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Meridiolithothamnion atlanticum gen. et sp. nov. (Hapalidiales, Rhodophyta), a rhodolith-forming non-geniculate coralline alga from Brazil and offshore the northern Gulf of Mexico

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Abstract

DNA sequence analysis of plastid-encoded *psb*A and *rbc*L loci of rhodolith-forming specimens of Hapalidiales from Brazil and the NW and NE Gulf of Mexico revealed them to belong to an unnamed species in a herein newly described genus named *Meridiolithothamnion atlanticum gen. et sp. nov.* that is sister to *Boreolithothamnion* (Hapalidiaceae). Detailed morpho-anatomical examination supports its taxonomic uniqueness, highlighting specific combination of vegetative and reproductive structures, including distinctive balloon-like basal pore canal cells within the tetrasporangial conceptacles. This genus contributes to understanding the biodiversity and biogeographic linkages of marine algae across the Western Atlantic, suggesting connectivity between Brazil and Gulf of Mexico regions.

Key words: biogeography, intertidal, isthmus of Panama, marine algae, marine biodiversity, mesophotic, salt dome, seaweeds

Abbreviations: BI = Bayesian Inference; GB = GenBank; ML = Maximum Likelihood; NWGMx = Northwestern Gulf of Mexico; NEGMx = Northeastern Gulf of Mexico; SEM = Scanning Electron Microscope.

Introduction

Over the past decade, coralline red macroalgal taxonomy, including the identification of new species in Brazil and in the northern region of the Gulf of Mexico, has been assisted by DNA sequencing analyses combined with morpho-anatomical studies. This combined morphological and molecular approach continues to reveal a wealth of species diversity that has yet to be fully described (Bahia *et al.* 2014, Richards *et al.* 2014, 2016, Vieira-Pinto *et al.* 2014, Leão *et al.* 2024). Interestingly, previous studies have shown that some species found in Brazil are also present in the Gulf of Mexico. Examples of species found in both in Brazil and in the Gulf of Mexico that have been confirmed by molecular evidence include *Melyvonnea erubescens* (Foslie) Athanasiadis & D.L. Ballantine (Hapalidiales) (reported from tropical northeastern and subtropical southeastern regions of Brazil), *Sporolithon amadoi* J.L. Richards & R.G. Bahia (Sporolithales), (reported from the tropical northeastern region of Brazil), and *Roseolithon occidentaleatlanticum* J.L. Richards & Fredericq (reported from the subtropical southeastern region of Brazil) (Sissini *et al.* 2014, 2022; Richards *et al.* 2019, 2020, Coutinho *et al.* 2021, Richards *et al.* 2022). Also, within the Corallinales, *Lithophyllum atlanticum* Vieira-Pinto, M.C. Oliveira & P.A. Horta (Corallinales) showed a similar distribution and has been recorded in both tropical (northeastern) and subtropical (southeastern) regions of Brazil as well as offshore North Carolina, U.S.A. (Sissini *et al.* 2014, 2022; Richards *et al.* 2018; Horta & Sissini 2024).

The Hapalidiaceae has been shown to be exceptionally species-rich, and numerous genera and species have been,

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and continue to be, described for this family. For example, Coutinho *et al.* (2022) recently described *Roseolithon*, which now includes 13 described species distributed worldwide. Richards *et al.* (2016) employed multi-locus DNA sequencing analyses of newly collected specimens and previously published sequences and demonstrated that the genus *Lithothamnion* was polyphyletic. The study showed that specimens from the Gulf of Mexico identified as *Lithothamnion* based on morpho-anatomy comprised numerous clades within the Hapalidiaceae (Richards *et al.* 2016). Gabrielson *et al.* (2023) clarified the status of the genus *Lithothamnion* by sequencing the generitype material (type locality Victoria, Australia) and showed that *Lithothamnion* is monophyletic, but exhibiting a distribution restricted in range to the Southern Hemisphere. Northern hemisphere species previously included in *Lithothamnion* were thus transferred to a newly erected genus, *Boreolithothamnion* (Gabrielson *et al.* 2023).

Richards *et al.* (2016) showed that a species (tentatively assigned as "*Lithothamnion* sp. I") from offshore NW Louisiana and NE Florida in the Gulf of Mexico was also present in northeastern Brazil. Phylogenetic analyses of single loci and concatenated alignments of *psb*A, COI, LSU and UPA showed this species did not form a clade with the other northern hemisphere species that are now placed in *Boreolithothamnion*, and that "*Lithothamnion* sp. I" instead formed a clade with a specimen from Pacific Panama (tentatively assigned as "*Lithothamnion* sp. J"). This clade comprised of "*Lithothamnion* spp. I and J" was fully supported in the concatenated analyses (Richards *et al.* 2016, pp. 93 fig 3.), but it was shown to be paraphyletic with respect to the clades *Boreolithothamnion* and *Phymatolithon* and the branching between these three clades was not resolved.

Ongoing DNA sequencing and analysis efforts from Brazilian collections identified additional specimens of "*Lithothamnion* sp. I" based on identical sequences of *psb*A. Herein, we describe this clade as a new genus of non-geniculate coralline algae within the family Hapalidiaceae and describe and characterize a new species from the Gulf of Mexico and Brazil.

Materials & Methods

Specimen collection. Gulf of Mexico non-geniculate coralline algal specimens were collected offshore Louisiana and Florida according to the protocols previously described in Richards *et al.* (2016). Brazilian non-geniculate coralline algal specimens were manually collected through SCUBA diving in the northeastern states of Ceará and Bahia (Richards *et al.* 2016), as well as in the southeastern state of Rio de Janeiro.

DNA extraction and sequencing. For Gulf of Mexico specimens (Table 1), genomic DNA was extracted and the chloroplast-encoded *psb*A (encodes photosystem II reaction center protein D1) and *rbc*L (encodes the large subunit of the enzyme ribulose l,5-bisphosphate carboxylase/oxygenase) genes were both sequenced according to protocols and primer combinations specified in Richards *et al.* (2014). For southeastern Brazil specimens (Table 1), the chloroplast-encoded *psb*A gene was selected for DNA analysis and was sequenced following the protocol used by Jesionek *et al.* (2020). DNA was extracted using Qiagen DNeasy Blood and Tissue Kit® (Qiagen, Crawley, UK) following a modified protocol described in Broom *et al.* (2008). The *psb*A gene was amplified using primers *psb*AF and *psb*AR2 (Yoon *et al.* 2002). Sequences were obtained commercially in Macrogen using the same primers of amplification.

TABLE 1. List of holotype, isotype, and paratype specimens of *Meridiolithothamnion atlanticum* with *psb*A, *rbc*L and LSU accession numbers in GenBank. Species, collection information and GenBank accession numbers in bold were determined for newly sequenced specimens in this study.

