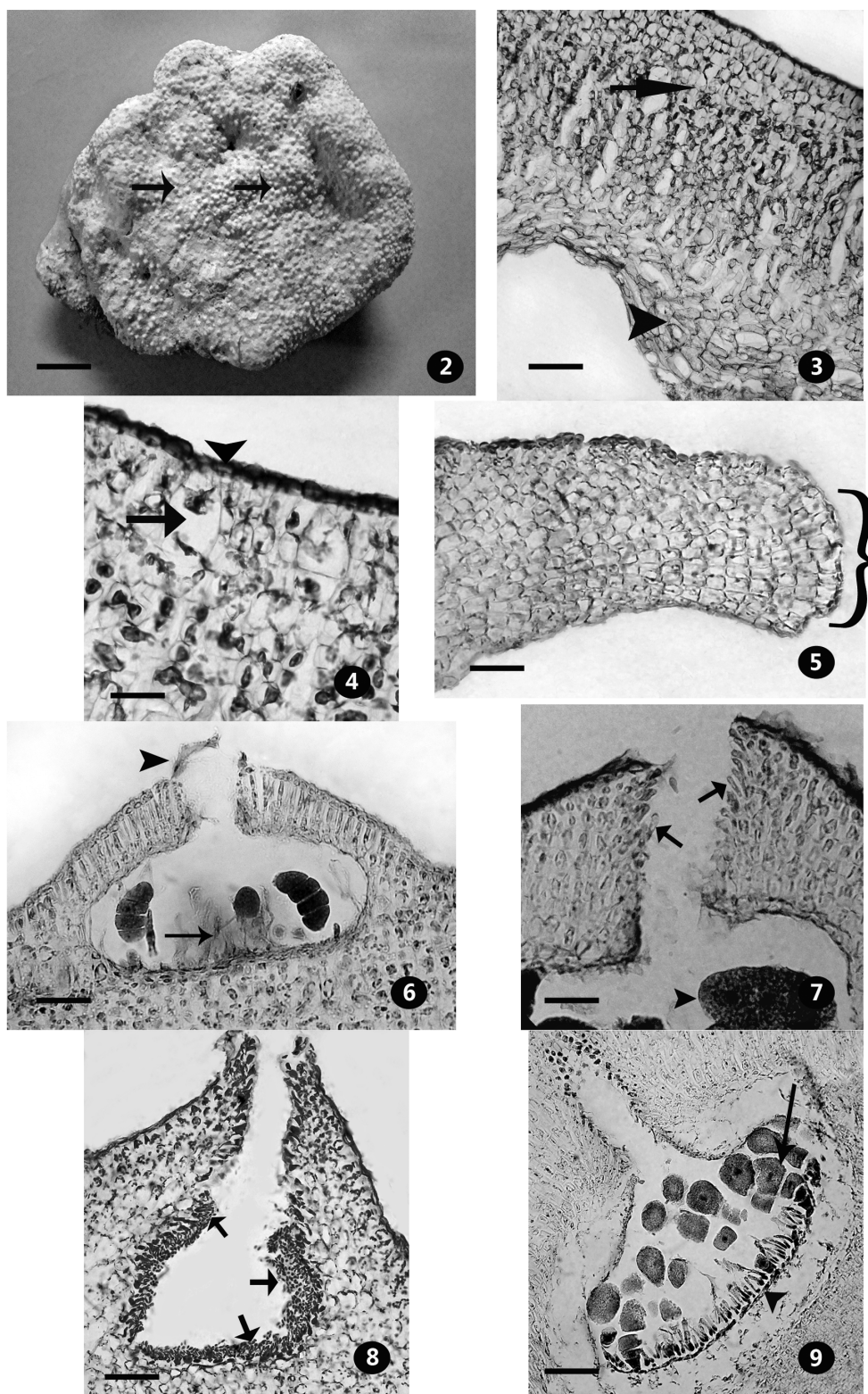
Type Locality: Sand Key, Florida, USA.

Geographical distribution: North America, Caribbean Islands, Brazil, Kenya, Japan (Wynne 2011, Guiry & Guiry 2014)

Specimens Examined Morpho-anatomically (Figs. 2–9). MÉXICO: *Veracruz*: Santiaguillo Island (Mendoza-González & Mateo-Cid, 1985: 15); Anegada de Adentro (96°06'17" W, 19°13'42" N), ⊕, Mateo-Cid & Mendoza-González, 08-07-2004 (ENCB 17454); Blanquilla Reef (96°05'54" W, 19°13'24" N), ⊕, Mateo-Cid & Mendoza-González, 24-04-2005 (ENCB 18830); Verde Island (96°04'06" W, 19°11'50" N), ⊕, Mateo-Cid & Mendoza-González, 16-11-1992, 24-04-2005 (ENCB 18834, 18837); Sacrificios Island (96°06'17" W, 19°10'26" N), ♀, ⊕, Mateo-Cid & Mendoza-González, 26-04-2005 (ENCB 18835). *Yucatán*: Alacranes Reef, Pérez Island (89°37'04" W, 21°17'55" N), ⊕, ♂, Huerta Múzquiz & Mateo-Cid, 15-10-1985 (ENCB 17435); Desertora Island (89°40'49" W, 22°23'08" N), ♀, ♂, Huerta Múzquiz & Mateo-Cid, 15-10-1985 (ENCB 17453). *Quintana Roo*: Cozumel Island, Punta Morena (86°51'12" W, 20°24'31" N), ♀, ♂ Mateo-Cid & Mendoza-González, 14-09-1993 (ENCB 19046), Mujeres Island (86°43'06" W, 21°12'44" N), ♂, Mateo-Cid & Mendoza-González, 14-09-1985 (ENCB 17447); 2 km. SE Boca Paila (87°33'00" W, 20°01'00" N), 20-06-2010, Mendoza-González, Mateo-Cid & Acosta Calderón (ENCB 20080); Pelicanos Beach (87°27'55" W, 19°59'38" N), ⊕, 21-01-2011, Mendoza-González, Mateo-Cid & Trinidad Calderón (ENCB 20079).

Habitat and Morphology. Epilithic on coral skeletons, intertidal and in pools. Thalli encrusting, following the contour of the substrate, without protuberances (Fig. 2), attached to the substratum ventrally by cell adhesion, 225 to 800 µm thick.

Anatomy. Thallus construction monomerous (Fig. 3), consisting of a multiaxial system of branched filaments that collectively contribute to a ventrally or centrally situated core (from 10–35% of the total thallus thickness) and a peripheral region where portions of core filaments or their derivatives curve outwards towards the thallus surface; ventral cells are oblong or rectangular 9–13 µm wide and 15–30 µm long; cortical cells are square (6–9 µm in diameter), rounded (12–20 µm diameter), or vertically elongate (8–18 µm wide and 18–24 µm long) each with



FIGURES 2–9. *Neogoniolithon accretum*, Anegada de Adentro (ENCB 17 454). 2) Thallus encrusting pebbles. Arrows indicate small conical conceptacles. Scale bar: 8 mm. 3) Thallus section showing monomerous construction, note medulla (arrowhead) and cortex (arrow). Scale bar: 45 μm . 4) Section through dorsal region showing single trichocyte (arrow), cell fusion (arrowhead) and flattened epithallial cell (triangle). Scale bar: 12 μm . 5) Thallus section showing terminal arrangement of meristem (brace). Scale bar: 35 μm . 6) Section through mature tetrasporangial conceptacle showing columella (arrow) and a lump of mucilage (arrowhead). Scale bar: 40 μm . 7) Enlarged section through tetrasporangial conceptacle showing pore canal lined by cells truncate-spatulate-shape projecting into the canal (arrows) and tetrasporangium (arrowhead). Scale bar: 45 μm . 8) Mature male conceptacle with spermatangial filaments on the floor, walls and roof (arrows) of the chamber. Scale bar: 50 μm . 9) Mature female conceptacle with the gonimoblast filaments developing dorsally from a central fusion cell (arrowhead) and bearing terminal carposporangia (arrow). Scale bar 35 μm .

several fusions to adjacent cells; epithallus unistratose with flattened cells 6–9 μm in wide and 12.5–15.0 μm long. Trichocytes occur singly and scattered in dorsal region, 25–35 μm wide and 35–50 μm long (Fig. 4). Thallus growing from intercalary meristematic cells located below the epithallus (Fig. 5).

Reproductive structures. Tetrasporangial conceptacles are scattered over the thallus, raised and rounded or apiculate, and their chambers measure 250–470 μm diameter and 100–180 μm high (Fig. 6). The pore canal measures 30–50 μm diameter and 200–300 μm long and is lined by cells orientated more or less parallel to roof surface, truncate-spatulate in shape and projecting into the canal (Fig. 7). Canal plugged with mucilage that obstructs pore canal (Fig. 6). Roof filaments 6–7 cells long (not including epithallial cell). Tetrasporangia are 35–50 μm wide and 80–130 μm long, and they develop peripheral to a columella.

Gametangial plants dioecious; spermatangial conceptacles uniporate and scattered over thallus, protruding and apiculate, chambers 210–310 μm in diameter and 80–110 μm high. Simple spermatangia develop on the floor, walls and roof of male chambers (Fig. 8). Female conceptacles uniporate, protruding, rounded and more frequent than males, chambers of 260–380 μm diameter and 140–200 μm high, canal 300–400 μm long. Gonimoblast filaments develop dorsally from a central fusion cell (Fig. 9). Carposporangia measure 40–60 μm in diameter and 90–100 μm long.

DNA sequences. The two sequenced specimens (Table 2) had identical *psbA* sequences.

Comments. This species was described by Foslíe & Howe (1906a) based on specimens collected in Florida and the Bahamas. The thallus was described as 80–340 μm thick; 1–3 mm for older thalli. They also measured medullary and cortical cells, as well as trichocytes. Although they measured the diameter of conceptacles, they did not say whether the conceptacles were carposporangial or tetrasporangial. Their figure (Foslíe & Howe 1906a, Pl. 91) shows monomerous thallus construction with a medulla that does not cover a significant proportion of the thickness of the thallus. In general, the features observed in our specimens are similar to those described by Foslíe & Howe (1906a), although we have not sequenced the holotype to see if it matches specimens described herein. Mexican plants of *N. accretum* are characterized by the following combination of features: 1) thallus adherent, lacking protuberances; 2) thallus monomerous; 3) trichocytes present, occurring singly; 4) tetrasporangial pore canal lined by narrow filaments that tilt into the pore canal and have a truncate-spatulate shape and 5) tetrasporangial conceptacle roof is 6–7 cells thick.

Neogoniolithon acropetum (Foslíe & M. Howe) W.H. Adey 1970: 8.

Basionym: *Goniolithon acropetum* Foslíe & M. Howe 1906b: 577.

Type Locality: Isle Culebra, Puerto Rico.

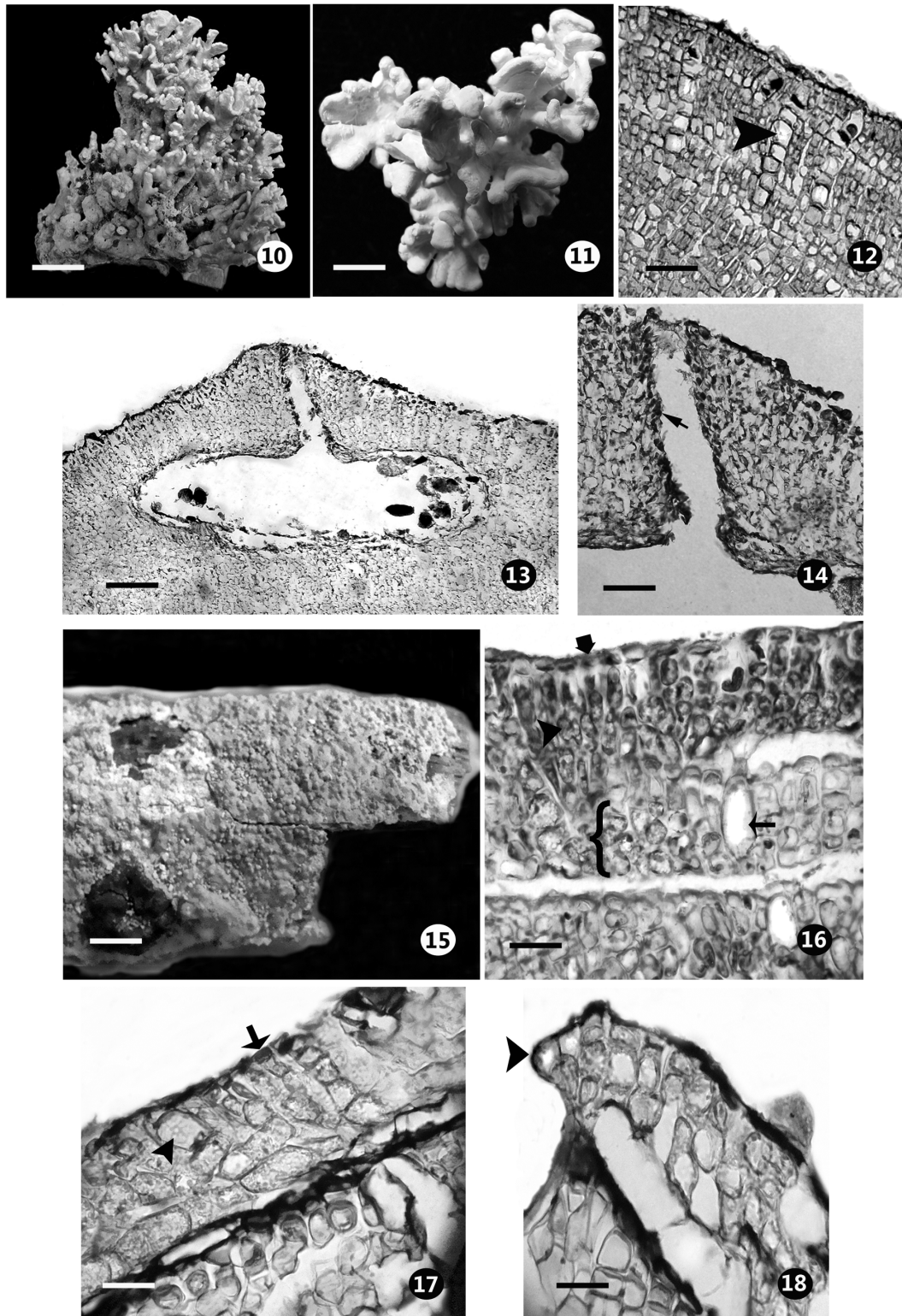
Distribution: Bahamas, Puerto Rico

Specimens Examined Morpho-anatomically (Figs. 10–14). MÉXICO: *Yucatán*: Alacranes Reef, Pérez Island (89°37'04" W, 21°17'55" N), ⊕, Huerta Múzquiz, 04-03-1989 (ENCB 19910). *Quintana Roo*: Ascensión Bay (87°25'28.5" W, 19°41'9.7" N), ⊕, Mateo-Cid & Mendoza-González, 17-05-1998 (ENCB 13484); El Zarzal (87°26'32.7" W, 19°55'47.7" N) ⊕; Mateo-Cid & Mendoza-González, 19-05-1998 (ENCB 17423).

