



Range extension of *Mesophyllum erubescens* (Foslie) Me. Lemoine (Hapalidiales, Rhodophyta): first report from mesophotic rhodolith beds in the northwestern Gulf of Mexico offshore Louisiana and Texas, including the Flower Garden Banks National Marine Sanctuary

Joseph L. Richards¹, Ronald P. Kittle III¹, Jaida R. Abshire¹, Dijel Fuselier¹, William E. Schmidt¹, Carlos F. D. Gurgel², Suzanne Fredericq¹

¹ University of Louisiana at Lafayette, Biology Department, 410 E. St. Mary Blvd., Billeaud Hall, Room 108, Lafayette, Louisiana 70503, USA.
² Centro de Ciências Biológicas, Departamento de Botânica, Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina 88040-900, Brazil.

Corresponding author: Joseph L. Richards, Joer207@gmail.com

Abstract

DNA sequence analysis of plastid-encoded *psbA* and UPA, mitochondrion-encoded COI, and nuclear-encoded LSU rDNA of rhodolith-forming crustose coralline algal specimens from the northwestern Gulf of Mexico reveals that *Mesophyllum erubescens* (Foslie) Me. Lemoine is present in mesophotic rhodolith beds offshore Louisiana and Texas at 39–57 m depth. Morpho-anatomical characters viewed with SEM support the identification of these specimens. *Mesophyllum erubescens* is reported for the first time offshore Louisiana at Ewing Bank, the Louisiana–Texas border at Bright Bank, and Texas in the Flower Garden Banks National Marine Sanctuary.

Keywords

CCA, COI, coralline algae, DNA, LSU rDNA, *psbA*, UPA.

Academic editor: Guilherme Henrique Pereira Filho | Received 6 January 2020 | Accepted 7 April 2020 | Published 6 May 2020

Citation: Richards JL, Kittle PR III, Abshire JR, Fuselier D, Schmidt WE, Gurgel CFD, Fredericq S (2020) Range extension of *Mesophyllum erubescens* (Foslie) Me. Lemoine (Hapalidiales, Rhodophyta): first report from mesophotic rhodolith beds in the northwestern Gulf of Mexico offshore Louisiana and Texas, including the Flower Garden Banks National Marine Sanctuary. Check List 16 (3): 513–519. <https://doi.org/10.15560/16.3.513>

Introduction

Previously, species identification and reports of coralline algal diversity in the northwestern Gulf of Mexico (NWGMx) have been based largely on morpho-anatomy. Few floristic studies of coralline algae were conducted in the region prior to 2014 (Minnery et al. 1985; Rezak 1985; Minnery 1990; Fredericq et al. 2009). Recently, DNA sequence-based floristic surveys and biodiversity

assessments of crustose coralline algae (CCA), including rhodoliths, have begun in the region (Richards et al. 2014, 2016). Though two new coralline species have been described from the region (Richards and Fredericq 2018; Richards et al. 2019), many other new species have yet to be described. Also, other species described from localities outside the region likely remain to be identified

from mesophotic collections in the NWGMx. Herein, we focus on documenting the presence of a described species that has yet to be reported from the region, *Mesophyllum erubescens* (Foslie) Me. Lemoine, whose identification has recently been clarified by comparative DNA sequence analyses including the holotype specimen (Sissini et al. 2014).

Methods

Rhodolith-forming specimens were collected (Table 1) offshore Louisiana and near the Texas–Louisiana border aboard the R/V *Pelican* using an Hourglass-design box dredge with minimum tows (Joyce and Williams 1969) as described in Richards et al. (2019) and from offshore Texas in the Flower Garden Banks National Marine Sanctuary (FGBNMS) via the ROV *Mohawk* aboard the R/V *Manta*, as described in Fredericq et al. (2019). Brazilian and Hawaiian specimens were collected from Arvoredo Island, Santa Catarina, southern Brazil, and at Richardson Ocean Park, Hilo, Hawai'i, respectively, to provide comparative loci among Brazilian, Hawaiian and NWGMx specimens. A distribution map was generated in R using package “ggplot2” (Wickham 2016; R Core Team 2019).