Species	psbA	rbcL	LSU	UPA	Collection information	Reference
***Meridiolithothamnion atlanticum* (Holotype)**	**PP929785**	-	-	-	**Saco do Cherne, Arraial do Cabo, Rio de Janeiro, Brazil, coll. R.G. Bahia (05. i.2016, RB 868638)**	**This study**
Meridiolithothamnion atlanticum	**PP977086**	-	-	-	**Papagaios Island, Cabo Frio, Rio de Janeiro, Brazil, coll. R. G. Bahia (08.i.2016, RB 868640)**	**This study**

...continued on the next page

TABLE 1. (Continued)

Species	psbA	rbcL	LSU	UPA	Collection information	Reference
Meridiolithothamnion atlanticum **(Isotype)**	**PP977087**	**-**	**-**	**-**	**Saco do Cherne, Arraial do Cabo, Rio de Janeiro, Brazil, coll. R.G. Bahia (05. i.2016, RB 868639)**	**This study**
Meridiolithothamnion atlanticum **(as "Lithothamnion sp. I" in Richards** ***et al.*****, 2016)**	**KP844864**	**PQ505128**	**KR075890**	**KU504274**	**Ewing Bank, NWGMx, coll. J. L. Richards (16.xi.2012, LAF6521)**	**This Study and Krayesky-Self** ***et al.*** **(2016), Richards** ***et al.*** **(2016)**
Meridiolithothamnion atlanticum (as "Lithothamnion sp. I" in Richards *et al.*, 2016)	KP844863	-	KR075888	KU504273	Florida Middle Grounds, NEGMx, coll. J. L. Richards (5.vii.2006, LAF1437A)	Krayesky-Self *et al.* (2016), Richards *et al.* (2016)
Meridiolithothamnion atlanticum (as "Lithothamnion sp. I" in Richards *et al.*, 2016)	-	-	KR075889	-	Florida Middle Grounds, NEGMx, coll. J. L. Richards (5.vii.2006, LAF1437B)	Richards *et al.* (2016)
Meridiolithothamnion atlanticum (as "Lithothamnion sp. I" in Richards *et al.*, 2016)	KU529477	-	-	KU519741	Banco da Panela, Salvador, Bahia, Brazil, coll. T. Vieira-Pinto, C. Azevedo, B. Torrano-Silva, M. Jamas (22. v.2013, SPF57882)	Richards *et al.* (2016)
Meridiolithothamnion atlanticum (as "Lithothamnion sp. I" in Richards *et al.*, 2016)	KU529478	-	-	-	Banco da Panela, Salvador, Bahia, Brazil, coll. T. Vieira-Pinto, C. Azevedo, B. Torrano-Silva, M. Jamas (22. v.2013, SPF 57883)	Richards *et al.* (2016)
Meridiolithothamnion atlanticum (as "Lithothamnion sp. I" in Richards *et al.*, 2016)	KU529479	-	-	-	Cabeço do Arrastado, Fortaleza, Ceará, Brazil, coll. M. Sissini & R. Morais (19. iv.2012, SPF57884)	Richards *et al.* (2016)

Sequence alignment and analysis.

The sequences obtained for the *psb*A gene of the Rio de Janeiro specimens were assembled and edited in BioEdit 7.2 and the sequence dataset for the *psb*A and *rbc*L analysis was built and aligned in MEGA6 (Tamura *et al.* 2013) using the ClustalW tool (Thompson *et al.* 1994; Larkin *et al.* 2007). The phylogenetic relationships between taxa were inferred using Maximum Likelihood (ML) performed with RAxML 8 (Stamatakis 2014) via the online analysis workbench CIPRES Science Gateway (Miller *et al.* 2010) with a bootstrap of 1,000 replicates (Felsenstein 1985) in IQTREE v2.3.4, and Bayesian Inference (BI) with four Monte Carlo–Markov chains in Mr. Bayes (Huelsenbeck, & Ronquist 2001), both using with a GTR+I+G model. For the Bayesian Inference analysis, 6 million generations were launched. The trees were sampled every 1,000 generations and trees saved after the first 1,500,000 generations were discarded as burn-in. The ML and BI Sequence database used were composed by the type sequences (i.e, holotype, isotype and the paratypes) and other sequences from Genbank: 37 for *psb*A and 43 for *rbc*L (Table S1). Pair-wise genetic distances were calculated using the p-distance in MEGA6 (Tamura *et al.* 2013).

Microscopy analysis. Gulf of Mexico specimens were fractured with a single-edge razor blade, mounted on metal stubs using conductive adhesive, and viewed with a Hitachi S-3000N scanning electron microscope (SEM) following the protocols of Richards *et al.* (2016). Specimens from southeastern Brazil were analyzed and imaged using embedding and sectioning methods as described by Maneveldt & van der Merwe (2012). Light microscopy analysis was performed with an Olympus BX43 microscope equipped with a digital camera. SEM analysis followed the methodology of Bahia *et al.* (2010) and was conducted using a Zeiss SEM EVO 40.

Growth forms were described following Woelkerling *et al.* (1993). Cell dimensions were measured from all images, following the methodology described in Maneveldt *et al*. (2017), except for medullary and cortical cells, for which 20-30 cells were measured per image. All mature conceptacles – both multiporate and uniporate – were measured individually, according to the criteria established by Adey & Adey (1973). Vegetative features were assessed in all specimens.

Results

Molecular Results

We generated three new *psb*A sequences from southeastern Brazil specimens and one new *rbc*L sequence from a NWGMx specimen herein described as *Meridiolithothamnion atlanticum*. ML and BI *psb*A results showed that the specimens from Brazil, the NWGMx, and NEGMx form a highly supported clade, which is also shown to be sister to the clade of the recently described species from the genus *Boreolithothamnion*, representing the new species and genus *Meridiolithothamnion atlanticum* (Fig. 1). This clade was also supported in the ML and BI analyses of *rbc*L (Fig. 2).

Meridiolithothamnion gen nov. J. Richards & Leão

Description: Thalli non-geniculate, pseudoparenchymatous, dorsiventral organization, construction monomerous non-coaxial; warty to fruticose in growth form, growing freely, unattached as rhodoliths. Filaments of medullary region composed of rounded to cylindrical cells. Cortical region is composed of filaments with rounded to cylindrical cells. Subepithallial initials (intercalary meristematic cells) cylindrical as long as, or longer than subtending cortical cells. Epithallial cells flattened and flared with thick lateral cell walls, a thin epithallial cell roof, and trapezoidal shaped lumen. Cells of adjacent cortical filaments joined by cell fusions but secondary pit-connections absent. Tetrasporangial conceptacles multiporate; pore canals bounded by filaments with basal bounding cells that are bigger than other conceptacle roof cells and resemble "balloons". Tetrasporangia zonately divided and produce an apical plug. Putative uniporate gametangial conceptacles mostly found post-spore release and buried within the thallus.