Habitat and Morphology. Epilithic and intertidal; thalli forming dense, branching masses 6–10 cm high (Fig. 10), these often confluent, primary crust inconspicuous. Erect branches repeatedly subdichotomous, terete, subterete to compressed (Fig. 11), often anastomosed, and showing high variation in branch shape and diameter. Basal branches terete 5–8 mm in diameter, subtruncate to flattened divisions 4–5 mm broad and 1–2 mm thick above; young branches decutescens, the exfoliations papyraceous, revolute, more or less zonate.

Anatomy. Thallus construction monomerous; in transverse section showing a prominent medullary region, these cells oblong or rectangular 12–18 μm wide and 9–30 μm long; cortical cells square or rounded 16–18 μm wide and 22–26 μm long; epithallus unistratose with rounded cells 18–20 μm wide and 14–16 μm long. In the medulla and cortex are numerous cell fusions. Trichocytes 30–35 μm wide and 45–50 μm long, scattered or in vertical rows (Fig. 12).

Reproductive structures. Tetrasporangial conceptacles scattered over the thallus, raised and rounded, and their chambers measure 750–850 μm diameter and 225–450 μm high (Fig. 13). The pore canal measures 30–40 μm diameter and 200–250 μm long and is lined by clavate-shaped cells that protrude laterally into the canal (Fig. 14). Roof filaments 10–14 cells long (not including epithallial cell). Tetrasporangia 40–50 μm diameter and 100–110 μm long, arranged across the floor of the conceptacle, and a central columella is absent. Male and female conceptacles not seen in Mexican specimens.



FIGURES 10–14. *Neogoniolithon acropetum*, El Zarzal, Quintana Roo (ENCB 17423). 10) Arborescent thalli growing on rocks. Scale bar: 1.3 cm. 11) Apical portions, becoming compressed. Scale bar: 5 mm. 12) Thallus section showing trichocytes in vertical rows (arrowhead). Scale bar: 45 μ m. 13) Section through mature tetrasporangial conceptacle showing tetrasporangium (arrow). Scale bar: 235 μ m. 14) Enlarged section through tetrasporangial conceptacle showing clavate-shaped pore canal cells that protrude laterally into the canal (arrow). Scale bar: 45 μ m. **FIGURES 15–18.** *Neogoniolithon erosum* Mujeres Island (ENCB 17 804). 15) Habit of encrusting thalli growing on *Rhizophora*. Scale bar: 4 mm. 16) Thallus section showing dimerous construction, note the medulla (brace), cortex, cell fusion (arrowhead), a single trichocytes (arrow) and epithallial cell (broad arrow). Scale bar: 20 μ m. 17) Thallus section showing superimposed crust, single layered epithallus (arrow) and single trichocyte (arrowhead). Scale bar: 40 μ m. 18) Thallus section showing two superimposed crusts, note the single basal cell (arrowhead). Scale bar: 15 μ m.

DNA sequences. The three sequenced specimens (Table 2) had identical *psbA* sequences.

Comments: In the original description, Foslie & Howe (1906b) noted that the thallus formed caespitose or deformed masses mostly 4–12 cm high, with branches repeatedly subdichotomous, much anastomosed, compressed or subterete, 1.25–3.10 mm in diameter and subtruncate-capitate, or very often much dilated either at apices only or throughout and forming flabellate or foliar lamina 10–25 mm broad, the dilated portions often anastomosed, younger branches all conspicuously decutescent. Medullary cells (hypothallium) measured 14–40 μm x 11–20 μm and the cortical cells (perithallium) 11–21 μm x 9–14 μm . Trichocytes were numerous. Sporangial conceptacles were subconical, becoming mammillate, about 1 mm in diameter, with tetrasporangia 90–168 μm x 40–102 μm . These authors mentioned that *N. acropetum* is nearly close to forms of *Neogoniolithon strictum*, but *N. acropetum* is coarser, less fragile, and has less tapering branches. By morpho-anatomy, Mexican specimens are very similar morpho-anatomically to *N. acropetum* but we have not sequenced the holotype specimen to confirm that our material is the same.

Mexican plants of *Neogoniolithon acropetum* are characterized by the following combination of features: 1) thallus adherent, branched, and morphologically variable; 2) thallus monomerous; 3) trichocytes present, occurring singly or in vertical series; 4) the tetrasporangial pore canal lined by narrow filaments that tilt into the pore canal and have a clavate shape and 5) the tetrasporangial conceptacle roof is more commonly 10–14 cells thick. This species is distributed in Puerto Rico and the Bahamas, and this is the third record for this species in the Caribbean Sea.

Neogoniolithon erosum (Foslie) W.H. Adey 1970: 8.

Basionym: *Lithophyllum erosum* Foslie 1906: 20.

Type locality: Magenbay, St. Thomas Island, Virgin Islands, USA.

Distribution: Virgin Islands (Taylor 1960, Guiry & Guiry 2014).

Specimens Examined Morpho-anatomically (Figs. 15–26). MÉXICO: *Veracruz*: Santiaguillo Island (Mendoza-González & Mateo-Cid, 1985:16). *Quintana Roo*: Mujeres Island, Extremo Norte (86°44'56" W, 21°15'52" N), ⊕, 16-11-1984, Mateo-Cid & Mendoza-González (ENCB 17 804); Xcalac (8753'15" W, 18°16'10" N), ♂, Huerta Múzquiz, 22-12-1971 (ENCB 19179).

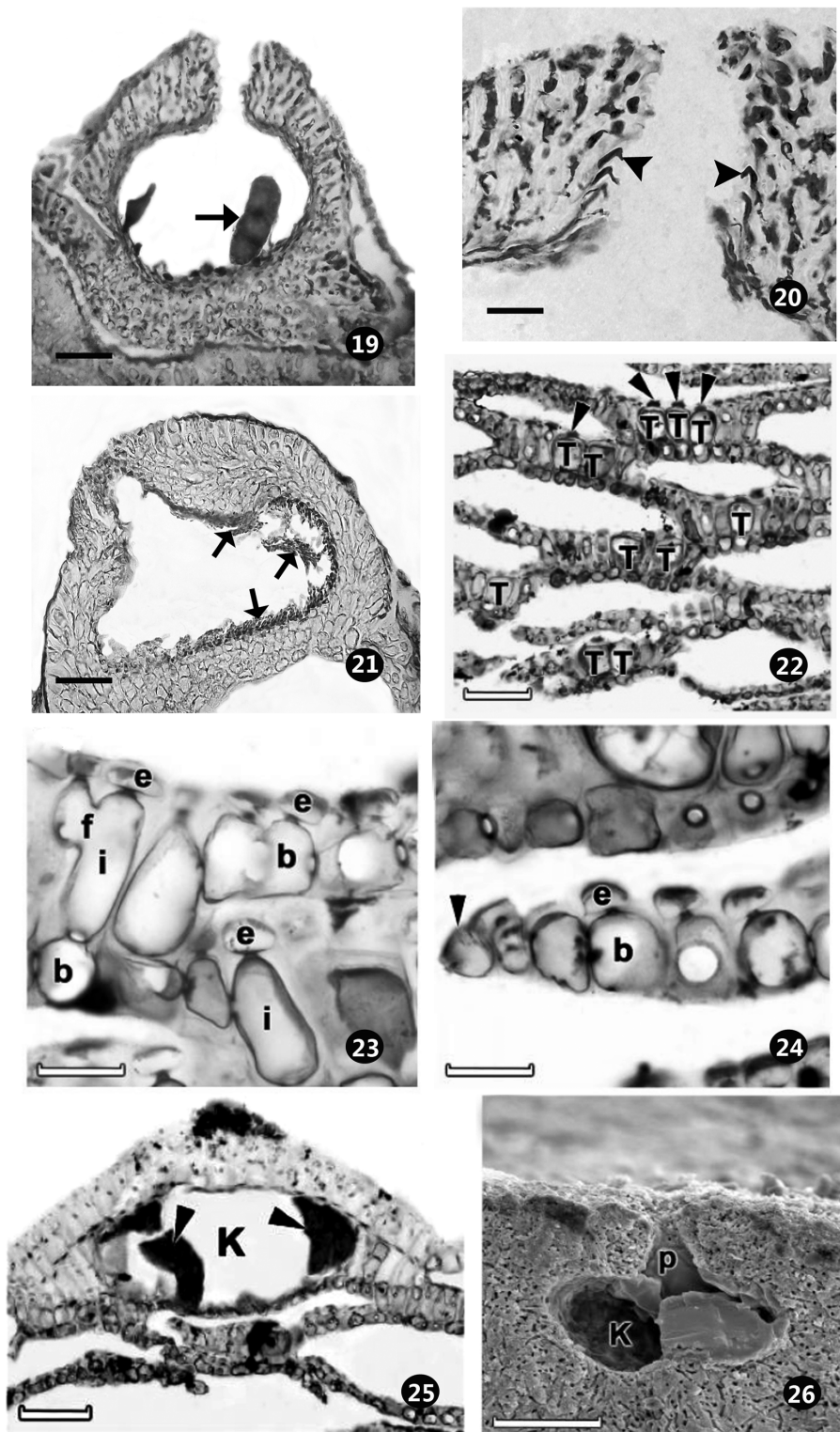
Habitat and Morphology. Intertidal. Thallus encrusting (Fig. 15), epiphytic, attached to hosts *Rhizophora mangle* Linnaeus and *Neogoniolithon strictum* (Foslie) Setchell & L.R. Mason ventrally by cell adhesion, 50 to 140 μm thick.

Anatomy. Thallus thin, 80–120 μm thick, construction dimerous (Fig. 16); medullary cells oblong or rectangular 7–12 μm wide and 10–15 μm long; cortical cells square or rounded 8–12 μm wide, 14–18 μm long with several fusions; epithallium unistratose with rounded cells 12–15 μm wide and 7–8 μm in long; numerous cell fusions present in medulla and cortex. Trichocytes occurred singly in dorsal region (Fig. 17), 18–22 μm wide and 30–40 μm long. Meristematic cells are the same size as cells immediately preceding (Fig. 18).

Reproductive structures. Tetrasporangial conceptacles abundant and scattered over thallus surface; conceptacles raised and rounded (Fig. 19), their chambers 170–180 μm diameter and 240–250 μm high. The pore canal measures 30–40 μm diameter and 80–100 μm long, and is lined by spike-shape cells protruding laterally into the canal (Fig. 20). Roof filaments 3–4 cells long (not including epithallial cell). Tetrasporangia measure 25–30 μm diameter and 75–80 μm long are arranged across the floor of the conceptacle, and a columella is absent.

Gametangial thalli are dioecious; spermatangial plants 70–100 μm thick with the same vegetative structure as the tetrasporangial plants. Conceptacles are uniporate, protruding, apiculate, scattered; conceptacle chambers 230–250 μm in diameter and 100–120 μm high, containing simple spermatangial branches on chamber floor, walls and roof (Fig. 21). Spermatangia ovoid, mostly 2 μm wide and 3 μm long. Female conceptacles not seen.

Comments. Mexican specimens assigned to *N. erosum* are very similar morpho-anatomically to type material of *Hydrolithon improcerum*. Maneveldt (2005) described the holotype material of *Goniolithon improcerum* Foslie & M. Howe housed at TRH as follows. The type fragments were extremely thin and adherent ranging from only 2 (typical) – 4 (when producing regenerated margins) cells thick. Individual thalli measured c. 60 μm thick but frequently occurred as applanate branches that overgrow one another measuring up to 500 μm thick (Fig. 22). Thalli were flat and smooth, lacking protuberances and had adherent margins that lacked orbital ridges. The surface texture was matte, and numerous small trichocyte fields occurred (Fig. 23). The thallus was dimerous with a



FIGURES 19–26: *Neogoniolithon erosum*, Mujeres Island (ENCB 17 804). 19) Section through tetrasporangial conceptacle showing zonately divided tetrasporangium (arrow). Scale bar: 55 μm . 20) Pore canal lined by spike-shape cells protruding laterally into the canal (arrowheads). Scale bar: 16 μm . 21) Mature male conceptacle with spermatangial filaments on chamber floor, walls and roof (arrows). Scale bar: 55 μm . Figures 22–26. Vegetative and reproductive anatomy of *Goniolithon improcerum* holotype in TRH. From Maneveldt (2005) used with permission of the author. 22) System of applanate branching showing solitary and small groups of trichocytes (T). Note trichocytes end abruptly at their dorsal surface and remains of darkly-staining hairs still visible (arrowheads) (scale bar = 60 μm). 23) Close-up of series of successive filaments showing single epithallial layer (e), subepithallial initials (i), non-palisade basal cell (b), and cell fusion between adjacent filaments (f) (scale bar = 15 μm). 24). Vertical section showing bistratose margin with terminating marginal initial (arrowhead), single epithallial layer (e) and single basal layer (b) (scale bar = 15 μm). 25). Raised tetrasporangial conceptacle showing open un-infilled chamber (K) and peripheral tetrasporangia (arrowheads) (scale bar = 60 μm). 26) Vertical fracture through tetrasporangial conceptacle showing open, unfilled chamber (K) and pore canal (p) (scale bar = 60 μm).

bistratose margin. The single basal layer comprised cells that were non-palisade and roughly squarish, measuring 9–21 μm long and 9–22 μm in diameter. Cell fusions were abundant; secondary pit connections were not seen. Epithallial cells were squat to elliptical and measured 4–9 μm long and 6–14 μm in diameter. Epithallial cells occurred as a single layer and stained darker than other cells (Fig. 24). Small groups of trichocytes occurred in horizontal rows. Trichocytes also occurred singly. Tetrasporangial conceptacles were raised above the thallus surface, but often appeared flush due to the regeneration of margins surrounding these conceptacles. Tetrasporangial conceptacles measured 200–375 μm in external diameter, their chambers were elliptical, and measured 130–250 μm in diameter and 54–105 μm high, with the roof 27–37 μm (2–4 cells; mostly 2, including the epithallial cell) thick. The conceptacle floor was usually flush with the thallus surface to 2 cells below the surface. From the orientation of the conceptacle roof cells, it appeared that the roof is formed from filaments interspersed among the sporangia (Fig. 25). A ring of enlarged, domed cells lined the base of the pore canal. The pore-canal filaments were oriented more-or-less vertically, and did not project into the pore. A central columella was not visible although zonately divided tetrasporangia were seen to be located more-or-less peripherally in the conceptacle chamber. Tetrasporangia measured 56–134 μm long and 16–69 μm in diameter.

Maneveldt (2005) was not certain that uniporate conceptacles were formed by filaments peripheral to the fertile area (type 1) or by filaments peripheral to the fertile area and interspersed among tetrasporangial initials (type 2), the former one of the defining characteristics of *Neogoniolithoideae* (Kato *et al.* 2011). Maneveldt's figures of tetrasporangial conceptacles do not show the shape of cells that line the canal pore, but the canal appears typical of *Neogoniolithon* tetrasporangial conceptacles (Fig. 26). In light of the description of *Goniolithon improcerum* by Maneveldt (2005), it is clear that the Mexican specimens assigned to *Neogoniolithon erosum* are very close to the concept of *G. improcerum*. Therefore it is necessary to re-examine the lectotype of *G. improcerum* and *Lithophyllum erosum* to elucidate the identity of both species.