DNA was extracted, amplified, and sequenced as described in Richards et al. (2014, 2016). The markers chosen for PCR included the plastid-encoded *psbA* (photosystem II reaction center protein D1 gene) and UPA (partial 23S rDNA), mitochondrion-encoded COI (cytochrome oxidase subunit I gene), and nuclear-encoded LSU (partial 28S rDNA). *Mesophyllum erubescens* sequences were initially identified using the Basic Local Alignment Search Tool (BLAST) (Altschul et al. 1990, available courtesy of the National Center for Biotechnology Information, U.S. National Library of Medicine) prior to alignment. *PsbA*, UPA, COI, and LSU sequences were aligned and concatenated, and the best partition scheme and model of evolution were determined according to the protocol of Richards et al. (2017). Published sequences were also downloaded from GenBank and included in the analysis for context, including sequences of *M. erubescens* that were verified by comparisons to type material, sequences of *Mesophyllum sphaericum*, and sequences of *Phymatolithon calcareum* as the outgroup. The final four-gene concatenated alignment was 2,414 base pairs (bp) long (*psbA* = 831 bp; UPA = 370 bp; COI = 613 bp; LSU = 600 bp). The alignment was analyzed for maximum likelihood (ML) using RAXML (Stamatakis 2006) implemented via “The CIPRES Science Gateway v. 3.3” (Miller et al. 2010) as described in Richards et al. (2017). Sequence divergence analyses were conducted in MEGA 5.2.2 (Tamura et al. 2011) by calculating *p*-distance. Alignments were cropped at the 5' and 3' ends prior to divergence analyses to remove missing data. Scanning electron microscopy (SEM) was performed as described in Richards et al. (2016).

Table 1. List of collection information, GenBank numbers, and reference information for sequences of taxa included in phylogenetic analyses.

Taxon	Voucher no.	Locality	Latitude	Longitude	Date	Depth (m)	Reference	GenBank accession no.			
								<i>psbA</i>	UPA	COI	LSU
<i>Mesophyllum erubescens</i>	LAF D1939	Bright Bank	27°53.418'N	093°18.219'W	25.v.2000	39	Present study	MN966834	MN966838	MN958887	MT025827
	LAF 7326 (Dive 700)	East Flower Garden Bank	27°56.314'N	093°36.027'W	24.ix.2018	52	Present study	—	—	—	MT025828
	LAF 7380	Ewing Bank	23°05.654'N	091°01.646'W	16.v.2019	56	Present study	MN966833	—	MN958886	MT025829
	LAF 7385	Ewing Bank	23°05.654'N	091°01.646'W	16.v.2019	56	Present study	MN966836	—	—	MT025830
	LAF 7386	Bright Bank	27°53.660'N	093°18.620'W	18.v.2019	56–57	Present study	MN966837	—	—	MT025831
	LAF 7459 (Dive 803)	East Flower Garden Bank	27°56.314'N	093°36.027'W	18.ix.2019	53	Present study	—	MN966839	—	—
	LAF 7323 (MS #13)	Arvoredo Island, SC, Brazil	23°58.000'S	046°10.077'W	17.i.2011	7–8	Present study	—	MN966840	—	MT025832
	LAF 7324 (MS #13)	Arvoredo Island, SC, Brazil	23°58.000'S	046°10.077'W	17.i.2011	7–8	Present study	—	MN966841	—	MT025833
	LAF 6921	Richardson Ocean Park, Hilo, Hawai'i	19°44.150'N	155°00.833'W	26.v.2013	1–2	Present study	MN966835	MN966842	MN958888	MT025834
	ARS 02835	O'ahu, Hawai'i	21°33.456'N	157°51.360'W	—	—	Sherwood et al. 2010	—	HQ420979	HQ422717	HQ421812
	ARS 02826	Lana'i, Hawai'i	20°54.87'N	156°54.00'W	—	—	Sherwood et al. 2010	—	HQ420974	HQ422718	HQ421803
	FLOR 14896	Fernando de Noronha, Brazil	03°51.1368'S	032°25.2562'W	08.viii.2013	—	Sissini et al. 2014	—	—	—	—
	FLOR 14919	Arvoredo Island, Brazil	23°58.000'S	046°10.077'W	28.xi.2012	—	Sissini et al. 2014	—	—	—	—
	FBCS 12791	Veracruz, Mexico	19°10.857'N	096°08.574'W	16.x.2012	—	Sissini et al. 2014	—	—	—	—
<i>Mesophyllum sphaericum</i>	CPNP 776	Galicia, Spain	42°36.036'N	008°52.459'W	14.x.2008	3	Pardo et al. 2014	KC819262	—	KC861526	—
	LBC 0001	France	47°38.3430'N	003°25.0002'E	01.viii.2007	—	Bittner et al. 2011	G0917436	—	G0917247	G0917309
<i>Phymatolithon calcareum</i>	BM 712373	Cornwall, United Kingdom	50°09.1544'N	005°03.9762'E	11.xii.1983	—	Peña et al. 2014, Hernández-Kantún et al. 2015	J0896231	—	KF808323	—