Etymology: "Meridio" comes from the Latin "meridionalis" which means 'southern', i.e. southern US (Gulf of Mexico) and southern hemisphere (Brazil), and "*lithothamnion*" referring to the morphoanatomical similarity to the genus *Lithothamnion*.

Meridiolithothamnion atlanticum sp. nov. J. Richards & Leão (Figures 3–5)

Holotype (designated here): RB 868638: Saco do Cherne, Arraial do Cabo, Rio de Janeiro, Brazil (22° 57' 39'' S; 42° 00' 18'' W), 05.i.2016, 2–8 m deep, collected by SCUBA, *leg.* Ricardo G. Bahia

Isotypes: RB 868639: Saco do Cherne, Arraial do Cabo, Rio de Janeiro, Brazil (22° 57' 39'' S; 42° 00' 18'' W), 05.i.2016, 2–8 m deep, collected by SCUBA, *leg.* Ricardo G. Bahia.

Additional material examined (Paratypes): RB 868640: Papagaios Island, Cabo Frio, Rio de Janeiro, Brazil (22° 53' 54" S; 41° 58' 58" W), 08.i.2016, 2–15 m deep, collected by SCUBA, *leg.* Ricardo G. Bahia; LAF1437A (7-5-06-2-2A) and LAF1437B (7-5-06-2-2B) from the Florida Middle Grounds, LAF6521 (11-16-12-5-1) from Ewing Bank; SPF57882 and SPF57883 from "Banco da Panela", Salvador, Bahia, Brazil (12° 57' 58" S; 38° 31' 36" W), 22.v.2013, 10–15 m deep, collected by SCUBA, *leg.* T. Vieira-Pinto, C. Azevedo, B. Torrano-Silva, M. Jamas; "Cabeço do arrastado", Fortaleza, Ceará, Brazil (3° 35' 20.70" S; 38° 24' 27.85" W), ≤10 m deep, collected by SCUBA, leg., M. Sissini & R. Morais. See Table 1 for additional paratype specimen details.

Etymology: The specific epithet is a reference to the geographical distribution of the species, being "*atlanticum*" referencing the Atlantic Ocean.

Description

DNA sequences:—Holotype *psb*A GB accession = PP929785; Isotype *psb*A GB accessions = PP977087. See Table 1 for GB accessions for *psb*A, *rbc*L, and LSU sequences of additional material examined (Paratypes).

Habit and external thallus characterization: Thallus light pink to lilac to red, dorsiventrally organized, with warty to fruticose growth form, forming rhodolith (Figures 3A-C). Presence of short nodular protuberances 1–3 mm x 1–4 mm, length x diameter (Figures 3A & B) in warty thallus and larger and wider protuberances (3–8 mm x 2–7 mm, length x diameter) in fruticose thallus (Figure 3C).

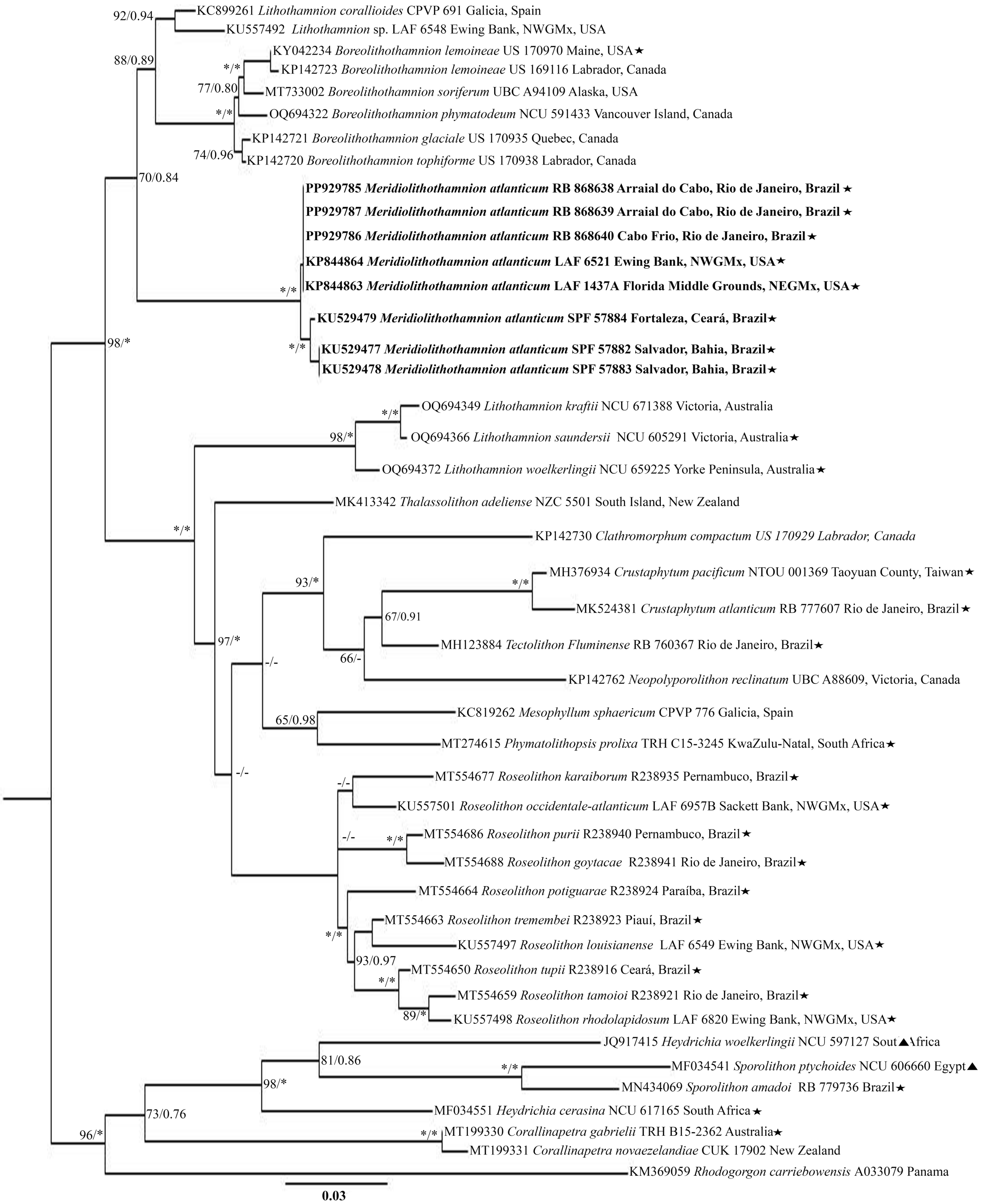

FIGURE 1. Phylogenetic tree based on ML analysis of *psb*A sequences. Numbers on branches indicate bootstrap values from ML analysis and posterior probabilities from BI analysis Specimens of *Meridiolithothamnion atlanticum* are marked in bold. Stars (★) indicate sequences from type material. Triangles (▲) denote topotypes. Bootstrap values lower than 65% and PP lower than 0.75 are not shown. * Indicates full support.