Neogoniolithon mamillare (Harvey) Setchell & L.R. Mason 1943: 91.

Basionym: *Melobesia mamillaris* Harvey 1849: 109.

Syntype localities: Bahía, Brazil; Tierra del Fuego; Ilhas do Cabo Verde; Algoa Bay, Cape Province, South Africa (Silva, Basson & Moe 1996: 263).

Homotypic Synonyms:

Lithothamnion mamillare (Harvey) Areschoug 1852: 521.

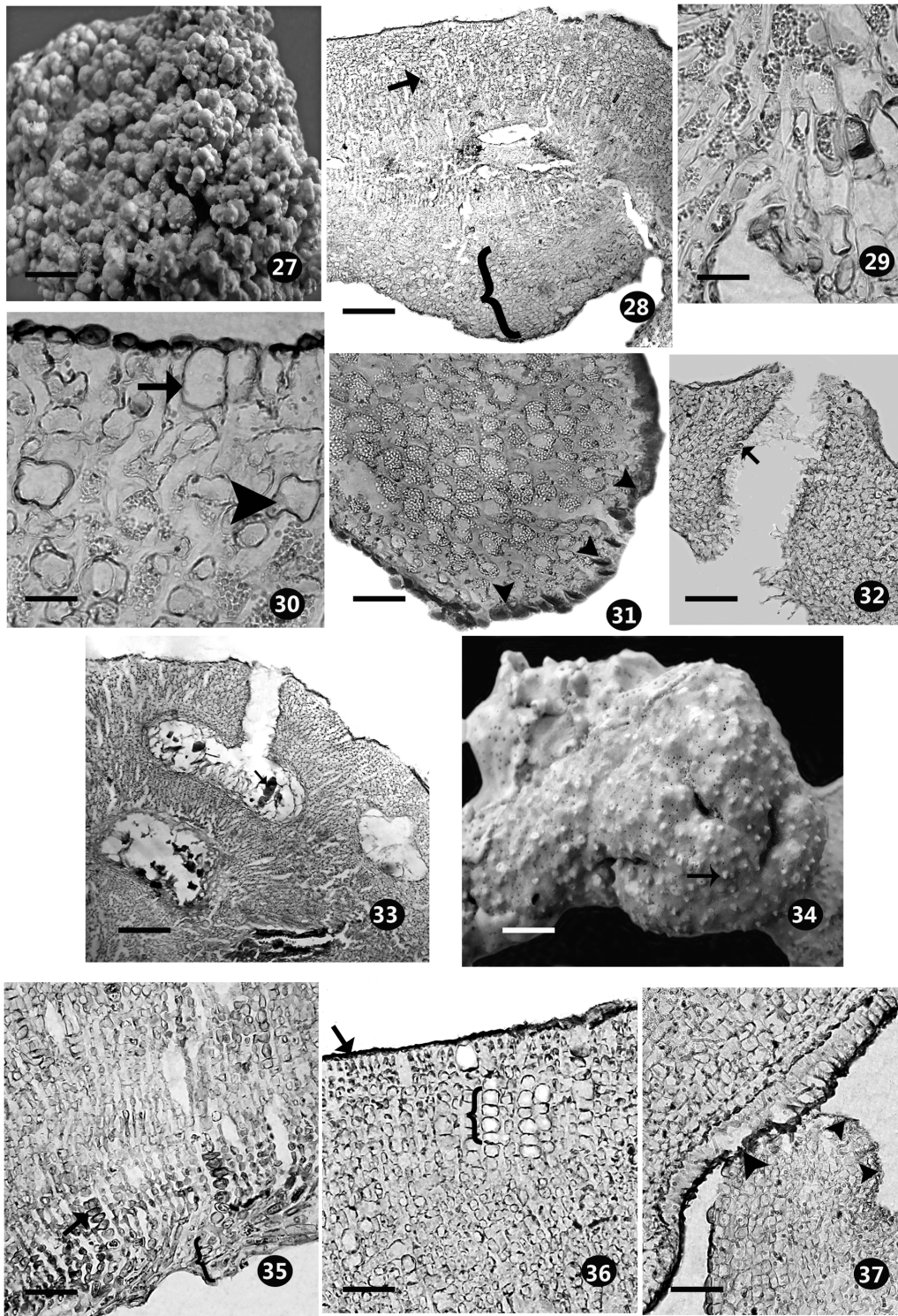
Goniolithon mamillare (Harvey) Foslie 1900: 16.

Distribution: Florida, Virgin Islands, Brazil, Japan, Cape Verde, Chile, Cameroon, Senegal, South Africa, Equatorial Guinea and Fuegia (Taylor 1960, Guiry & Guiry 2014).

Specimens Examined Morpho-anatomically (Figs. 27–33). MÉXICO: *Quintana Roo*: Mujeres Island, Parte Este (86°43'06" W, 21°12'44" N), ⊕, 21-05-1998, Mateo-Cid & Mendoza-González (ENCB 17424); Cozumel Island, Maya Beach (87°0'57.6" W, 20°24'24.6" N), ⊕, 23-03-1994, Mendoza-González & Mateo-Cid (ENCB 19176); San Francisco Beach ⊕, 19-05-1993, Mateo-Cid & Mendoza-González (ENCB 17428); Chankanab Reef (86° 59' 41.36" W, 20° 26' 36.13"N), ⊕, 15-05-1993, Mateo-Cid & Mendoza-González (ENCB 17430); Santa Rosa Reef (86°58'55" W, 20°29'03" N), ⊕, 02-06-1995, Mateo-Cid & Mendoza-González (ENCB 17427), Paraíso Reef (20°16'04" N, 87°00'08" W), ⊕, 18-09-1993, Searles (ENCB 13420); 2km SE of Boca Paila, 20-06-2010, Mendoza-González, Mateo-Cid & Acosta Calderón (ENCB 20083).

Habitat and Morphology. Epilithic, intertidal to 30 m deep. Thallus encrusting to warty to lumpy to fruticose, protuberances mammillate, rounded 2–6 mm diameter and 3–5mm high (Fig. 27).

Anatomy. Internal organization dorsiventral in encrusting portions of thallus, radial in protuberances. Encrusting base 600–800 μm thick, construction monomerous (Fig. 28). Medulla composed of filaments oriented parallel to the thallus surface, medullary cells 18–22 μm wide and 35–40 μm long, constituting 50–60% of the thallus thickness. Dorsal region (cortex) composed of filaments that bend away from the ventral region and gradually become oriented perpendicular to the thallus surface. Cortical cells ovoid or subrectangular, 7–14 μm in wide and 12–15 μm long, and cells of adjacent filaments connected laterally by cell fusions (Fig. 29). Dorsal filaments terminated by a roundish epithallial cell, 15–18 μm wide and 11–12 μm long. Trichocytes common, occurring singly or in horizontal rows at thallus surface, sometimes becoming buried, individual trichocytes 20–22 μm wide and 24–30 μm long (Fig. 30). Thallus growing from intercalary meristematic cells (Fig. 31).



FIGURES 27–33: *Neogoniolithon mamillare*, Cozumel Island, Paraíso Reef (ENCB 13420). 27) Thallus habit with numerous mammillate excrescences. Scale bar: 6 mm. 28) Thallus section showing monomerous construction, note medulla (brace) and cortex (arrow). Scale bar: 145 μ m. 29) Section through ventral region, showing enlarged medullary cells. Scale bar: 20 μ m. 30) Dorsal region showing single trichocyte (arrow) and cell fusion (arrowhead). Scale bar: 30 μ m. 31) Thallus section showing meristematic region of growth (arrowheads). Scale bar: 90 μ m. 32) Section through pore canal showing elongated cells protruding laterally into canal (arrow). Scale bar: 125 μ m. 33) Section through mature tetrasporangial conceptacle showing tetrasporangium (arrow). Scale bar: 180 μ m.

FIGURES 34–37: *Neogoniolithon propinquum*, Chopas Reef (ENCB 18839). 34) Habit of encrusting thallus growing on pebble; note prominent apiculate conceptacles (arrows). Scale bar: 7 mm. 35) Thallus section showing monomerous construction, note medulla (brace) and trichocytes in vertical rows (arrow). Scale bar: 45 μ m. 36) Section through dorsal region showing profuse trichocytes in vertical rows (brace) and flattened epithallial cells (arrow). Scale bar: 40 μ m. 37) Thallus section showing meristematic region of growth (arrowheads). Scale bar: 50 μ m.

Reproductive structures. Tetrasporangial conceptacles raised, scattered and apiculate, their chambers 500–700 µm in diameter and 300–380 µm high (Fig. 32). The pore canal measures 50–60 µm diameter and 200–300 µm long and is lined by elongate cells protruding laterally into the canal (Fig. 33). Roof filaments 14–16 cells long (not including epithallial cell). Tetrasporangia 20–25 µm diameter and 65–75 µm long, arranged across conceptacle floor, and a columella is present.

Female and male conceptacles not seen.

DNA sequence. A *psbA* sequence was obtained for only one specimen (Table 2).

Comments: We apply this name with caution to material from Mexico as type material from each of the syntype localities needs be sequenced to unambiguously apply this named. In the Mexican Caribbean *N. mamillare* occurs intertidally on reefs and to depths of 30 m. Mexican plants are characterized by the following combination of features: 1) thallus adherent, warty to mammillate; 2) thallus monomerous; 3) trichocytes present, occurring singly or in horizontal rows; 4) meristematic cells intercalary below the epithallus; 5) tetrasporangial pore canal lined by narrow filaments that tilt into the pore canal and have an elongated shape and 6) tetrasporangial conceptacle roof is more commonly 14–16 cells thick.

Neogoniolithon propinquum (Foslie) Me. Lemoine 1966: 12.

Basionym: *Goniolithon notarissii* f. *propinquum* ('*propinqua*') Foslie 1900: 21–22.

Homotypic Synonym:

Goniolithon propinquum (Foslie) Foslie 1903: 4

Lectotype Locality: St. Croix, Virgin Islands (Silva *et al.* 1996: 264).

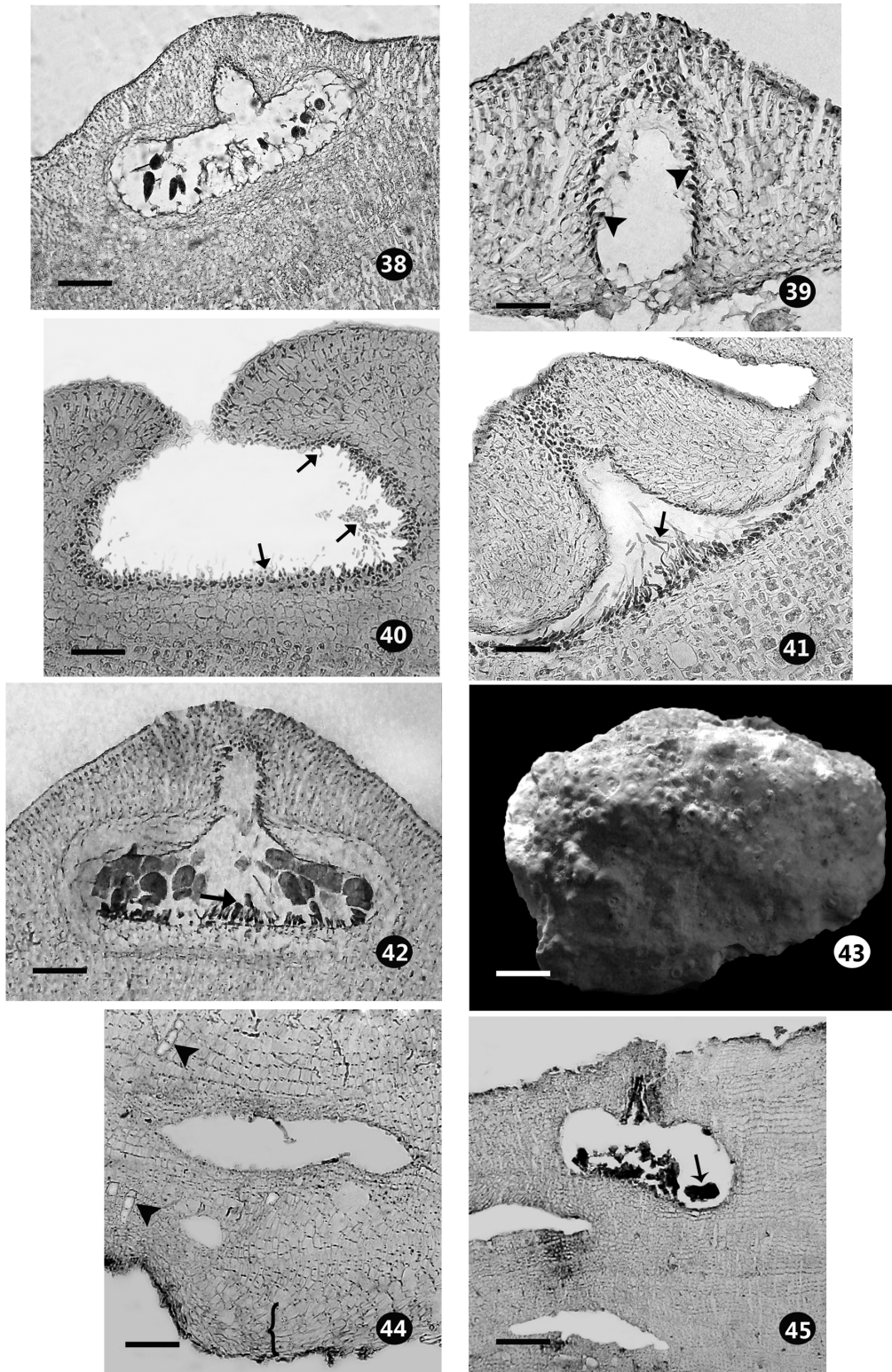
Distribution: Western Atlantic, Japan, Israel, Comoros and Mayotte (Silva *et al.* 1996, Guiry & Guiry 2014).

Specimens Examined Morpho-anatomically (Figs. 34–45). MÉXICO: *Veracruz*: Sacrificios Island⊕, Mateo-Cid & Mendoza-González, 24-11-1986, (ENCB 17421); Blanquilla Reef, Huerta Múzquiz & Garza, 03-05-1964, (ENCB 17417); Verde Island⊕, Mateo-Cid & Mendoza-González, 23-11-1986, (ENCB 7933); Chopas Reef (96° 00' 29.48" W 19° 03' 32.11" N), ♀, ♂, ⊕, Mateo-Cid & Mendoza-González, 23-11-1986, (ENCB 18840); Anegada de Adentro ♀, Mateo-Cid & Mendoza-González, 08-07-2004, (ENCB 17402); Enmedio Island (95°56'19.5" W, 19°06'01" N), ♀, Mateo-Cid & Mendoza-González, 09-07-2004, (ENCB 17403). *Yucatán*: Alacranes Reef, Pérez Island♂, 14-10-1985, Huerta Múzquiz (ENCB 17413); Pájaros Island (89°39'34" W, 22°22'31" N), ⊕, ♀, 12-10-1985, Huerta Múzquiz, Hidalgo & Mateo-Cid (ENCB 17409). *Quintana Roo*: Mujeres Island⊕, 13-09-1985, Mateo-Cid & Mendoza-González (ENCB 17407); Cozumel Island⊕, 10-03-1994, Mendoza-González & Mateo-Cid (ENCB 17402); Azul Beach (87°06'01" W, 20°24'05" N), ⊕, 22-05-1993, Mateo-Cid & Mendoza-González (ENCB 17415); Ascensión Bay⊕, Mateo-Cid & Mendoza-González, 17-05-1998 (ENCB 17405); El Zarzal ♀, Mateo-Cid & Mendoza-González, 19-05-1998 (ENCB 17416); 12 km NE Punta Allen, 22-06-2010, Mendoza-González, Mateo-Cid & Acosta Calderón (ENCB 20081); Akumal (87°18'41" W, 20°23'48" N), ⊕, 16-09-1993, Mendoza-González, Mateo-Cid & Searles (ENCB 17408).