Results

Mesophyllum erubescens (Foslie) Me. Lemoine

New records. USA; offshore Louisiana; Ewing Bank; 23°05.654'N, 091°01.646'W; 56 m; 16 May 2019; collected by S. Fredericq, W.E. Schmidt, R.P. Kittle III; 2 individuals (vouchers LAF 7380, LAF 7385, tetrasporophytes). USA; offshore Louisiana–Texas border; Bright Bank; 27°53.660'N, 093°18.620'W; 56–57 m; 16 May 2019; collected by S. Fredericq, W.E. Schmidt, R.P. Kittle III; 1 individual (voucher LAF 7386). USA; offshore Louisiana–Texas border; Bright Bank; 27°53.418'N, 093°18.219'W; 39 m; 25 May 2000; collected by S. Fredericq, Brigitte Gavio; 1 individual (voucher LAF D1939). USA; offshore Texas; East Flower Garden Bank; 27°56.314'N, 093°36.027'W; 52 m; 24 September 2018; collected by S. Fredericq, J.L. Richards, R.P. Kittle III, Dijel Fuselier; 1 individual (voucher LAF 7326, tetrasporophyte). USA; offshore Texas; East Flower Garden Bank; 27°56.314'N, 093°36.027'W; 53 m; 18 September 2019; collected by S. Fredericq, J.L. Richards; 1 individual (voucher LAF 7459, tetrasporophyte). USA; Hawai'i; Hawai'i Island; Richardson Ocean Park, Hilo; 19°44.15'N, 155°00.833'W; 1–2 m (collected by snorkeling); 26 May 2013; collected R.P. Kittle III; 1 individual (voucher LAF 6921, tetrasporophyte). See Table 1 for collection information and GenBank accession numbers corresponding to specimen voucher numbers and Figure 1 for distribution map.

Identification. The identification of specimens was confirmed by analysis of DNA sequences (Fig. 2), including sequences of specimens whose identifications were previously verified by comparisons to type material. *PsbA* sequences of NWGMx specimens were 0–0.1% divergent from sequences of Brazilian specimens, and

NWGMx and Brazilian specimens were 0.3–0.4 % divergent from the Hawaiian specimen. UPA sequences of the NWGMx specimens were identical to the Brazilian specimens, and 0.3% divergent from the Hawaiian specimens. LSU sequences of the NWGMx, Brazilian, and Hawaiian specimens were all identical to each other. COI sequences of the NWGMx specimens were 3.4–3.7 % divergent from the Hawaiian specimens.

Observation of habit and SEM imaging (Fig. 3) showed characters congruent with *M. erubescens*, e.g., protuberant habit (Fig. 3A), presence of cell fusions (Fig. 3B), lack of secondary pit connections, a single layer of non-armored (ie. not “flared”) epithallial cells (Fig. 3C), and abundant multiporate conceptacles (Fig. 3D–G). Conceptacle roofs flat to slightly rounded (Fig. 3D, F, G.), with pore canals showing apical pore plugs (Fig. 3E). Longitudinal sections of protuberances showed radial construction and layers of multiporate conceptacles that became infilled with adventitious vegetative cells after spore release (Fig. 3F, G).

Discussion

Results of the ML analyses (Fig. 2) show *Mesophyllum erubescens* is present in mesophotic rhodolith beds offshore Louisiana and Texas in the NWGMx. Specimens were collected at Ewing Bank, Bright Bank, and East Flower Garden Bank in the FGBNMS. These are the first confirmed reports of *M. erubescens* in the northern Gulf of Mexico. Minnery (1990) reported *Mesophyllum* sp. from the FGBNMS, but did not list a specific epithet. The image in Minnery (1990: 998, fig. 5I), shows an algal nodule from West Flower Garden Bank that may correspond to *M. erubescens*, considering that the image shows layers of overgrown conceptacles infilled with adventitious vegetative cells. *Mesophyllum erubescens*