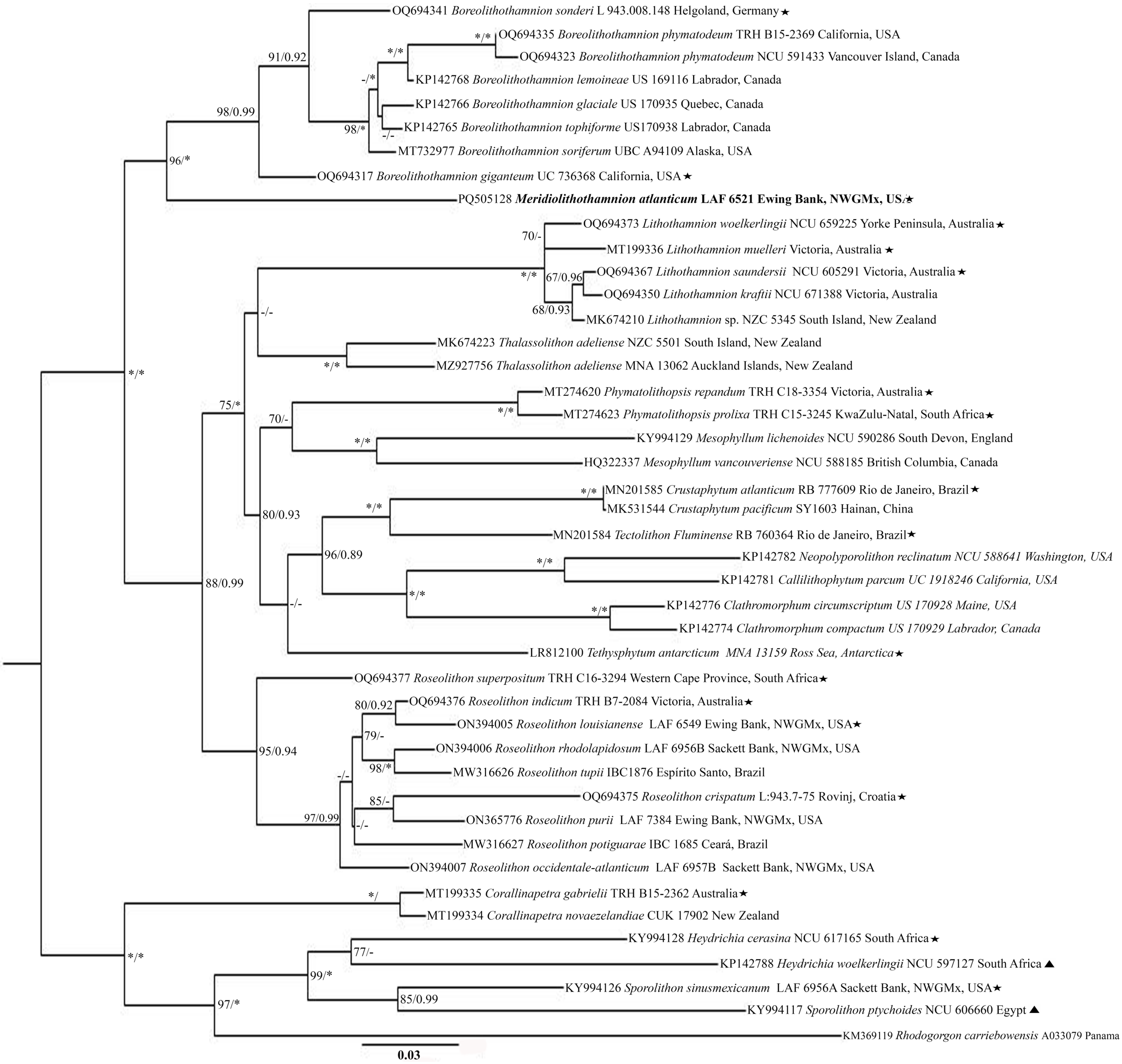

FIGURE 2. Phylogenetic tree based on ML analysis of *rbc*L sequences. Numbers on branches indicate bootstrap values from ML analysis and posterior probabilities from BI analysis Specimens of *Meridiolithothamnion atlanticum* are marked in bold. Stars (★) indicate sequences from type material. Triangles (▲) denote topotypes. Bootstrap values lower than 65% and PP lower than 0.75 are not shown. * Indicates full support.

Vegetative anatomy:—Thallus pseudoparenchymatous and non-geniculate, 100–440 µm thick. Thallus construction monomerous non-coaxial type (Figure 3D). Medullary filaments with rounded to cylindrical cells - 9–27 µm x 6–13 µm, length x diameter (Figure 3D). Cortical filaments with rounded to cylindrical cells - 5–25 µm x 4–14 µm, length x diameter (Figure 3F). Subepithallial initials (intercalary meristematic cells) cylindrical - 8–16 µm x 6–11 µm, length x diameter, as long as, longer than, or shorter subtending cortical cells (Figure 3E). Epithallial layer with cells flattened and flared - 3–6 µm x 5–9 µm, length x diameter (Figure 3E), with a trapezoidal shaped cell lumen and thin epithallial cell roofs that appear pentagonal in surface view (Figure 5D). Contiguous cortical filaments joined by cell fusions (Figure 3F). Secondary pit-connections absent.

Reproduction:—Multiporate tetrasporangial conceptacles slightly raised above the surrounding thallus surface (Figures 4A & B). Conceptacles chambers - 180–290 µm x 320–780 µm, length x diameter. Roof is 50–65 µm thick, 6–7 celled (including epithallial cells) (Figure 4D). Conceptacles pore canals bounded by filaments with cells similar in size and shape to the other conceptacle roof cells, except by the basal ones (Figure 4D) which are bigger and resemble "balloons" (Figures 4C-E). Tetrasporangia develop scattered on the conceptacle floor (Figure 4F). Tetrasporangia zonately divided - 120–175 µm x 45–70 µm, length x diameter (Figure 4F). In surface view, tetrasporangial conceptacle pores are surrounded by 6–8 rosette cells and measure 12–17 µm in diameter (Figures 4G & H).