Habitat and Morphology. Plants encrusting on rocks and dead coral, intertidal to 3 m deep, attached to the substratum ventrally by cell adhesion, without rhizoids, with flattened dorsal surface, lacking protuberances (Fig. 34), 300–2500 µm thick.

Anatomy. Construction monomerous and dorsiventral (Fig. 35), with cells of adjacent filaments connected laterally by fusions and secondary pit connections not seen. Ventral region (medulla) composed of several layers of filaments oriented parallel to the thallus surface. Medullary cells 12–22 µm wide and 20–32 µm long, constituting 10–40% of the thallus thickness. Dorsal region (cortex) composed of filaments that bend away from the ventral region and gradually become oriented perpendicularly to the thallus surface. Cells of cortex flattened or subrectangular, 8–15 µm wide and 10–18 µm long. Dorsal filaments terminated by an ovoid epithallial cell flattened, 10–13 µm wide and 6–10 µm long. Trichocytes frequent, occurring single or in vertical or horizontal rows at thallus surface (Fig. 36), sometimes becoming buried; individual trichocytes 26–30 µm wide and 30–50 µm long. Meristematic cells intercalary (Fig. 37).

Reproductive structures. Tetrasporangial thalli 600–2500 µm thick with uniporate, protruding, scattered and apiculate conceptacles, their chambers 500–900 µm in diameter and 170–300 µm high (Fig. 38). The pore canal measures 40–60 µm diameter and 180–230 µm long and is lined by sigmoid-shaped cells (Fig. 39) protruding laterally into the canal. Roof filaments 10–12 cells long (not including epithallial cell). Tetrasporangia 40–50 µm wide and 110–125 µm long and arranged across the floor of the conceptacle. A columella is absent.



FIGURES 38–45. *Neogoniolithon propinquum*, Chopas Reef (ENCB 18839). 38) Section through mature tetrasporangial conceptacle showing tetrasporangia. Scale bar: 140 μm . 39) Enlarged section through tetrasporangial conceptacle pore showing pore canal lined by sigmoid-shaped cells protruding laterally into canal (arrowhead). Scale bar: 60 μm . 40) Mature male conceptacle with spermatangial filaments on floor, walls and roof of chamber (arrows). Scale bar: 60 μm . 41) Section through female conceptacle with carpogonial branches (arrow). Scale bar: 42 μm . 42) Section through mature carposporangial conceptacle showing a terminal carposporangium (arrow) borne on a several-celled gonimoblast filament and remains of old carpogonial branches. Scale bar: 60 μm . 43) Lectotype of *N. propinquum* (in TRH). Scale bar: 6 mm. 44) Thallus section of lectotype showing monomerous construction; note medulla (brace) and trichocytes in vertical rows (arrowhead). Scale bar 45 μm . 45) Section through sporangial conceptacle and remains of sporangia (arrow). Scale bar: 60 μm .

Gametangial thalli are dioecious, spermatangial plants 600–800 µm thick with the same vegetative structure as tetrasporangial plants. Uniporate conceptacles protruding, not apiculate, scattered, conceptacle chambers usually 350–400 µm in diameter and 150–200 µm high containing simple spermatangial branches on the chamber floor, the walls and the roof (Fig. 40). Spermatangia ovoid, mostly 2 µm wide and 3–4 µm long. Carposporangial conceptacles uniporate, protruding, rounded and more frequent than males (Fig. 41), the chambers without columella, chambers 500–620 µm diameter and 150–170 µm high, canal 250–360 µm long. Carposporangia develop on the floor of the chamber (Fig. 42) and measure 50–60 µm in wide and 80–90 µm long.

DNA sequences. The four sequenced specimens (Table 2) varied by up to 0.9% (8 bp) in their *psbA* sequences.

Comments. The examined specimens are broadly in line with the description of Foslie (1900), but Foslie did not provide a detailed description of many species that he described for the first time. Our morpho-anatomical observations of the lectotype (Fig. 43) compare well with Mexican material in terms of vegetative cell measurements and trichocytes in horizontal and vertical rows (Fig. 44). In addition, the measurements of conceptacle chambers in the lectotype (Fig. 45) match those of tetrasporangial chambers of Mexican specimens. We have not matched our field-collected material to the type by DNA sequence. Mexican plants of *N. propinquum* are characterized by the following combination of features: 1) thallus adherent, lacking protuberances; 2) construction monomerous; 3) trichocytes present, occurring singly and in vertical and horizontal rows; 4) tetrasporangial pore canal lined by narrow filaments that tilt into the pore canal and have a sigmoid shape and 5) tetrasporangial conceptacle roof is more commonly 10–12 cells thick. This is the first record of *N. propinquum* from the Gulf of Mexico and Caribbean Sea Mexican coasts. *Neogoniolithon propinquum* is a tropical species and has been recorded from Japan, Comoros, Israel, Virgin Islands, and other localities from the Caribbean (Guiry & Guiry 2014). All reports outside the western Atlantic need to be confirmed by DNA sequences.

Neogoniolithon rhizophorae (Foslie & M. Howe) Setchell & L.R. Mason 1943: 91.

Basionym: *Goniolithon rhizophorae* Foslie & M. Howe 1906a: 130–131, Pl. 82, Fig. 2.

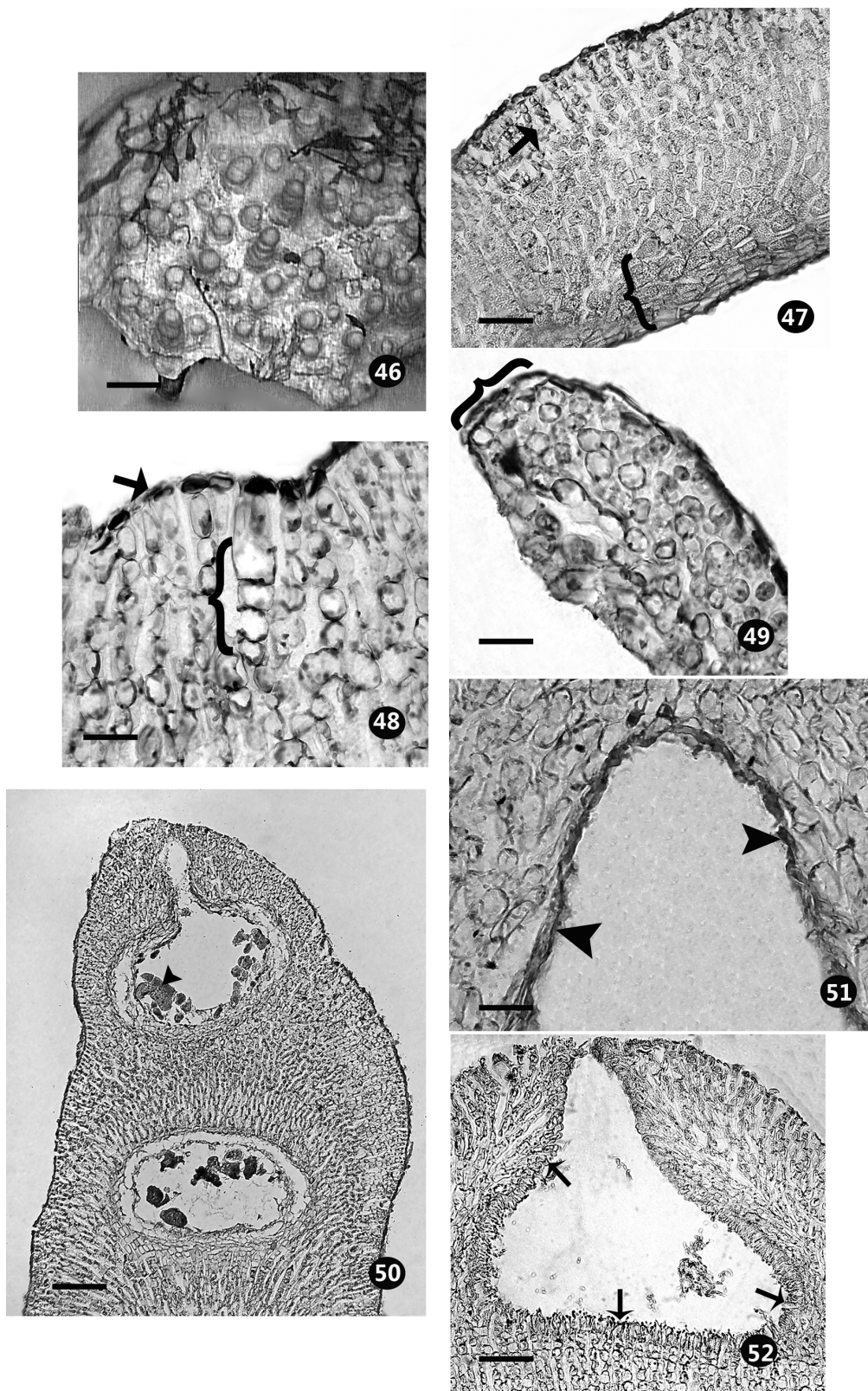
Type locality: Bahamas, Stocking Island, Great Exuma.

Distribution: Bermuda, Colombia (Guiry & Guiry 2014).

Specimens Examined Morpho-anatomically (Figs. 46–52). MÉXICO: *Veracruz*: Sacrificios Island⊕, Huerta Múzquiz, 07-05-1965, (ENCB 17363); Chopas Reef, Mateo-Cid & Mendoza-González, 27-06-2005, (ENCB 19119); Verde Island♀, Mateo-Cid & Mendoza-González, 27-09-1985 (ENCB 17355), Ortega Garduño, 13-05-2000, (IZTA 1038); Enmedio Island♀, Mateo-Cid & Mendoza-González, 09-07-2004, (ENCB 19047); Anegada de Adentro ♀, Mateo-Cid & Mendoza-González, 08-07-2004, (ENCB 19042). *Campeche*: Cayo Arcas (91°58'00" W, 22°12'00" N), ⊕, 23-04-1986, Huerta Múzquiz & Hidalgo (ENCB 17351). *Yucatán*: Alacranes Reef, Pérez Island, ♂, 16-07-1960, Huerta Múzquiz (ENCB 17364); Chica Island (89°06'36" W, 22°01'00" N), ⊕, ♀, 16-02-1985, Huerta Múzquiz & Hidalgo (ENCB 17458). *Quintana Roo*: Akumal, ⊕, 18-09-1993, Mendoza-González, Mateo-Cid & Searles (ENCB 17359); Banco Chinchorro, Cayo Norte (87°19'25" W, 18°46'37" N), 11-07-1992, Huerta Múzquiz (ENCB 17333); Banco Chinchorro, Cayo Centro, 24-06-1984, Huerta Múzquiz & Mateo-Cid (ENCB 17361); Banco Chinchorro, Cayo Lobos (87°22'53" W, 18°23'11" N), ⊕, 05-07-1982, Huerta Múzquiz (ENCB 17353).

Habitat and Morphology. Epiphytic on *Rhizophora mangle*, on rocks, and encrusting dead coral, intertidal to 2 m deep. Plants encrusting sometimes with protuberances; attached to the substratum ventrally by cell adhesion, without rhizoids; encrusting base conspicuous and 100–950 µm thick; protuberances terete, once or twice branched, 0.8–1.0 mm in diameter and 3–7 mm high (Fig. 46).

Anatomy. Construction monomerous (Fig. 47), with cells of adjacent filaments connected laterally by fusions, secondary pit connections not seen. Ventral region (medulla) composed of several layers of filaments oriented parallel to the thallus surface. Medullary cells 15–17 µm wide and 20–25 µm long, constituting 40–50% of the thallus thickness. Dorsal region composed of filaments that bend away from the ventral region and gradually become oriented perpendicular to thallus surface. Cortical cells flattened 11–13 µm in wide and 18–21 µm long. Dorsal filaments terminated by flattened epithallial cells, 10–13 µm wide and 5–7 µm long. Trichocytes common, occurring in horizontal and vertical rows at thallus surface, sometimes becoming buried. Individual trichocytes 25–30 µm wide and 40–45 µm long (Fig. 48), the initial meristematic cell is the same size as the cells immediately preceding (Fig. 49).



FIGURES 46–52. *Neogoniolithon rhizophorae*, Banco Chinchorro (ENCB 17361). 46) Habit showing encrusting basal portion and some enlarged and terete excrescences. Scale bar: 3 mm. 47) Thallus section showing monomerous construction; note medulla (brace) and cortex (arrow). Scale bar: 140 μm . 48) Section through dorsal region showing trichocytes in vertical row (brace) and epithallial cell (arrow). Scale bar: 20 μm . 49) Section through encrusting base of thallus showing the meristematic region of growth (brace). Scale bar: 35 μm . 50) Section through mature tetrasporangial conceptacle showing tetrasporangium (arrow). Scale bar: 220 μm . 51) Pore canal lined by arcuate-shaped cells that protruding laterally into canal (arrowhead). Scale bar: 135 μm . 52) Mature male conceptacle with spermatangial filaments on floor, walls and roof of chamber (arrows). Scale bar: 80 μm .

Reproductive structures. Tetrasporangial conceptacles terminal on excrescences, apiculate, their chambers 600–700 µm diameter and 250–320 µm high (Fig. 50). The pore canal measures 30–40 µm diameter and 250–400 µm long and is lined by arcuate cells that do not protrude laterally into the canal (Fig. 51). Roof filaments 15–18 cells long (not including epithallial cell). Tetrasporangia 50–55 µm wide and 90–100 µm long and arranged across the floor of the conceptacle; central columella is absent.

Spermatangial plants with the same vegetative structure as tetrasporangial plants. Conceptacles uniporate, protruding, not apiculate, scattered; conceptacle chambers usually 350–450 µm in diameter and 150–250 µm high containing simple spermatangial branches on chamber floor, walls and roof (Fig. 52). Spermatangia ovoid, mostly 3 µm wide and 3–4 µm long. Female plants not found.

DNA sequences. The four sequenced specimens (Table 2) varied by up to 1.06% (9 bp) in their *psbA* sequences.