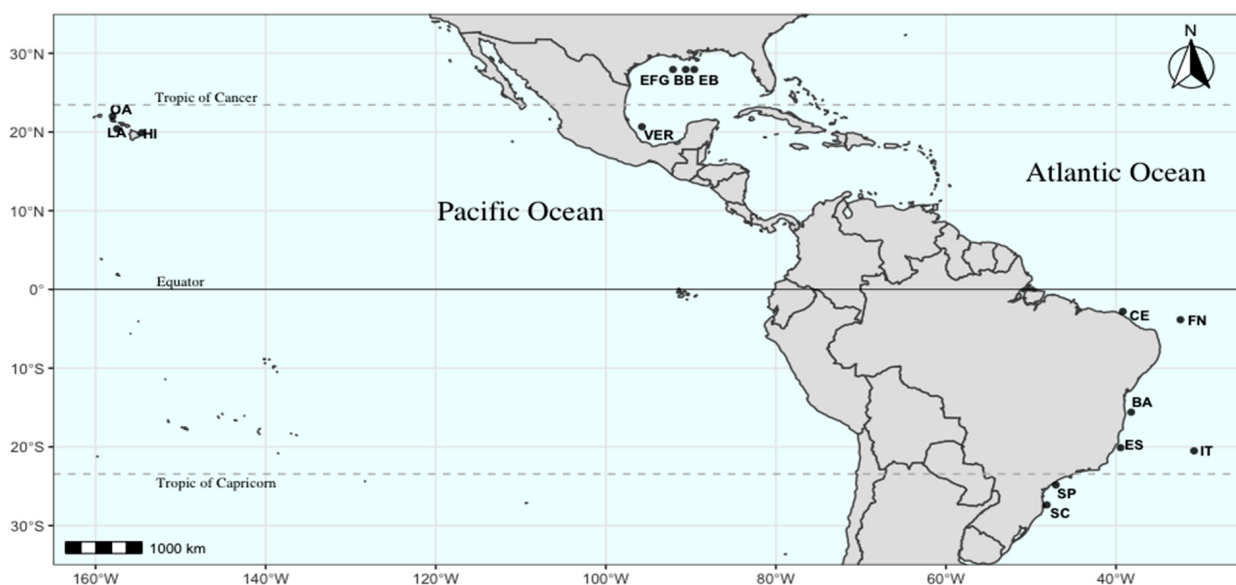


Figure 1. Distribution map showing records of *Mesophyllum erubescens* verified by DNA sequence analyses. EFG = East Flower Garden Bank; BB = Bright Bank; EB = Ewing Bank; VER = Veracruz; HI = Hawai'i; LA = Lāna'i; OA = O'ahu; CE = Ceará; FN = Fernando de Noronha; BA = Bahia; ES = Espírito Santo; IT = Trindade Island; SP = São Paulo; SC = Santa Catarina.

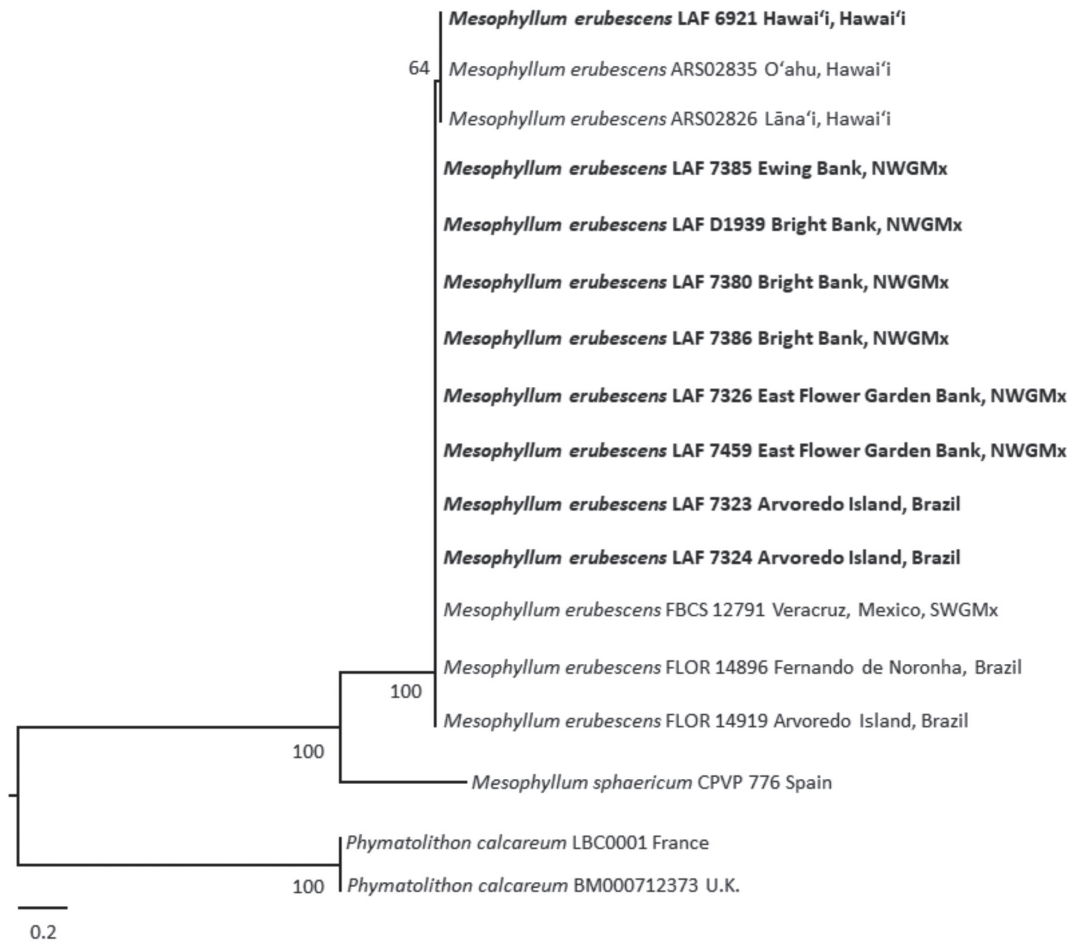


Figure 2. Maximum likelihood phylogenetic analyses of concatenated *psbA*, *UPA*, *COI*, and *LSU* (2,414 bp) DNA sequences of *Mesophyllum erubescens* and *Mesophyllum sphaericum*, with *Phymatolithon calcareum* as outgroup. Sequences shown in bold are newly generated in this study. Numbers at nodes are bootstrap values (1,000 replicates). NWGMx = northwestern Gulf of Mexico; SWGMx = southwestern Gulf of Mexico.

was recently placed in a new genus, *Melyvonnea* Athanasiadis & D.L.Ballantine, along with a few other species of *Mesophyllum* (Athanasiadis and Ballantine 2014). Because there are no DNA sequences available of the generitype, *Melyvonnea canariensis*, we here retained *M. erubescens* in *Mesophyllum* pending further molecular evidence.