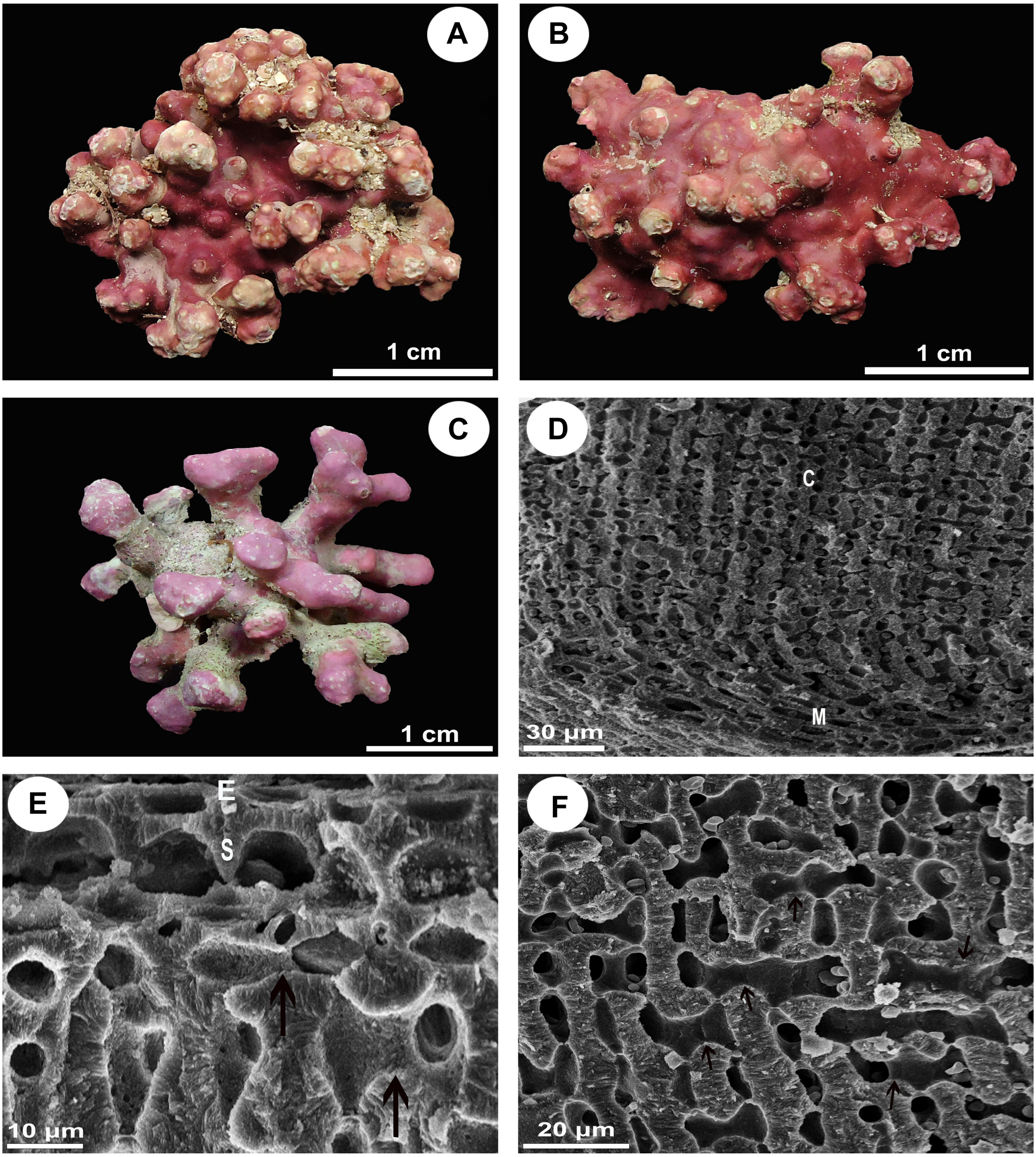

FIGURE 3 (**A–F**). External morphology and vegetative anatomy of *Meridiolithothamnion atlanticum*. (**A** and **B**) Holotype (RB 868638) and Isotype (RB 868639) specimens with warty to fruticose growth form. (**C**) Paratype (RB 868640) specimen with fruticose growth form. (**D**) SEM view of the Isotype specimen showing non-coaxial monomerous construction. M = medullary. C = cortical. (**E**) SEM view of the upper portion of the Isotype specimen thallus showing flattened and flared epithallial cells ("E") and subepithallial initials ("S") as long as or longer than subtending cells. Presence of cell fusion (black arrows) joining two subtending cells. (**F**) SEM of Paratype specimen of a vertical section showing vegetative cortical filaments. Notice that the contiguous cortical filaments are joined by cell fusions (black arrows).