Comments. *Neogoniolithon rhizophorae* is a rare species in the Caribbean Sea. The only previous Caribbean record is from Colombia (Díaz-Pulido & Díaz-Ruiz 2003, Wynne 2011). The Mexican plants are in general agreement with the dimensions reported from type material from Bermuda, (Foslie & Howe 1906a), but we have not confirmed the application of this name by DNA sequencing of type material. Mexican plants of *N. rhizophorae* are characterized by the following combination of features: 1) thallus adherent, with terete protuberances to 7 mm high; 2) construction monomerous; 3) trichocytes present, occurring singly or in horizontal and vertical rows; 4) the meristematic cells are grouped in the margin, located below the epithallus; 5) tetrasporangial pore canal lined by narrow filaments that tilt into the pore canal and have an arcuate shape and 6) tetrasporangial conceptacle roof more commonly 15–18 cells thick. This species occurs along the Mexican coasts of the Gulf of Mexico and Caribbean Sea and is the first record from these coasts.

***Neogoniolithon siankanensis* Mateo-Cid, Mendoza-González & P.W. Gabrielson**

Holotype: ENCB 20148 and NCU 624415, intertidal encrusting coral rubble, 18 Dec. 2011, *leg.* A.C. Mendoza-González & Luz Elena Mateo-Cid.

Type Locality: MEXICO, Quintana Roo, Playa Hualapich (19°53'20" N, 87°25'50" W). Reserva Biosfera Sian Ka'an.

Paratype: ENCB 20159, MEXICO, Quintana Roo, Río Indio (18°49'02" N, 87°39'46" W), intertidal on coral skeletons, 13 Nov. 2013, *leg.* A.C. Mendoza-González, Luz Elena Mateo-Cid & Julio A. Acosta.

Etymology: The species epithet is named for the Reserva de la Biosfera de Sian Ka'an where the plants were collected.

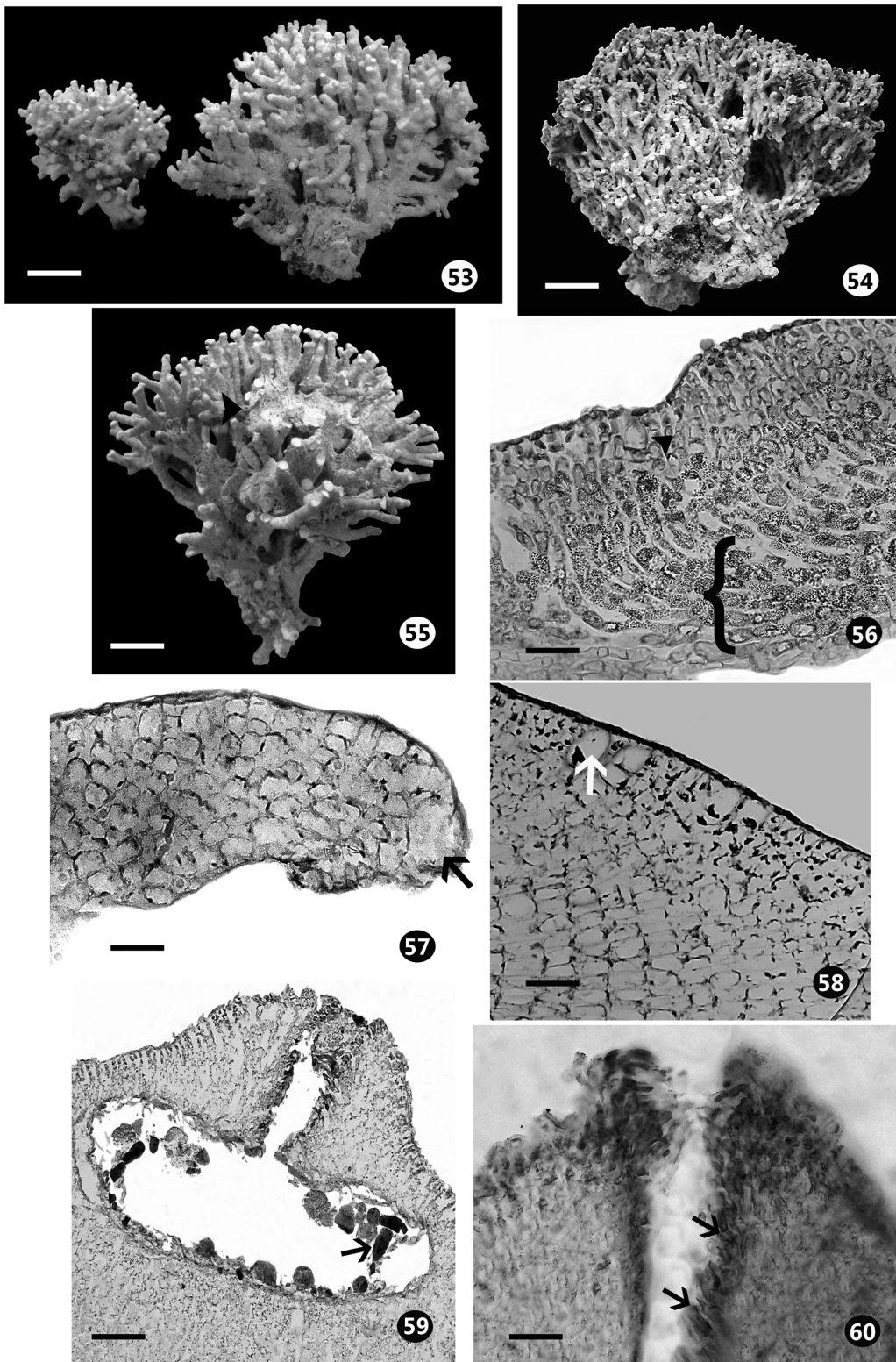
Diagnosis. Thallus non-geniculate, fruticose, branches trichotomous or irregularly subdichotomous, terete and uniform in diameter along their entire length but sometimes anastomosing; construction monomerous, basal layer without palisade cells; trichocytes singly or in vertical and horizontal fields; tetrasporangial conceptacles terminal on branches; tetrasporangial pore canal lined by narrow filaments that tilt into the pore canal and have a lanceolate shape; tetrasporangial conceptacle roof 10–12 cells thick.

Distribution: Quintana Roo, Yucatán.

Specimens Examined Morpho-anatomically (Figs. 53–60). MÉXICO: *Yucatán:* Alacranes Reef, Pérez Island, ⊕, 18-07-1960, Huerta Múzquiz (ENCB 17341). *Quintana Roo:* Isla Mujeres, Extremo norte, 01-03-1983, Mateo-Cid & Mendoza-González (ENCB 17332); Isla Cozumel, recorrido, ⊕, 20-05-1993, Mendoza-González & Mateo-Cid (ENCB 17339), Banco Chinchorro, Cayo Norte, ⊕, 09-07-1982, Huerta Múzquiz & Mateo-Cid (ENCB 17362); Ascensión Bay, Punta Solimán, ⊕, 17-05-1998, Mateo-Cid & Mendoza-González (ENCB 17352).

Habitat and Morphology. Thallus fruticose, growing on rocks and encrusting dead coral, intertidal to 5 m deep, consists two well-defined portions: basal smooth crust firmly attached to substrate 400–500 µm thick, and a branched thalli that arise from crust, these branches are terete and 1–1.5 mm in diameter and 2–8 cm long, are essentially uniform in diameter along their entire length and trichotomous, irregularly subdichotomous or anastomosing (Fig. 53,54,55). Branch apices often terminate in conical to dome-shaped conceptacles.

Anatomy. Construction monomerous in encrusting portions of thallus (Fig. 56), radial in protuberances. Medulla composed of several layers of filaments oriented parallel to the thallus surface. Medullary cells 12–15 µm wide and 15–18 µm long and comprising approximately 20–40% of thallus thickness. The initial meristematic cell is bigger than the cells immediately preceding (Fig. 57). Dorsal region (cortex) composed of filaments that bend away from the ventral region and gradually become oriented perpendicular to thallus surface. Cortical cells flattened 8–10 µm wide and 13–15 µm long; cells of adjacent filaments connected laterally by cell fusion. Dorsal filaments terminated by one layer of flattened epithallial cells, 11–13 µm wide and 7–8 µm long. Trichocytes common, occurring singly at thallus surface (Fig. 58); individual trichocytes 25–30 µm wide and 35–55 µm long.



FIGURES 53–60. *Neogoniolithon siankanensis*, (ENCB 20148, ENCB 20159). 53) Habit of holotype, Hualapich, Reserva Biosfera Sian Ka'an (ENCB 20148). Scale bar: 5 mm. 54) Habit of holotype, Hualapich, Reserva Biosfera Sian Ka'an (ENCB 20148); note anastomosing branches (arrowhead). Scale bar: 1 cm. 55) Habit of isotype, Río Indio, Majahual, Quintana Roo (ENCB 20159), with encrusting basal portion and terete branches. Scale bar: 9 mm. 56). Section through encrusting base showing monomerous construction; note medulla (brace) and cortex (arrowhead). Scale bar: 65 μ m. 57) Section through the encrusting base of thallus showing single terminal cell (arrow). Scale bar: 100 μ m. 58) Section through dorsal region of branch; trichocytes single (arrow). Scale bar: 50 μ m. 59) Tetrasporangial conceptacle section showing tetrasporangium (arrow). Scale bar: 95 μ m. 60) Enlarged section through tetrasporangial conceptacle; pore canal lined by lanceolate-shaped cells protruding laterally into canal (arrows). Scale bar: 60 μ m.

Reproductive structures. Tetrasporangial conceptacles terminal on excrescences, conical to dome-shaped, their chambers 600–750 µm diameter and 200–400 µm high (Fig. 59). The pore canal measures 90–130 µm diameter and 200–300 µm long and is lined by lanceolate-shaped cells that protruding laterally into the canal (Fig. 60). Roof filaments 10–12 cells long (not including epithallial cell). Tetrasporangia 30–40 µm wide and 90–135 µm long arranged across the floor of the conceptacle; a central columella is not present.

DNA sequences. The three sequenced specimens, all from Quintana Roo (Table 2), have identical *psbA* sequences.

Comments. *Neogoniolithon siankanensis* is morphologically similar to *Goniolithon decutescens* (Heydrich) Foslie ex M. Howe, as described and illustrated by Heydrich (1901, as *Lithothamnion decutescens*). *Goniolithon decutescens* exhibits a basal layer to 0.4–1.0 mm thick, bearing simple or subsimple, terete or subterete, occasionally anastomosed branches 5–10 mm long and 0.8–1.0 mm diameter. Anatomically, branches have a massive medulla and a relatively poorly developed cortex. Tetrasporangial conceptacles are lateral on protuberances, 0.8–1.0 mm diameter. In contrast, *N. siankanensis* possesses a thin basal layer, branching is trichotomous or irregularly subdichotomous, branches reach a length of 2–8 cm, tetrasporangial conceptacles are terminal on branches and their chambers are 600–750 µm in diameter. *N. siankanensis* has a sequence divergence in *psbA* of only 1.6% compared to specimens that we call *N. strictum* (Table 2). Sequencing of type material of both *Goniolithon decutescens* and *N. strictum* is needed as well as additional field-collected specimens to determine if *N. siankanensis* is a distinct species.

Neogoniolithon solubile (Foslie & M. Howe) Setchell & L.R. Mason 1943: 90.

Basionym: *Goniolithon solubile* Foslie & M. Howe in Foslie 1907: 21.

Type locality: Culebra Island (Puerto Rico).

Synonym: *Paragoniolithon solubile* (Foslie & M. Howe) W.H. Adey, R.A. Townsend & Boykins 1982: 12.

Distribution: Caribbean Islands (Cuba, Hispaniola); Brazil; Colombia (Taylor 1960, Guiry & Guiry, 2014)

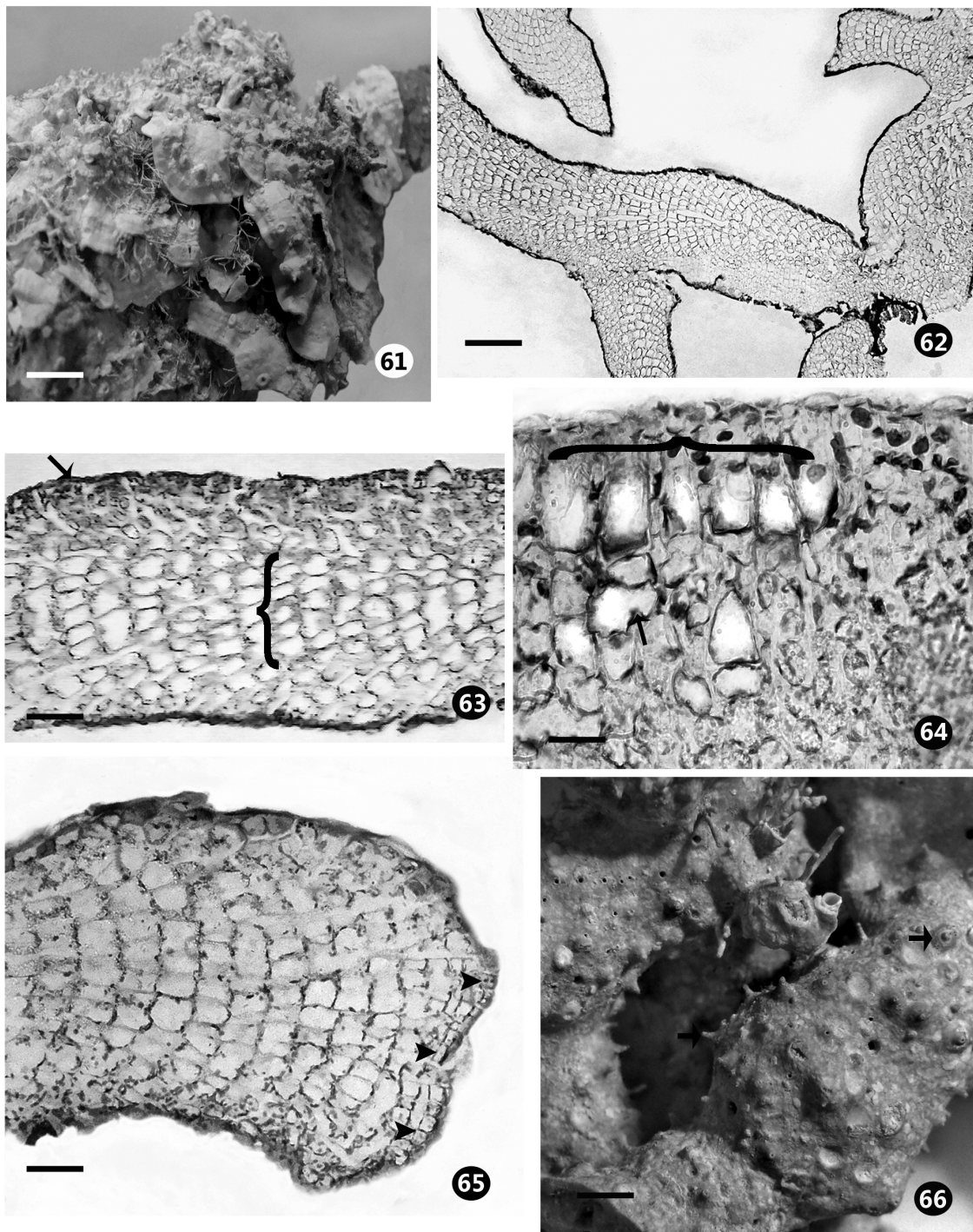
Specimens Examined Morpho-anatomically. (Figs. 61–69): MÉXICO: *Veracruz*: Verde Island, ⊕, Mateo-Cid & Mendoza-González, 27-11-1983, (ENCB 17444) (Mateo-Cid & Pedroche 2004: 187). *Yucatán*: Alacranes Reef, Pérez Island, ♂, 14-10-1985, Huerta Múzquiz (ENCB 17438); Desertora Island, 15-10-1985, Huerta Múzquiz, Hidalgo & Mateo-Cid (ENCB 16850). *Quintana Roo*: Mujeres Island, Lancheros Beach (86°43'41" W, 21°12'59.4" N), ⊕, 13-08-1997, Mateo-Cid & Mendoza-González (ENCB 17434), Garrafón Reef, ⊕, 20-05-1998, Mendoza-González & Mateo-Cid (ENCB 20096); Cozumel Island, Caracol Beach (86°58'03" W, 20°17'05" N), ⊕, 16-10-1983, Mendoza-González & Mateo-Cid (ENCB 13270); San Francisco Beach (87°01'6.3" W, 20°24'04" N), ⊕, 17-05-1993, Mateo-Cid & Mendoza-González (ENCB 17443); Punta Morena (86°51'12" W, 20°24'31" N), ⊕, 21-03-1994, Mateo-Cid & Mendoza-González (ENCB 19046); Palancar Reef (87° 01' 21" W, 20° 23' 21.13" N), ⊕, 16-05-1993, Searles (ENCB 12141); Tormentos Reef (87°01'51" W, 20°25'57" N), ⊕, 30-03-1995, Searles (ENCB 17440); Banco Chinchorro, Cayo Norte (87°19'25" W, 18°46'37" N), ⊕, 27-06-1984, Huerta Múzquiz & Mateo-Cid (ENCB 17433); Xcalak, ⊕, 22-12-1973, Huerta Múzquiz (ENCB 16848); Akumal (87°18'41" W, 20°23'48" N), ⊕, 16-09-1993, Mendoza-González, Mateo-Cid & Searles (ENCB 17435).