Reports based on DNA sequence analyses show that the known distribution of *Mesophyllum erubescens* currently includes Brazil, the southwestern Gulf of Mexico (SWGMx), the NWGMx, and Hawai'i (Fig. 1) (Sherwood et al. 2010; Sissini et al. 2014; Jesionek et al. 2016; present study). Sissini et al. (2014) noted that the identification of the Hawaiian population of *M. erubescens* needs confirmation with *psbA*, *rbcL*, or *COI*. We show here in this study that *psbA* sequences of the Brazilian and NWGMx specimens were only 0.3–0.4% divergent (2–3 base pairs) from the Hawaiian specimen, suggesting that the Hawaiian population is conspecific with *M. erubescens*. For context, previous phylogenetic studies of taxa within the Hapalidiales have reported minimum interspecific divergence values of 0.7 % or greater for *psbA* (Adey et al. 2015; Jesionek et al. 2020). However, considerable

divergence was observed for the *COI* marker indicating that further studies need to be performed to clarify the relationship between the Pacific and Atlantic populations of this species. *COI* sequences were 3.4–3.7 % divergent between NWGMx and Hawaiian specimens, which is greater than the maximum intraspecific divergence value of 1.8% reported in a previous study for *Phymatolithon* spp. (as “infralineage variation”; Peña et al. 2015). However, Peña et al. (2014) reported that intraspecific divergence (as “infralineage variation”) between *Mesophyllum* spp. was as high as 3.24 %.

Observation of habit and SEM imaging (Fig. 3) supports the identification of these NWGMx specimens and showed characters congruent with the *Mesophyllum erubescens* description (Sissini et al. 2014). It is important to note that although these characters support the species identification, the morpho-anatomical characters alone can not be used to identify this species, because the characters are shared by other members of the Hapalidiales. For example, both *M. erubescens* and *M. sphaericum* tetrasporophytes possess protuberances with radial construction and abundant multiporate conceptacles with flat roofs that become overgrown after spore release