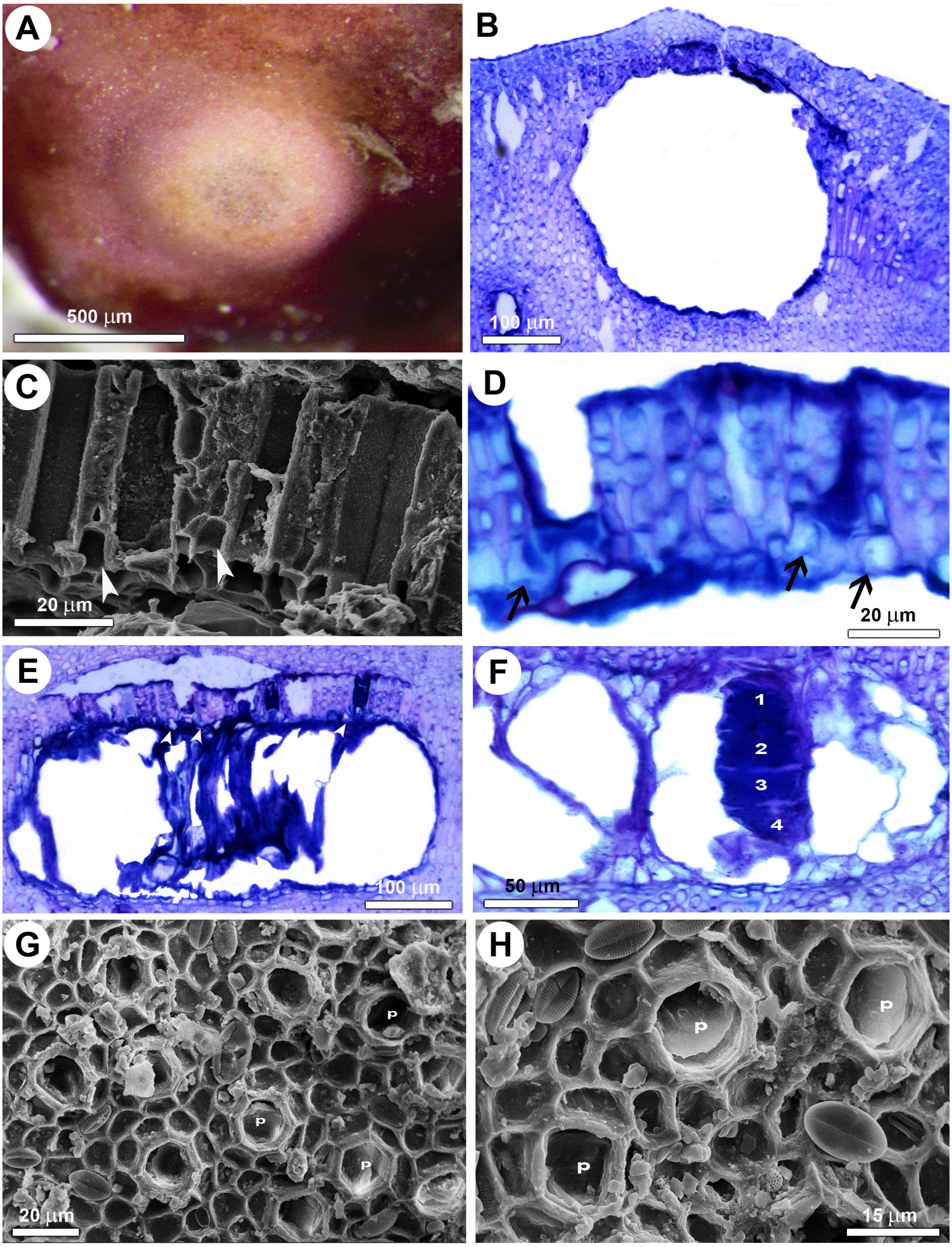

FIGURE 4 (**A–F**). Reproductive anatomy of *Meridiolithothamnion atlanticum*. (**A**) Multiporate tetrasporangial conceptacle in stereoscope microscope view, showing they are subtly elevated above the surrounding thallus surface. (**B**) Longitudinal section of the Holotype specimen showing a multiporate tetrasporangial conceptacle slightly raised above the surrounding thallus surface. (**C**) SEM view of the Paratype specimen showing multiporate tetrasporangial conceptacle pore canals evidencing the bounding cells (white arrowheads). (**D**) Longitudinal section of the Holotype specimen showing a conceptacle roof showing balloon-like pore canals basal bounding cells (black arrows), which are different in shape and size from the other conceptacle roof cells. (**E**) Longitudinal section of the Holotype specimen showing a multiporate tetrasporangial conceptacle, evidencing the presence of the basal pore canals bounding cells (white arrowheads). (**F**) Longitudinal section of the Holotype specimen showing a zonately divided tetrasporangia (1, 2, 3 and 4). (**G and H**) SEM surface views of the Isotype specimen showing the multiporate tetrasporangial conceptacle roof surface with tetrasporangial conceptacle pores ("P") surrounded by 6–8 rosette cells.