Habitat and Morphology. Epilithic and on dead coral, intertidal to 30 m deep. Thalli encrusting, layered to foliose, attached to the substratum ventrally by cell adhesion, without rhizoids, with flattened dorsal surface, lacking protuberances (Fig. 61), 400–1000 µm thick.

Anatomy. Construction monomerous (Fig. 62); ventral region (medulla) composed of several layers of filaments oriented parallel to thallus surface and cells arranged strongly coaxially (Fig. 63); medullary cells 12–16 µm wide and 12–20 µm long, constituting 50–75% of the thallus thickness. Cells of the adjacent filaments connected laterally by frequent fusions; secondary pit connections not seen. Dorsal region (cortex) composed of filaments that bend away from the ventral region and gradually become oriented perpendicular to the thallus surface. Cortical cells ovoid or subrectangular, 10–14 µm wide and 12–15 µm long. Dorsal filaments terminated by one layer of roundish or flattened epithallial cells, 12–15 µm wide and 6.0–11 µm long. Trichocytes common, occurring individually or in horizontal and vertical rows at thallus surface (Fig. 64), sometimes becoming buried; individual trichocytes 20–28 µm wide and 30–45 µm long. Meristematic cells intercalary, below the epithallus (Fig. 65).

Reproductive structures. Tetrasporangial conceptacles abundant, protruding, scattered and apiculate (Fig. 66). Their chambers measure 500–900 µm in diameter and 200–340 µm high (Fig. 67). The pore canal measures 50–70

μm diameter and 500–700 μm long and is lined by papillae-like cells that protrude laterally into the canal (Fig. 68). Roof filaments 8–12 cells long (not including epithallial cell). Tetrasporangia 30–40 μm wide and 80–120 μm long arranged across the floor of the conceptacle; columella absent.



FIGURES 61–66: *Neogoniolithon solubile*, Cozumel Island (ENCB 19 046). 61) Habit of foliose thalli attached to dead coral. Scale bar: 7 mm. 62) Section through thalli showing several superimposed crusts. Scale bar: 250 μm . 63) Thallus section showing coaxial medulla (brace) and epithallial cell (arrow). Scale bar: 100 μm . 64) Section through dorsal region; trichocytes in horizontal rows (brace) and cell fusion (arrow). Scale bar: 36 μm . 65) Thallus section showing arrangement of meristematic region at margin (arrowheads). Scale bar: 60 μm . 66) Thallus with prominent apiculate conceptacles (arrows). Scale bar: 1.5 cm.

Gametangial thalli are dioecious; spermatangial (male) plants 400–600 µm thick with the same vegetative structure as tetrasporangial plants. Conceptacles uniporate, protruding, apiculate or not; scattered, chambers usually 250–300 µm in diameter and 130–150 µm high, containing simple spermatangial branches on chamber floor, walls and roof (Fig.69). Spermatangia ovoid, mostly 2–2.5 µm diameter and 3–4 µm long. Female conceptacles not found.

Comments. The isotype collection at TRH consisted of three fragments of a non-geniculate coralline attached to the substratum ventrally by cell adhesion, without rhizoids, with a flattened dorsal surface, lacking protuberances, and 600–900 µm thick, (reported as 200–800 µm thick in the protologue). Thallus construction is monomerous with cells of adjacent filaments connected laterally by fusions, and secondary pit-connections were not seen. Cells of the ventral region (medulla) arranged coaxially, occupying 50–75% of the thallus thickness. Medullary cells 12.5–17.5 µm wide and 25–30 µm long (in the protologue said to be 11–24 µm wide and 18–46 µm long. Dorsal regions (cortex) composed of filaments that become oriented perpendicularly to the thallus surface. Cortical cells ovoid, 10–15 µm in wide and 10–12.5 µm long (in the protologue said to be 11–14 µm in diameter and 11–18 µm long). Each dorsal filament terminated by an ovoid epithallial cell, 10–12.5 µm in diameter and 8–10 µm tall. Trichocytes common at the surface (in the protologue said to occur in small numbers), occurring singly or in vertical and horizontal rows. Trichocytes 20–25 µm in wide and 30–35 µm long. Tetrasporangial conceptacles projected and apiculate, tetrasporangial chambers 540–800 µm in diameter and 180–300 µm high, and pore canals lined by cells oriented parallel to the thallus surface. Tetrasporangia are 30–40 µm in wide and 70–80 µm long.

The characters observed in the type material of *Goniolithon solubile* were nearly the same as those of *Neogoniolithon fosliei* (Heydrich) Setchell & L.R. Mason including: thallus construction monomerous, ventral region (medulla) with cells arranged coaxially, occupying 50–75% of the thallus thickness; each dorsal filament terminated by an ovoid epithallial cell, 12.5–15 µm in diameter and 12–16 µm tall; trichocytes singly or in vertical and horizontal rows, each measuring 20–25 µm in wide and 30–40 µm long. Despite these similarities, we have used the name *N. solubile* with a Caribbean Sea type locality (Culebra, Puerto Rico) rather than *N. fosliei* (type locality: Tor, Egypt) for the local species.

Neogoniolithon spectabile (Foslie) Setchell & L.R. Mason 1943: 92.

Basionym: *Goniolithon spectabile* Foslie 1901: 16–18.

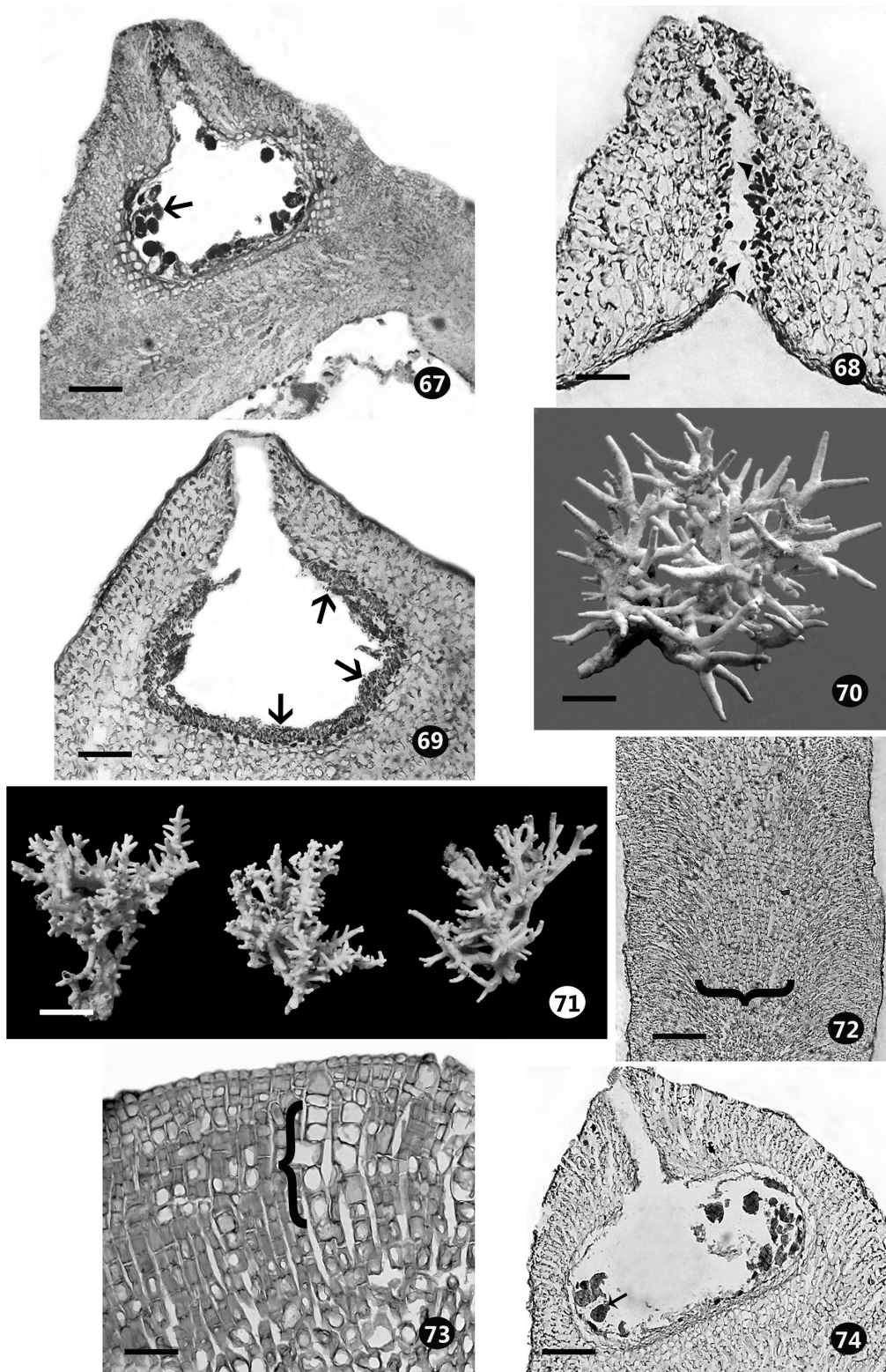
Type locality: Bermuda (Lectotype: C.V. Forsstrand, ex Naturhistoriska Riksmuseum, Stockholm (S); TRH unnumbered, includes slide 437; designated by Adey in Adey & Lebednik, 1967: 29)

Distribution: Florida, Belice, Bermudas, Bahamas and Colombia (Taylor 1960).

Specimens Examined Morpho-anatomically (Figs. 70–75). MÉXICO: *Yucatán*: Alacranes Reef, Pérez Island, ⊕, 23-05-1964, Huerta Múzquiz (ENCB 17392). *Quintana Roo*: Cozumel Island, Maya Beach (87°0'57.604" W, 20°24'24.6" N), ⊕, 27-02-1985, Mendoza-González & Mateo-Cid (ENCB 17391); Banco Chinchorro, Cayo Centro ⊕, 24-06-1984, Huerta Múzquiz & Mateo-Cid (ENCB 17398); Ascensión Bay (87°26'52" W, 19°38'57" N), ⊕, 18-05-1998, Mateo-Cid & Mendoza-González (ENCB 17400); Vigía Chico (87°29'27" W, 19°42'25.8" N), ⊕, 19-05-1998, Mateo-Cid & Mendoza-González (ENCB 17920); Punta Pájaros (87°30'38.8" W, 19°48'4.3" N), 17-05-1998, Mateo-Cid & Mendoza-González (ENCB 17399); Punta Sacrificios, Espíritu Santo Bay, 19-01-2011, Mendoza-González, Mateo-Cid & Acosta Calderón (ENCB 20082); Xcalak, ⊕, 22-12-1971, Huerta Múzquiz (ENCB 17390).

Habitat and Morphology. Thalli branching, unattached and free living as rhodoliths, intertidal to 5 m deep, thalli are up 3.0 to 6 cm high (Fig. 70–71). Branching irregular to subdichotomous, branches terete to subterete, 2–4 mm in diameter, the apical portions 1–1.5 mm diameter.

Anatomy. Internal organization radial in branches (Fig. 72). Medulla composed of several layers of filaments radially organized. Medullary cells 18–20 µm wide and 30–40 µm long. Dorsal region (cortex) composed of filaments, cortical cells ovoid, 16–21 µm wide and 14–18 µm long and cells of adjacent filaments connected laterally by cell fusions. Dorsal filaments terminated by flattened epithallial cell, 15–18 µm wide and 10–12 µm long. Trichocytes common, these occurring singly, in vertical rows at thallus surface or sometimes becoming buried (Fig. 73); individual trichocytes 35–40 µm wide and 55–65 µm long.



FIGURES 67–69. *Neogoniolithon solubile*, Cozumel Island (ENCB 19 046). 67) Section through tetrasporangial conceptacle showing tetrasporangium (arrow). Scale bar: 240 μ m. 68) Enlarged section through tetrasporangial conceptacle showing pore canal lined by papillae-like cells orientated perpendicular to canal (arrowheads). Scale bar: 140 μ m. 69) Mature male conceptacle with spermatangial filaments on floor, walls and roof of chamber. Scale bar: 70 μ m.

FIGURES 70–74. *Neogoniolithon spectabile*, Ascensi3n Bay (ENCB 17 399). 70) Habit of freely growing branched thallus with terete branches narrowing toward apices. Scale bar: 8 mm. 71) Habit of three branched thalli. Scale bar: 10 mm; 72) Longitudinal section through branch showing prominent medullary region (brace). Scale bar: 250 μ m. 73) Section through cortex; trichocytes in vertical rows (brace). Scale bar: 75 μ m. 74) Section through tetrasporangial conceptacle showing remains of tetrasporangia (arrow). Scale bar: 120 μ m.

Reproductive structures. Tetrasporangial conceptacles originating laterally on terminal branches, apiculate, their chambers 500–800 µm diameter and 250–370 µm high (Fig. 74). The pore canal 70–80 µm diameter and 300–350 µm long and is lined by elliptical cells that protrude laterally into the canal (Fig. 75). Roof filaments 16–20 cells long (not including epithallial cell). Tetrasporangia 40–60 µm wide and 90–100 µm long, arranged across conceptacle floor; central columella absent. Gametangial plants not found.