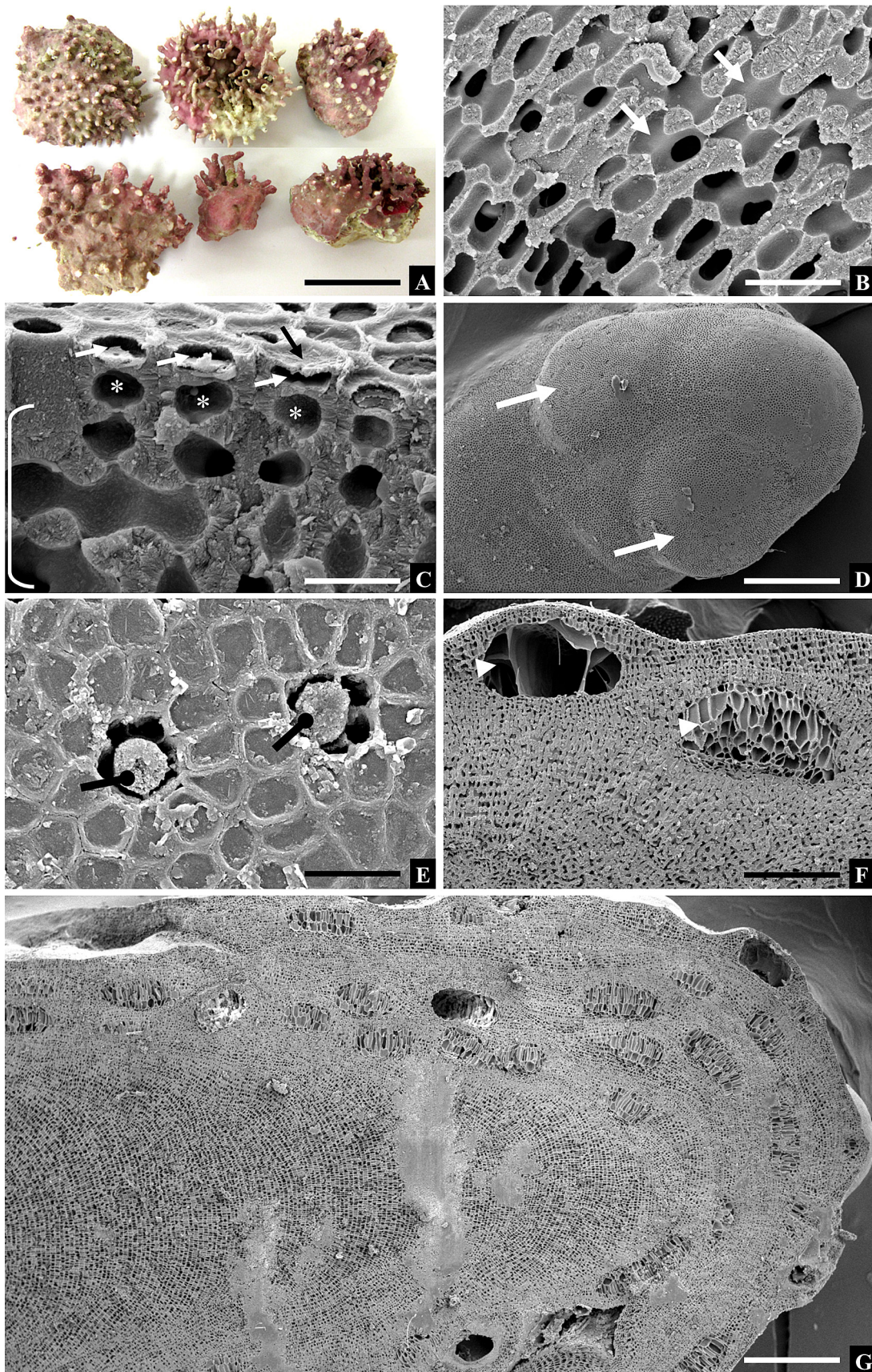


Figure 3. *Mesophyllum erubescens*. **A.** Thallus habit of northwestern Gulf of Mexico specimens. Top (left to right): LAF 7385, LAF 7326, LAF D1939. Bottom (left to right): LAF 7380, LAF 7459, LAF 7386. **B.** Perithallium with cell fusions (arrows). **C.** Partial surface view and section view showing perithallium (bracket), intercalary meristematic cells (*), and epithallial cells (white arrows), one with intact epithallial cell roof (black arrow). **D.** LAF 7326. Surface view of protuberance with multiporate conceptacles (arrows). **E.** LAF 7326. Conceptacle pores with intact apical pore plugs (circle pointers). **F.** LAF 7326. Longitudinal fracture of protuberance showing conceptacles (arrowheads), one infilled with adventitious vegetative cells (right arrowhead). **G.** LAF 7380. Longitudinal fracture of protuberance with layers of overgrown conceptacles infilled with adventitious vegetative cells. Scale bars: A = 2.5 cm; B = 27.5 μ m; C = 11 μ m; D = 280 μ m; E = 14 μ m; F = 150 μ m; G = 400 μ m.

(Horta et al. 2011; Peña et al. 2011; Sissini et al. 2014). Interestingly, empty conceptacles of *M. erubescens* become infilled with adventitious vegetative cells after spore release (Fig. 3D, E), which is different from other members of the Hapalidiales present in the NWGMx that become infilled with aragonite crystals (e.g. *Lithothamnion* spp.; Krayesky-Self et al. 2016). The findings in this study help to better delineate the true diversity and define the precise taxonomic composition of crustose coralline red algal flora of the Flower Garden Banks National Marine Sanctuary and offshore Louisiana.

Acknowledgements

This work was funded by NSF grant DEB-1754504 for rhodolith research to SF. The authors thank Emma Hickerson and FGBNMS permit no. FGBNMS-2018-007 for facilitating collections taken in the marine sanctuary. CFDG thanks CNPq grants 437115/2018-6 and 309658/2-16-0. JLR acknowledges Tom Pesacreta and Mike Purpera at the UL Lafayette Microscopy Center for help using the SEM. RPK acknowledges Karla McDermid and UH Hilo Marine Science Department (Special Activity Permit SAP 2013-27). We thank the crews of the R/V *Pelican* and R/V *Manta* for help with sampling, and Jason White and Eric Glidden from the University of North Carolina Wilmington-Undersea Vehicle Program (UNCW-UVP) for ROV-collections at the FGBNMS. We also thank Marina Sissini for the Brazilian collections (SISGEN # R8B145D) and the three reviewers of this article for their helpful comments and suggestions.

Authors' Contributions

JLR, RPK, and SF conceived the idea for the project. JLR, RPK, DF, WES, CFDG and SF assisted in specimen collection. JLR, JA, CFDG generated SEM data; JLR, RPK, JA, and DF generated DNA sequence data. JLR, RPK, JA, DF and WES analyzed and interpreted the data. RPK generated the distribution map. JLR, RPK, CFDG, WES, and SF wrote the manuscript. All authors critically reviewed the final manuscript.