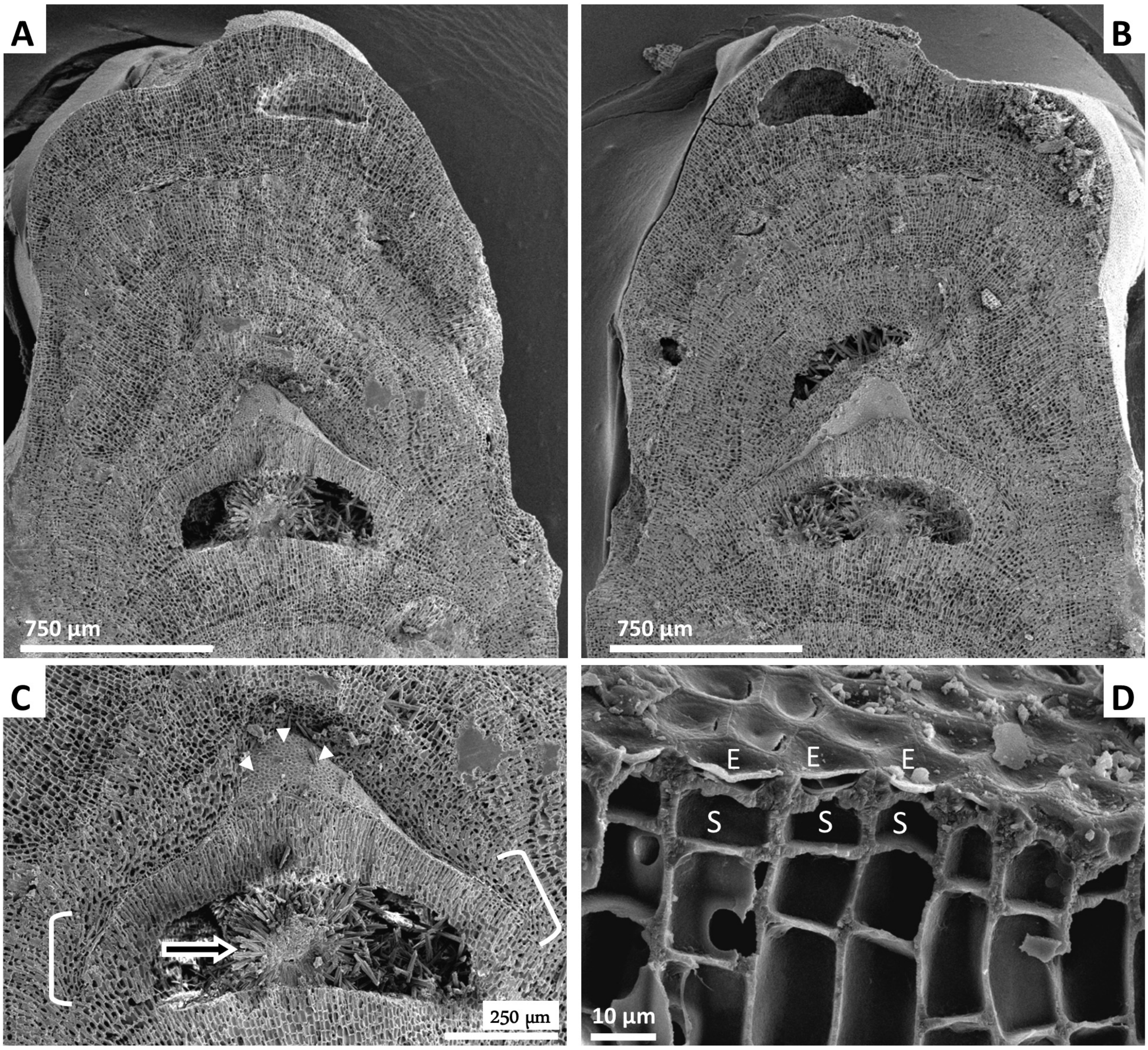

FIGURE 5 (A–D). Vegetative and reproductive anatomy of Gulf of Mexico paratype specimen (LAF1437B) of *Meridiolithothamnion atlanticum*. (A-B) Longitudinal section of thallus protuberance, each image showing mirror image views of each half of the resulting fractured fragments. (C) Magnified view of uniporate conceptacle (infilled with aragonite, arrow) that was overgrown by a secondary hypothallium (brackets) and new layers of cortical filaments. Image shows fracture with both section view and partial surface of conceptacle roof (arrowheads). (D) Section view and partial surface view showing flattened and flared epithallial cells ("E") with a trapezoidal shaped cell lumen and intact, thin epithallial cell roofs and subepithallial initials (meristematic cells) ("S") shorter than subtending cortical cells.

Vegetative remarks:—Subepithallial initials (intercalary meristematic cells) showed two distinct patterns relative to the subtending cells: one pattern was subepithallial initial cells as long as, or longer than subtending cortical cells (uppermost perithallial cells), observed exclusively in specimens from southeastern Brazil. The other developmental sequence included subepithallial initials as long as, longer than, or shorter than subtending cortical cells (uppermost perithallial cells) and was seen in specimens from northeastern Brazil and the Gulf of Mexico. All other vegetative features were similar in all specimens from both regions of Brazil and the Gulf of Mexico.

Reproductive remarks:—Longitudinal sections of the Gulf of Mexico specimens showed protuberances with numerous overgrown conceptacles infilled with aragonite crystals (Figures 5A-C). New growth layers were observed over the conceptacle roofs in the reproductive specimens that developed from a secondary hypothallium comprised of 2–4 layers of filaments that grew over the older conceptacle roofs (Figure 5C) and gave rise to upwardly branched tiers of perithallial filaments. These specimens showed subepithallial initials (intercalary meristematic cells) cylindrical to quadratic - 6–12 µm x 4–11 µm, length x diameter, as long as, or shorter than subtending cortical cells (Figure 5D). Some conceptacles were identified as gametangial in Gulf of Mexico specimens, evidenced by a unipore that was observed, a tapered roof suggesting a uniporate shape, and/or a lack of multiporate structures in the roof section views (Figures 5A-C). Conceptacle chambers 165–290 µm x 315–675 µm, length x diameter. It was not determined if Gulf of Mexico specimens were male or female.

Note:—*psb*A and *rbc*L sequences diagnostic for this genus and species. The balloon-like pore canal basal bounding cells (Figures 4C-E) in *Meridiolithothamnion atlanticum* also help differentiate this species from other closely related species in Brazil and the Gulf of Mexico, such as *Roseolithon* spp., which this character has not been reported in. In addition to this aspect, the tetrasporangial conceptacles of *M. atlanticum* also showed a relatively larger maximum diameter, up to 780 µm. The presence of subepithallial initials sometimes being shorter than subtending cortical cells in *Meridiolithothamnion atlanticum* is a supporting character state that, when present, may also help distinguish this new genus from the closely related *Lithothamnion* and *Boreolithothamnion*, genera in which this character state has not been reported.

Distribution: Previously known to be present in biogenic reefs and in rock formations known as "riscas" ('stripes') of northeastern region of Brazil and from mesophotic rhodolith beds offshore Louisiana and Florida in the Gulf of Mexico (Richards *et al.* 2016). Additionally, the genus is also herein reported to be present in shallow reefs and along the shores of nearby islands of the southeastern region of Brazil (present study).

Discussion

Ongoing global DNA sequencing efforts are demonstrating that there are not enough described genus names verified by DNA sequencing to apply to all the newly revealed clades of coralline algae based molecular analyses (Leão *et al.* 2024). For example, in the Hapalidiaceae, Sciuto *et al.* (2021) recently described the genus *Tethysphytum* and Trentin *et al.* (2023) described the genus *Thalassolithon* to accommodate non-geniculate coralline algal species from Antarctica that were shown to not belong to any other named genera verified based on DNA sequences.

The new genus and species described here shows a highly similar morphoanatomy to "*Lithothamnion* sp." described by Bahia (2014) for the Vitória-Trindade Seamount Chain, with small differences in conceptacles and tetrasporangia measurements. However, since Bahia (2014) specimens were exclusively preserved in 4% diluted formalin, a molecular comparison with the ones from the present study was not possible.

Interspecific and intergeneric divergences remain a subject of debate in the taxonomy of non-geniculate coralline algae, especially as new genera and species are continuously described. Jeong *et al*. (2019) reported interspecific divergence for the for *psb*A marker ranging from 5.3–8.0%, with the highest values (7.9–8.0%) observed between *Phymatolithon dosungii* S.Y. Jeong, B.Y. Won & T.O. Cho and *P. koreanum* S.Y. Jeong, B.Y. Won & T.O. Cho. Liu & Lin (2023) found intergeneric divergence values for *psb*A that were ≥ 7.56%, which are lower than the highest interspecific divergence reported by Jeong *et al.* (2019). In studies involving other coralline orders, such as Sporolithales, Bahia *et al*. (2015) reported higher intergeneric divergence values between *Sporolithon* and *Heydrichia*, ranging from between 9.44–13.94%. Jesionek *et al.* (2020) observed an intergeneric divergence of 6.3% for *psb*A between *Crustaphytum* and *Tectolithon*. These findings highlight that thresholds in interspecific/intergeneric divergence can vary considerably based on the study, the taxa involved, geographical distance and even when the same molecular marker is used.

Meridiolithothamnion atlanticum split (branched) basally from the *Boreolithothamnion* clade. The *psb*A divergence between *Meridiolithothamnion atlanticum* and species previously described within *Boreolithothamnion* (*e.g.*, *Boreolithothamnion glaciale*) ranged from 7.12 to 7.37%, which we consider intergeneric genetic distances. Additionally, the *rbc*L sequence from a Gulf of Mexico specimen (LAF 6521) showed a divergence of 10.47–13.18% compared to *Boreolithothamnion* sequences for the same marker. This exceeds the interspecific divergence range of 2.1 to 7% reported by Gabrielson *et al*. (2023) for *Boreolithothamnion*, providing strong support for recognizing *Meridiolithothamnion atlanticum* as both a new species and new genus that is distinct from its sister genus *Boreolithothamnion*. Three Hapalidiales genera—*Lithothamnion*, *Roseolithon*, and *Boreolithothamnion*—exhibit morpho-anatomical features similar to *Meridiolithothamnion*, namely: thallus construction of the monomerous non-coaxial type; contiguous cortical filaments joined by cell fusions; 1–2 layers of epithallial cells; epithallial layer with flattened and flared cells exhibiting trapezoidal-shaped cell lumen; and multiporate conceptacle chambers.