DNA sequences. The three sequenced specimens, (Table 2), vary maximally by 1.06%.

Comments. Foslie (1901) described *Goniolithon spectabile* as subhemispheric, about 32 cm long and 24 broad, it seems at first to have been attached showing however a tendency little by little to loosen itself from the substratum. In addition he mentioned that the thallus exhibited a wide variation in the form of branches and branching type. As well as *Goniolithon strictum* (Foslie 1901), the specimen of *G. spectabile* was sterile and Foslie referred it into *Goniolithon* because trichocytes were present. According to Taylor (1960) *Neogoniolithon spectabile* could readily be distinguished from other branched species of *Neogoniolithon* mainly by its size, type of branching and shape of the branches. Mexican plants of *N. spectabile* are characterized by the following combination of features: 1) thalli are fruticose rhodoliths, with great morphological variation and branching subdichotomous to irregular; 2) thallus radial in branches; 3) trichocytes present, occurring singly or in vertical rows; 4) tetrasporangial pore canal lined by narrow filaments that tilt into the pore canal and have an elliptical shape and 5) tetrasporangial conceptacle roof is more commonly 16–20 cells thick.

Neogoniolithon strictum (Foslie) Setchell & L.R. Mason 1943: 92

Basionym: *Goniolithon strictum* Foslie 1901: 14

Type Locality: Florida, USA.

Distribution: Florida, Bahamas, Hispaniola, Jamaica, Puerto Rico, Virgin Islands, Cuba, Colombia, Venezuela and Indonesia (Taylor, 1960; Silva *et al.* 1996).

Specimens Examined Morpho-anatomically (Figs. 76–80): MÉXICO: *Yucatán:* Alacranes Reef, Pérez Island, ⊕, 25-01-1986, Huerta Múzquiz (ENCB 17367); Desertora Island, ⊕, 15-10-1985, Huerta Múzquiz, Hidalgo & Mateo-Cid (ENCB 17374). *Quintana Roo:* Mujeres Island, ⊕, 12-10-1983, Mateo-Cid & Mendoza-González (ENCB 17382); Cozumel Island, Maya Beach, 08-11-1984, Mendoza-González & Mateo-Cid (ENCB 17370); Banco Chinchorro, Cayo Centro, ⊕, 09-06-1982, Huerta Múzquiz (ENCB 14236); Ascensión Bay, ⊕, 17-05-1998, Mateo-Cid & Mendoza-González (ENCB 13486); El Zarzal, ⊕, Mateo-Cid & Mendoza-González, 19-05-1998 (ENCB 17371); Xcalak, 22-12-1971, Huerta Múzquiz (ENCB 17366).

Habitat and Morphology. Thalli branching, growing on rocks or unattached and free living as rhodoliths are up to 6 to 8 cm high, forming very fragile masses (Fig. 76), intertidal to 8 m deep. Repeatedly subdichotomous branching, branches compressed to subterete 3–4 mm in diameter, the apical portions 1–2 mm broad.

Anatomy. Internal organization radial in the branches. Medulla composed of several layers of filaments oriented perpendicularly to the thallus surface (Fig. 77). Medullar cells 13–20 µm wide and 25–40 µm long. Dorsal region (cortex) composed of filaments, cortical cells ovoid, 15–18 µm wide and 13–18 µm long, cells of adjacent filaments connected laterally by cell fusion. Dorsal filaments terminated by an ovoid or flattened epithallial cell, 13–18 µm wide and 7–10 µm long. Trichocytes common, occurring singly and 25–35 µm wide and 35–50 µm long (Fig. 78).

Reproductive structures. Tetrasporangial conceptacles originating laterally on terminal branches, apiculate (Fig. 79), their chambers measure 750–1000 µm diameter and 200–300 µm high. The pore canal measures 100–120 µm diameter and 300–350 µm long, and is lined by semilunate-shape cells that protruding laterally into the canal (Fig. 80). Roof filaments 10–14 cells long (not including epithallial cell). Tetrasporangia measures 30–45 µm wide and 90–100 µm long, they are arranged across the floor of the conceptacle and central columella is absent. Gametangial plants not found.

DNA sequences. Both specimens (Table 2) have identical *psbA* sequences.

Comments: In its original description, Foslie (1901) indicated that *N. strictum* formed large masses repeatedly subdichotomously branched, branches terete to slightly compressed 1–1.5 mm thick, with rounded ends. A median longitudinal section of a branch exhibited regular radiating cells-rows, cells 15–25 µm wide and 35–55 µm long. Although the specimen was sterile, Foslie inclined to refer it into *Goniolithon* because the trichocytes were present. Mexican plants of *N. strictum* are characterized by the following combination of features: 1) Thallus grows adherent or as rhodoliths, branching subdichotomous; 2) trichocytes present, occurring singly or in horizontal rows; 3) the tetrasporangial pore canal lined by narrow filaments that tilt into the pore canal and have an semilunate shape and

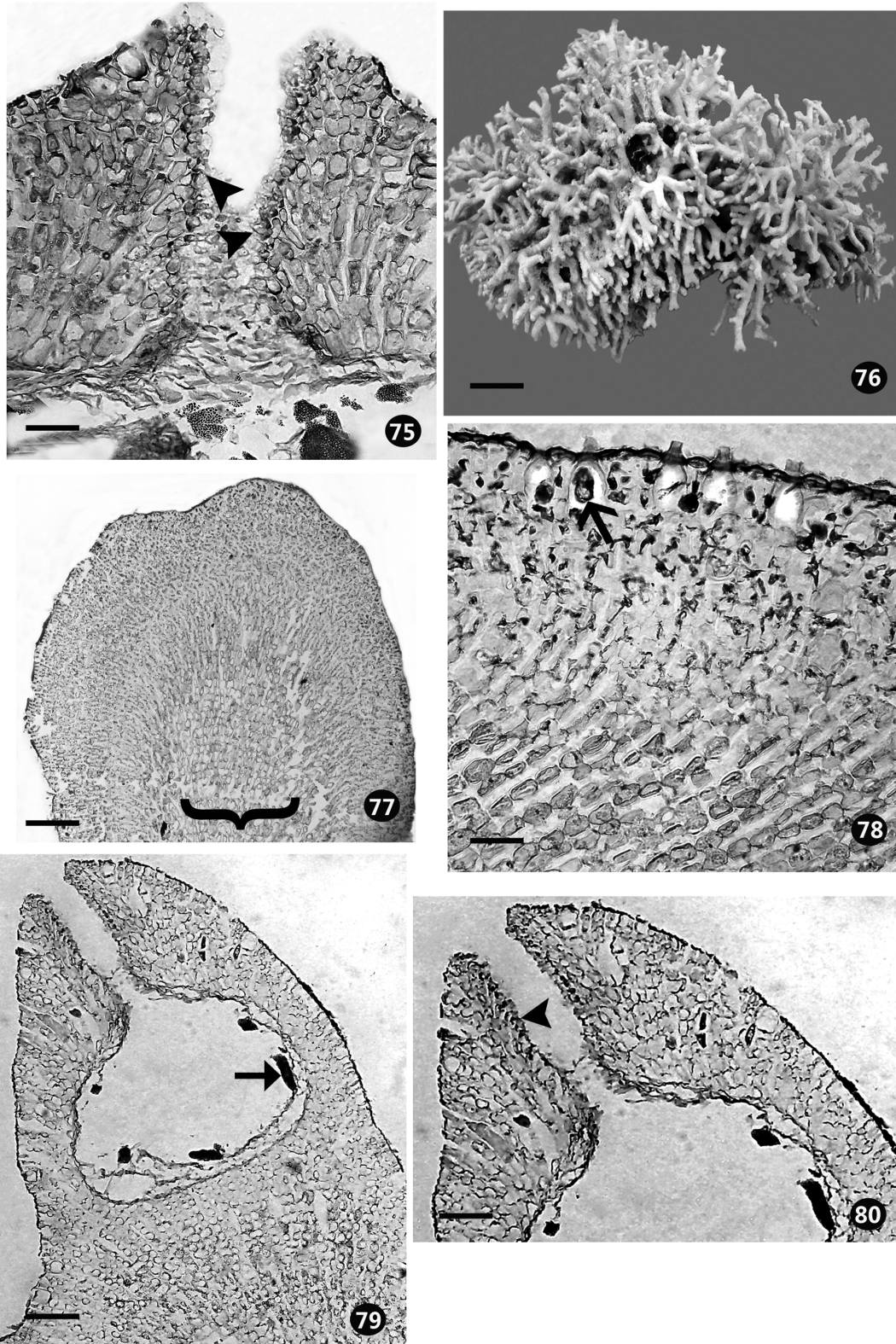


FIGURE 75. *Neogoniolithon spectabile*, 75) Enlarged section through tetrasporangial conceptacle showing pore canal lined by elliptical cells protruding laterally into canal (arrowhead). Scale bar: 40 μm . **FIGURES 76–80.** *Neogoniolithon strictum*, Banco Chinchorro (ENCB 14 235). 76) Habit of a branched thallus; note dense branching and compressed branches. Scale bar: 16 mm. 77) Section through thallus apex showing medullary region (brace) and cortex. Scale bar: 340 μm . 78) Section through the dorsal region showing trichocytes (arrow). Scale bar: 100 μm . 79) Section through tetrasporangial conceptacle; tetrasporangium (arrow). Scale bar: 250 μm . 80) Enlarged section through tetrasporangial pore canal lined by semilunate-shaped cells protruding laterally into canal (arrowhead). Scale bar: 70 μm .

4) the tetrasporangial conceptacle roof is more commonly 10–14 cells thick. Unlike specimens of *N. spectabile*, *N. strictum* specimens can grow unattached, their branching pattern is subdichotomous and branches are compressed and may be delimited based on their anatomical and reproductive features. One of the principal differences between *N. spectabile* and *N. strictum* is their habit, with the former always occurring as rhodoliths in our collections whereas the latter occurs both unattached and on rocks. Tetrasporangial conceptacle chambers are 500–800 µm diameter and 250–370 µm high and roof filaments are 16–20 cells long in *N. spectabile*, whereas in *N. strictum* tetrasporangial chambers are 750–1000 µm diameter and 200–300 µm high and roof filaments are 10–14 cells long (Table 4). Both species are conspicuous components of coral reefs of Quintana Roo.

Discussion

We consider the species treated herein as belonging to *Neogoniolithon* primarily because they are in the same clade with other species treated as *Neogoniolithon* (Fig. 1) and because they conform to the diagnostic characters proposed by Kato *et al.* (2011) for Neogoniolithoideae. We do not know, however, if some of the diagnostic features that characterize *Neogoniolithon* are present in the generitype species, *N. fosliei* (type locality: Tor, Egypt). All observations of diagnostic reproductive features in the generitype species have been based on material collected from localities far distant from the type locality and said to belong to *N. fosliei* based on morpho-anatomical similarities. Moreover, *N. fosliei* has been considered a synonym of *N. brassica-florida* (Harvey) Setchell & L.R. Mason (type locality: Algoa Bay, South Africa) for the past 17 years (Penrose 1996). Kato *et al.* (2013) cast doubt on the synonymy of *N. fosliei* with *N. brassica-florida* by showing that numerous distinct crustose species as well as fruticose species were passing under this single name in the Ryukyu Islands, Japan. But we also don't know if *N. fosliei* is correctly applied to specimens from Japan, as the name is linked to those specimens only by morpho-anatomy (Kato *et al.* 2013) and not by DNA sequence to type or topotype material. From a taxonomic standpoint, the assignment of all species to *Neogoniolithon*, and even the validity of Neogoniolithoideae need to be confirmed by DNA sequencing of type or topotype material of the generitype species.

For Mexican Gulf of Mexico and Caribbean Sea *Neogoniolithon* species, we faced the same problems as Kato *et al.* (2013) in the Ryukyu Islands, Japan: 1) species diversity is higher than we thought with the presence of several cryptic species, and 2) using morpho-anatomical characters to link field-collected specimens to validly published species names has proved problematic. Based on sequencing only 32 specimens from the rather narrow study area, we have recovered 14 species, four of which are based on only one or two specimens that lack many morpho-anatomical characters needed to adequately describe them, particularly those characters associated with reproduction. We have not sequenced any specimens that morpho-anatomically we call *N. erosum*. We have only used the names of species whose type locality is in the subtropical and tropical western Atlantic, a province from which all of our specimens were collected. For example, we have used the name *N. solubile* (type locality: Culebra, Puerto Rico) rather than *N. fosliei* (type locality: Tor, Egypt) for a species in our local area, even though Woelkerling (1987) placed *N. solubile* in synonymy under *N. fosliei* based on morpho-anatomy. We recognize that acceptance of each of these names for our local species will depend upon sequencing type or topotype specimens. *Morphological characters useful in segregating Mexican Gulf of Mexico and Caribbean Sea Neogoniolithon species.* Despite the difficulty of applying names, we have found a suite of morpho-anatomical characters that we believe can be used to segregate many Mexican Gulf of Mexico and Caribbean Sea *Neogoniolithon* species. These characters include habit (branched versus unbranched; encrusting versus warty), thallus construction (monomerous versus dimerous), disposition of trichocytes (single and/or in horizontal rows and/or in vertical rows), and, of particular use, characters associated with tetrasporangial conceptacles, including size of conceptacle chambers, number of cells in roof filaments and the shapes of cells lining pore canals (Tables 3 and 4).

Conclusions

Based on the limited sampling that we have done along the eastern coast of Mexico, primarily in the states of Veracruz and Quintana Roo, Mexico, 14 species of *Neogoniolithon* are present and more likely will be found. One

new species, *N. siankanensis* is described herein, with another four needing to be described when reproductive specimens of each species have been found. The applications of all species names need to be confirmed by sequencing type or topotype material. A suite of morpho-anatomical characters, particularly those associated with tetrasporangial conceptacles, appears to be useful in delineating Mexican east coast species of *Neogoniolithon*.