References

- Adey, WH, Hernandez-Kantun, JJ, Johnson, G, Gabrielson, PW (2015) DNA sequencing, anatomy, and calcification patterns support a monophyletic, subarctic, carbonate reef-forming *Clathromorphum* (Hapalidiaceae, Corallinales, Rhodophyta). *Journal of Phycology* 51 (1): 189–203. <https://doi.org/10.1111/jpy.12266>
- Altschul, SF, Gish, W, Miller, W, Myers, EW, Lipman, DJ (1990) Basic local alignment search tool. *Journal of Molecular Biology* 215 (3): 403–410. [https://doi.org/10.1016/S0022-2836\(05\)80360-2](https://doi.org/10.1016/S0022-2836(05)80360-2)
- Athanasiadis A, Ballantine DL (2014) The genera *Melyvonnea* gen. nov. and *Mesophyllum* s.s. (Melobesioideae, Corallinales, Rhodophyta) particularly from the central Atlantic Ocean. *Nordic Journal of Botany* 32 (4): 385–436. <https://doi.org/10.1111/njb.00265>
- Bittner L, Payri CE, Maneveldt GW, 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 (3): 697–713. <https://doi.org/10.1016/j.ympev.2011.07.019>
- Fredericq S, Cho TO, Earle SA, Gurgel CF, Krayesky DM, Mateo-Cid LE, Mendoza González AC, Norris JN, Suárez AM (2009) Seaweeds of the Gulf of Mexico. In: Felder DL, Camp DK (Eds) *Gulf of Mexico: its Origins, waters, and biota*. I. Biodiversity. Texas A&M University Press, 187–259.
- Fredericq S, Krayesky-Self S, Sauvage T, Richards J, Kittle R, Arakaki N, Hickerson E, Schmidt WE (2019) The critical importance of rhodoliths in the life cycle completion of both macro- and microalgae, and as holobionts for the establishment and maintenance of biodiversity. *Frontiers in Marine Science* 5: 502. <https://doi.org/10.3389/fmars.2018.00502>
- Hernández-Kantún JJ, Riosmena-Rodríguez R, Hall-Spencer JM, Peña V, Maggs CA, Rindi, F (2015) Phylogenetic analysis of rhodolith formation in the Corallinales (Rhodophyta). *European Journal of Phycology* 50 (1): 46–61. <https://doi.org/10.1080/09670262.2014.984347>
- Horta PA, Scherner F, Bouzon ZL, Riosmena-Rodrigues R, Oliveira ECD (2011) Morphology and reproduction of *Mesophyllum erubescens* (Foslie) Me. Lemoine (Corallinales, Rhodophyta) from southern Brazil. *Brazilian Journal of Botany* 34 (1): 125–134. <https://doi.org/10.1590/S0100-84042011000100011>
- Joyce, EA, Williams J (1969) Rationale and pertinent data. *Memoirs of the Hourglass Cruises* 1 (1): 11–50.
- Jesionek MB, Bahia RG, Lyra MB, Leão LA, Oliveira MC, Amado-Filho GM (2020) Newly discovered coralline algae in southeast Brazil: *Tectolithon fluminense* gen. et sp. nov. and *Crustaphytum atlanticum* sp. nov. (Hapalidiales, Rhodophyta). *Phycologia* 59 (2): 101–115. <https://doi.org/10.1080/00318884.2019.1702320>
- Jesionek MB, Bahia RG, Hernández-Kantún JJ, Adey WH, Yoneshigue-Valentin Y, Longo LL, Amado-Filho GM (2016) A taxonomic account of non-geniculate coralline algae (Corallinophycidae, Rhodophyta) from shallow reefs of the Abrolhos Bank, Brazil. *Algae* 31 (4): 317–340. <https://doi.org/10.4490/algae.2016.31.11.16>
- Krayesky-Self S, Richards JL, Rahmatian M, Fredericq S (2016) Aragonite infill in overgrown conceptacles of coralline *Lithothamnion* spp. (Hapalidiaceae, Hapalidiales, Rhodophyta): new insights in biomineralization and phylomineralogy. *Journal of Phycology* 52 (2): 161–173. <https://doi.org/10.1111/jpy.12392>
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010. New Orleans, LA, 1–8.
- Minnery GA (1990) Crustose coralline algae from the Flower Garden Banks, Northwestern Gulf of Mexico; controls on distribution and growth morphology. *Journal of Sedimentary Research* 60 (6): 992–1007. <https://doi.org/10.1306/d4267663-2b26-11d7-864800102c1865d>
- Minnery GA, Rezak R, Bright TJ (1985) Depth zonation and growth form of crustose coralline algae: Flower Garden Banks, Northwestern Gulf of Mexico. In: Toomey DF, Titecki MH (Eds) *Paleoalgology: contemporary research and applications* Springer-Verlag, Berlin, 238–246.
- National Center for Biotechnology Information, US National Library of Medicine. Bethesda MD. <https://www.ncbi.nlm.nih.gov/>
- Pardo C, Lopez L, Peña V, Hernández-Kantún J, Le Gall L, Bárbara I, Barreiro R (2014) A multilocus species delimitation reveals a striking number of species of coralline algae forming maerl in the OSPAR maritime area. *PLoS ONE* 9: e104073. <https://doi.org/10.1371/journal.pone.0104073>
- Peña V, Adey WH, Riosmena-Rodríguez R, Jung MY, Afonso-Carrillo J, Choi HG, Barbara I (2011) *Mesophyllum sphaericum* sp. nov. (Corallinales, Rhodophyta): a new maerl-forming species from the northeast Atlantic. *Journal of Phycology* 47 (4): 911–927. <https://doi.org/10.1111/j.1529-8817.2011.01015.x>

- Peña V, Hernández-Kantún JJ, Grall J, Pardo C, López L, Bárbara I, Le Gall L, Barreiro R (2014) Detection of gametophytes in the maerl-forming species *Phymatolithon calcareum* (Melobesioideae, Corallinales) assessed by DNA barcoding. *Cryptogamie, Algologie* 35 (1): 15–25. <https://doi.org/10.7872/crya.v35.iss1.2014.15>
- Peña V, Pardo C, López L, Carro B, Hernandez-Kantun J, Adey WH, Barreiro R, Le Gall L. (2015) *Phymatolithon lusitanicum* sp. nov. (Hapalidiales, Rhodophyta): the third most abundant maerl-forming species in the Atlantic Iberian Peninsula. *Cryptogamie, Algologie* 36 (4): 429–459. <https://doi.org/10.7872/crya/v36.iss4.2015.429>
- R Core Team (2019) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Rezak R, Bright TJ, McGrail DW (1985) Reefs and banks of the Northwestern Gulf of Mexico: their geological, biological, and physical dynamics. Wiley, New York, 259 pp.
- Richards JL, Gabrielson PW, Fredericq S (2014) New insights into the genus *Lithophyllum* (Lithophylloideae, Corallinales, Corallinales) from deepwater rhodolith beds offshore the NW Gulf of Mexico. *Phytotaxa* 190 (1): 162–175. <https://doi.org/10.11646/phytotaxa.190.1.11>
- Richards JL, Vieira-Pinto T, Schmidt WE, Sauvage T, Gabrielson PW, Oliveira MC, Fredericq S (2016) Molecular and morphological diversity of *Lithothamnion* spp. (Hapalidiales, Rhodophyta) from deepwater rhodolith beds in the Northwestern Gulf of Mexico. *Phytotaxa* 278 (2): 81–114. <https://doi.org/10.11646/phytotaxa.278.2.1>
- Richards JL, Sauvage T, Schmidt WE, Fredericq S, Hughey JR, Gabrielson PW (2017) The coralline genera *Sporolithon* and *Heydrichia* (Sporolithales, Rhodophyta) clarified by sequencing type material of their genotypes and other species. *Journal of Phycology* 53 (5): 1044–1059. <https://doi.org/10.1111/jpy.12562>
- Richards JL, Fredericq S (2018) *Sporolithon sinismexicanum* sp. nov. (Sporolithales, Rhodophyta): a new rhodolith-forming species from deepwater rhodolith bed in the Gulf of Mexico. *Phytotaxa* 350 (2): 135–46. <https://doi.org/10.11646/phytotaxa.350.2.2>
- Richards JL, Bahia RG, Jesionek MB, Fredericq S (2019) *Sporolithon amadoi* sp. nov. (Sporolithales, Rhodophyta), a new rhodolith-forming non-geniculate coralline alga from offshore the north-western Gulf of Mexico and Brazil. *Phytotaxa* 423 (2): 49–67. <https://doi.org/10.11646/phytotaxa.423.2.1>
- Sherwood AR, Kurihara A, Conklin KY, Sauvage T, Presting GG (2010) The Hawaiian Rhodophyta Biodiversity Survey (2006–2010): a summary of principal findings. *BMC Plant Biology* 10 (1): 258. <https://doi.org/10.1186/1471-2229-10-258>
- Sissini MN, Oliveira MC, Gabrielson PW, Robinson NM, Okolodkov YB, Riosmena-Rodríguez R, Horta PA (2014) *Mesophyllum erubescens* (Corallinales, Rhodophyta)—so many species in one epithet. *Phytotaxa* 190 (1): 299–319. <https://doi.org/10.11646/phytotaxa.190.1.18>
- Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22 (21): 2688–2690. <https://doi.org/10.1093/bioinformatics/btl446>
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28 (10): 2731–2739. <https://doi.org/10.1093/molbev/msr121>
- Wickham H. (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, 1–260 pp.