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References

- Adey, W.H. (1970) A revision of the Foslie crustose coralline herbarium. *Kongelige Norske Videnskabers Selskabs Skrifter* 1: 1–46.
- Adey, W.H., Townsend, R.A. & Boykins, W.T. (1982) The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. *Smithsonian Contributions to the Marine Science* 15: 1–74.
<http://dx.doi.org/10.5479/si.01960768.15.1>
- Areschoug, J.E. (1852) *Ordo XII: Corallineae* In Agardh JG (ed.) *Species genera et ordines algarum* Vol 2, Part 2 C.W.K. Gleerup: Lund, pp. 506–576.
- Athanasiadis, A. (1997) On the typification and taxonomic status of *Melobesia notarisii* Dufour (Rhodophyta, Corallinales). *Phycologia* 36: 410–15.
<http://dx.doi.org/10.2216/i0031-8884-36-5-410.1>
- Babbini, L. & Bressan, G. (1997) Recensement de Corallinacées de la Mer Méditerranée et considérations phytogéographiques. *Bibliotheca Phycologica* 103: 1–421.
- Bittner, L., Payri, C.E., Maneveldt, G.W., Couloux, A., Cruaud, C., de Reviers, B. & Le Gall, L. (2011) Evolutionary history of the Corallinales (Corallinophycidae, Rhodophyta) inferred from nuclear, plastidial and mitochondrial genomes. *Molecular Phylogenetics and Evolution* 61: 697–713.
<http://dx.doi.org/10.1016/j.ympev.2011.07.019>
- Braga, J. C. & Aguirre, J. (2004) Coralline algae indicate Pleistocene evolution from deep, open platform to outer barrier reef environments in the northern Great Barrier Reef margin. *Coral Reefs* 23: 547–58.
<http://dx.doi.org/10.1007/s00338-004-0414-x>
- Cabioch, J. (1972) Etude sur les corallinacées II. La morphogenèse; conséquences systématiques et phylogénétiques. *Cahiers de Biologie Marine* 13: 137–288.
- Chamberlain, Y.M. (1983) Studies in Corallinaceae with special reference to *Fosliella* and *Pneophyllum* in the British Isles. *Bulletin of the British Museum (Natural History). Botany* 11: 291–463.
- Chamberlain, Y.M. (1994) Masthophoroideae Setchell. In: *Seaweeds of the British Isles. 1. Rhodophyta, part 2B Corallinales, Hildenbrandiales*. (Eds. Irvine, L.M. & Y. Chamberlain) pp. 113–158. *The Natural History Museum, London*.
- Díaz-Pulido, G. & Díaz-Ruíz, M. (2003) Diversity of benthic marine algae of the Colombian Atlantic. *Biota Colombiana* 4: 203–246.
- Foslie, M. (1898) List of species of the lithothamnia. *Kjelder Norske Videnskabers Selskab skrifter*. 1898. (2): 1–7.
- Foslie, M. (1900) New or critical calcareous algae. *Kongelige Norske Videnskabers Selskabs Skrifter* 1899 (5): 1–34.
- Foslie, M. (1901) New Melobesiae. *Kjelder Norske Videnskabers Selskab skrifter*. 1900 (6): 1–24.
- Foslie, M. (1903) Two new lithothamnia. *Kjelder Norske Videnskabers Selskab skrifter*. [1903] (2): 1–4.
- Foslie, M. (1906) Algologiske notiser II. *Kjelder Norske Videnskabers Selskab skrifter*. 1906. (2): 1–28.
- Foslie, M. & Howe, M.A. (1906a) New American coralline algae. *Bulletin of the New York Botanical Garden* 4: 128–136, Plates 80–93.
- Foslie, M. & Howe, M.A. (1906b) Two new coralline algae from Culebra, Porto Rico. *Bulletin of the Torrey Botanical Club* 33: 577–580.
- Foslie, M. (1907) Algologiske notiser IV. *Det Kongelige Norske Videnskabers Selskabs Skrifter* 1907 (6): 1–30.

- Foslie, M. (1909) Algologiske notiser VI. *Kongelige Norske Videnskabers Selskabs Skrifter* 1909 (2): 1–63.
- Guiry, M.D. & Guiry, G.M. (2014) AlgaeBase version 4.2. World-wide electronic publication, National University of Ireland, Galway. Available from: <http://www.algaebase.org>.
- Hamel, G. & Lemoine, M. (1953) Corallinacées de France et d’Afrique de Nord. [Séries 7] *Archives du Muséum National d’Histoire Naturelle* 1: 15–136.
- Harvey, W.H. (1849) *Nereis australis, or algae of the southern ocean: being figures and descriptions of marine plants, collected on the shores of the Cape of Good Hope, the extra-tropical Australian colonies, Tasmania, New Zealand, and the Antarctic regions; deposited in the Herbarium of the Dublin University*. Part 2. London: Reeve Brothers, pp. 65–124, pls. XXVI–L.
- Harvey, A.S., Phillips, L.E., Woelkerling, W.J. & Millar, J.K. (2006) The Corallinaceae, subfamily Mastophoroideae (Corallinales, Rhodophyta) in south-eastern Australia. *Australian Systematic Botany* 19: 387–429. <http://dx.doi.org/10.1071/sb05029>
- Harvey, A.S., Woelkerling, W.J. & Millar, J.K. (2009) The genus *Lithophyllum* (Lithophylloideae, Corallinaceae, Rhodophyta) in south-eastern Australia, with the description of *L. riosmenae*, sp. nov. *Australian Systematic Botany* 22: 296–317. <http://dx.doi.org/10.1071/sb08051>
- Heydrich, F. (1897) Neve kalkalgen von Deutsch-Neu-Guinea (Kaiser Wilhelms-Land). *Bibliotheca Botanica*. 41: 1–11, pl.1.
- Heydrich, F. (1901) Die Lithothamniën des Museum d’ Histoire Naturelle in Paris. *Botanical Journal*. 28: 529–545, pl. 11.
- Howe, M.A. (1920) Class 2. Algae. In: Britton, N.L. & Millspaugh, C.F. (Ed.) *The Bahama Flora*. Privately published, New York, pp. 553–631.
- Huerta-Múzquiz, L., Mendoza-González, A.C. & Mateo-Cid, L.E. (1987) Avance sobre un estudio de las algas marinas de la Península de Yucatán. *Phytologia* 62(1): 23–53.
- Hughey, J. & Gabrielson, P.W. (2012) Comment on “Acquiring DNA sequence data from dried archival red algae (Florideophyceae) for the purpose of applying available names to contemporary genetic species: a critical assessment” *Botany* 90: 1191–1194. <http://dx.doi.org/10.1139/b2012-102>
- Hughey, J.R., Silva, P.C. & Hommersand, M.H. (2001) Solving taxonomic and nomenclatural problems in Pacific Gigartinaeae (Rhodophyta) using DNA from type material. *Journal of Phycology* 37: 1091–1109. <http://dx.doi.org/10.1046/j.1529-8817.2001.01048.x>
- Iryu, Y. & Matsuda, S. (1994) Taxonomic studies of the *Neogoniolithon fosliei* complex (Corallinaceae, Rhodophyta) in the Ryukyu Islands. *Transactions Proceedings Paleontology Society of Japan. N. S.* 174: 426–448.
- Johansen, H.W. (1970) The diagnostic value of reproductive organs in some genera of articulated coralline red algae. *British Phycological Journal* 5(1):79–86. <http://dx.doi.org/10.1080/00071617000650101>
- Johansen, H.W. (1981) *Coralline algae, a first synthesis*. CRC Press, Boca Raton, Florida 239 pp.
- Kato, A., Baba, M. & Suda, S. (2011) Revision of the Mastophoroideae (Corallinales, Rhodophyta) and polyphyly in nongeniculate species widely distributed on Pacific coral reefs. *Journal of Phycology* 47: 662–672. <http://dx.doi.org/10.1111/j.1440-1835.2012.00665.x>
- Kato, A., Baba, M. & Suda, S. (2013). Taxonomic circumscription of heterogeneous species *Neogoniolithon brassica-florida* (Corallinales, Rhodophyta) in Japan. *Phycological Research* 61: 15–26. <http://dx.doi.org/10.1111/j.1440-1835.2012.00665.x>
- Keats, D.W. & Chamberlain, Y.M. (1994) Three species of *Hydrolithon* (Rhodophyta, Corallinaceae): *Hydrolithon onkodes* (Heydrich) Penrose and Woelkerling, *Hydrolithon superficiale* sp. nov., and *H. samoëense* (Foslie) comb. nov. from South Africa. *South African Journal of Botany* 60: 8–21.
- Lemoine, M. (1917) Corallinaceae. Subfam. I. Melobesieae. In: Børgesen, F. (Ed.) *The marine algae of the Danish West Indies III. Rhodophyceae. Part C*. pp. 147–182. Dansk Botanisk Arkiv.
- Lemoine, M. (1929) Melobesieae. *Det Kongelige Danske Videnskabernes Selskab Biologiske Meddelelser* 8: 19–68, 6 plates.
- Lemoine, M. (1966) Algues calcaires recueillies dans la Mer Rouge, en particulier dans le Golfe d’Eilat. *Bulletin of the Sea Fisheries Research Station [Haifa]* 42: 28.
- Littler, M.M. (1972) The crustose Corallinaceae. Oceanography and Marine Biology. *Annals Review* 10: 1–311.
- Littler, D.S. & Littler, M.M. (2000) *Caribbean reef plants*. Offshore Graphic, Inc. Washington, 542 pp.
- Maneveldt, G.W. (2005) A global revision of the nongeniculate coralline algal genera *Porolithon* Foslie (defunct) and *Hydrolithon* Foslie (Corallinales, Rhodophyta). PhD Thesis Department of Biodiversity & Conservation Biology, University of The Western Cape, South Africa, 492 pp. 286 pls.
- Martoja, R. & Martoja-Pierson, M. (1970) *Técnicas de Histología Animal*. Barcelona: Toray-Masson, 370 pp.
- Masaki, T. (1968) Studies on the Melobesioideae of Japan. *Memoirs of the Faculty of Fisheries, Hokkaido University* 16: 1–80.
- Mateo-Cid, L.E. & Mendoza-González, A.C. (1991) Algas marinas bénticas de la Isla Cozumel, Quintana Roo, México. *Acta Botánica Mexicana* 16: 57–87.
- Mateo-Cid, L.E. & Pedroche, F.F. (2004) The occurrence of *Neogoniolithon fosliei* (Heydrich) Setchell et Mason in the Mexican Caribbean and the relationship of this species to *N. solubile* (Foslie et Howe) Setchell et Mason (Corallinales, Rhodophyta). *Caribbean Journal of Science* 40: 182–191.
- Mendoza-González, A.C. & Mateo-Cid, L.E. (1985) Contribución al conocimiento de la flora marina bentónica de las Islas

- Sacrificios y Santiaguillo, Veracruz, México. *Phytologia* 59: 9–16.
- Mendoza-González, A.C. & Mateo-Cid, L.E. (1992) Algas marinas bentónicas de Isla Mujeres, Quintana Roo, México. *Acta Botánica Mexicana* 19: 37–62.
- Mendoza-González, A.C. & Mateo-Cid, L.E. (2007) Cinco nuevos registros de algas rojas (Rhodophyta) para el Caribe mexicano. *Polibotánica* 23: 101–119.
- Ortega, M.M., Godínez, J.L. & Garduño-Solórzano, G. (2001) *Catálogo de algas bénticas de las costas mexicanas del Golfo de México y Mar Caribe*. Comisión Nacional para el Estudio de la Biodiversidad y Universidad Nacional Autónoma de México, México, D.F., 594 pp.
- Penrose, D.L. (1996) Genus *Neogoniolithon* Setchell & Mason 1943: 90. In: Womersley, H.B.S. (ed.) *The marine benthic flora of southern Australia. Rhodophyta. Part IIIB, Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales*. Canberra: Australian Biological Resources Study, pp. 280–283.
- Peña, V., Adey, W.H., Riosmena-Rodríguez, R., Jung, M.Y., Afonso-Carillo, J., Choi, H.G. & Bárbara, I. (2011) *Mesophyllum sphaericum* sp. nov. (Corallinales, Rhodophyta): a new maerl-forming species from the northeast Atlantic. *Journal of Phycology* 47: 911–927.
<http://dx.doi.org/10.1111/j.1529-8817.2011.01015.x>
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML web-servers. *Systematic Biology* 57: 758–771.
- Setchell, W.A. (1943) *Mastophora* and the Mastophorae: Genus and subfamily of Corallinaceae. *Proceedings of the National Academy of Science of the United States of America* 29: 127–135.
- Setchell, W.A. & Mason, L.R. (1943) *Goniolithon* and *Neogoniolithon*: two genera of crustaceous coralline algae. *Proceedings of the National Academy of Science of the United States of America* 29: 87–92.
- Silva, P.C., Basson, P.W. & Moe, R.L. (1996) Catalogue of the benthic marine algae of the Indian Ocean. *University of California Publications in Botany* 79: 1–1259.
- South, G.R. & Skelton, P.A. (2003) Catalogue of the marine benthic macroalgae of the Fiji Islands, South Pacific. *Australian Systematic Botany* 16: 699–758.
- Taylor, W.R. (1960) *Marine algae of the eastern tropical and subtropical coasts of the Americas*. pp. xi + 870, 14 figs, 80 plates. Ann Arbor: The University of Michigan Press.
- Thiers, B. (2014) (continuously updated) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium.
- Townsend, R.A. (1981) Tetrasporangial conceptacle development as a taxonomic character in the Mastophoroideae and Lithophylloideae (Rhodophyta). *Phycologia* 20: 407–414.
<http://dx.doi.org/10.2216/i0031-8884-20-4-407.1>
- Verheij, E. (1994) Nongeniculate Corallinaceae (Corallinales, Rhodophyta) from the Spermonde Archipelago, SW Sulawesi, Indonesia. *Blumea* 39: 95–137.
- Weber-Van Bosse, A. (1904) Corallinaceae verae of the Malay Archipelago. In: Weber-van Bosse A. & Foslie, M. *The Corallinaceae of the Siboga Expedition-Siboga-Expeditie* Monographic 61. Leiden. Pp. 78–110, pls. XIV–XVI.
- Woelkerling, W.J. (1985) A taxonomic reassessment of *Spongites* (Corallinaceae, Rhodophyta) based on studies of Kützing's original collections. *British Phycological Journal* 20: 123–153.
<http://dx.doi.org/10.1080/00071618500650151>
- Woelkerling, W.J. (1988) *The Coralline Red Algae: An Analysis of the Genera and Subfamilies of Non-geniculate Corallinaceae*. Oxford: Oxford University Press and London: British Museum (Natural History), 268 pp.
- Woelkerling, W.J. (1993) Type collections of Corallinales (Rhodophyta) in the Foslie Herbarium (TRH). *Gunneria* 67: 1–289.
- Woelkerling, W.J., Penrose, D.L. & Chamberlain, Y.M. (1993) A reassessment of type Collections of non-geniculate Corallinaceae (Corallinales, Rhodophyta) described by C. Montagne and L. Dufour, and of *Melobesia brassica-florida* Harvey. *Phycologia* 32: 323–331.
<http://dx.doi.org/10.2216/i0031-8884-32-5-323.1>
- Woelkerling, W.J., Gustavsen, G., Myklebost, H.E., Prestø, T. & Sastad, S.M. (2005) The coralline red algal herbarium of Mikael Foslie: revised catalogue with analyses. *Gunneria* 77: 1–625.
- Womersley, H.B.S. (1996) *The marine benthic flora of southern Australia - Part IIIB - Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales*. Vol. 5. Canberra & Adelaide: Australian Biological Resources Study & the State Herbarium of South Australia, 392 pp., 160 figs.
- Wynne, M.J. (2011) A check-list of benthic marine algae of the tropical and subtropical western Atlantic: second revision. *Beihefte zur Nova Hedwigia* 129: 1–152.
- Yoon, H.S., Hackett, J.D., Ciniglia, C., Pinto, G. & Bhattacharya, D. (2002) A Molecular Timeline for the Origin of Photosynthetic Eukaryotes. *Molecular Biology and Evolution* 21: 809–818.