Using the 3P-*rbc*L gene sequence from the lectotype of the genus *Lithothamnion*, *Lithothamnion muelleri* Lenormand ex Rosanoff, along with type-sequence data and newly generated sequences, Gabrielson *et al.* (2023) re-circumscribed *Lithothamnion*, leading to the establishment of a new genus, *Boreolithothamnion*, for Northern hemisphere species previously included in *Lithothamnion* but not molecularly fitting into *Roseolithon*, namely:

Boreolithothamnion glaciale (Kjellman) P.W. Gabrielson, Maneveldt, Hughey & V. Peña, *B. lemoineae* P.W. Gabrielson, Maneveldt, Hughey & V. Peña, *B. sonderi* (Hauck) P.W. Gabrielson, Maneveldt, Hughey & V. Peña)¸*B. soriferum* (Kjellman) P.W. Gabrielson, Maneveldt, Hughey & V. Peña, and *B. tophiforme* (Esper) P.W. Gabrielson, Maneveldt, Hughey & V. Peña. Additionally, these authors described the new species *Boreolithothamnion giganteum* (L.R. Mason) P.W. Gabrielson, Maneveldt, Hughey & V. Peña and *B. phymatodeum* (Foslie) P.W. Gabrielson, Maneveldt, Hughey & V. Peña. Gabrielson *et al.* (2023) provided only a general genus description for *Lithothamnion* and *Boreolithothamnion*. Gabrielson *et al.* (2023) also identified only gametangial and carposporangial conceptacles for the species described in their study, making tetrasporangial morpho-anatomical species-specific comparisons with *Boreolithothamnion*, *Lithothamnion*, *Roseolithon*, and *Meridiolithothamnion* difficult. Due to this limitation, the tetrasporangial anatomy of *Meridiolithothamnion* and its type species were primarily compared, at the generic level, to those of *Boreolithothamnion*, *Lithothamnion* and *Roseolithon* (Table 2). Additionally, *B. glaciale* , *B. lemoineae* ¸ *B. soriferum* and *B. tophiforme* were previously re-circumscribed, but still under the name *Lithothamnion*, in Peña *et al.* (2021). Although Gabrielson *et al.* (2023) did not provide new tetrasporophytic anatomical descriptions for these species, morpho-anatomical comparison with previous descriptions associated to these species (under the name *Lithothamnion*) is possible (Table 3).

TABLE 2. Morpho-anatomical comparative analysis focusing on the principal diagnostic characters of four phylogenetically close genera: *Boreolithothamnion*, *Lithothamnion*, *Roseolithon*, and *Meridiolithothamnion*.

Character type	Features	*Boreolithothamnion*	*Lithothamnion*	*Roseolithon*	*Meridiolithothamnion*
Vegetative	Epithallial cells	flattened and flared with trapezoidal lumens	quadratic with rounded lumens; flattened with elongate lumens; flared (trapezoidal lumens)	flattened and flared with trapezoidal lumens	flattened and flared with trapezoidal lumens
Vegetative	Subepithallial initials	as long as or longer than inward derivatives	as long as or longer than inward derivatives	as long as or longer than inward derivatives; as long as or shorter than inward derivatives	as long as or longer than inward derivatives; as long as or shorter than inward derivatives
Vegetative	Trichocytes	absent	common to rare	absent	absent
Reproductive (multiporate tetrasporangial conceptacles)	Rosette cells	basal cells disintegrated or flush with the surface	basal cells disintegrated or flush with the surface	in depression	flush with the surface
Reproductive (multiporate tetrasporangial conceptacles)	Pore canals	flush with the surface	in depression or flush with the surface	in depression	flush with the surface
Reproductive (multiporate tetrasporangial conceptacles)	Pore canal bounding cells	cylindrical to elongate	cylindrical	cylindrical	basal cell "ballon-like"

As shown in Tables 2 and 3, the shape of the pore canal bounding cells in *Boreolithothamnion*, *Lithothamnion*, and *Roseolithon* differs from that of *Meridiolithothamnion*, particularly regarding the basal cell. This distinction supports the recognition of a key diagnostic feature for *Meridiolithothamnion*: tetrasporangial conceptacle pore canals bounded by "balloon-like" cells. However, future studies involving additional specimens are needed to determine whether this character is consistent or exhibits plasticity within the genus. *Roseolithon* can be distinguished from other closely related genera, such as *Lithothamnion* and the new genus *Meridiolithothamnion*, by its multiporate tetrasporangial conceptacles bordered by rosette cells in depressions (Coutinho *et al.* 2021). In contrast, *Meridiolithothamnion* exhibit rosette cells that are flush with the surface, lacking the depression of the pore plate and degeneration of surrounding cell filaments.

TABLE 3. Morphoanatomical comparison based on reproductive features of *Meridiolithothamnion atlanticum* and species of the genus *Boreolithothamnion*. 1. *Meridiolithothamnion atlanticum* (this study). 2. Irvine & Chamberlain (1994), as *Lithothamnion glaciale*, *L. lemoineae* and *L. sonderi*. 3. Adey & Adey (1973), as *Lithothamnion glaciale* and *L. sonderi*. 4. Henriques *et al.* (2012), as *Lithothamnion glaciale*. 5. Adey (1966), as *Lithothamnion lemoineae*. 6. Chamberlain (1992), as *Lithothamnion sonderi*. 7. Melbourne *et al.* (2017), as *Lithothamnion erinaceum*. 8. Adey (1970), as *Lithothamnion tophiforme*. 9. Adey *et al.* (2005), as *Lithothamnion tophiforme*. 10. Wilks & Woelkerling (1995). - = no data, not informed.

Features	***Meridiolithothamnion atlanticum***[1]	***Boreolithothamnion glaciale***[2,3]	***Boreolithothamnion glaciale***[4]	***Boreolithothamnion lemoineae***[2,5]	***Boreolithothamnion sonderi***[2,6,3]	***Boreolithothamnion soriferum***[7]	***Boreolithothamnion tophiforme***[8,9]	***Lithothamnion muelleri***[4,10]
Tetra/bisporangial conceptacles x surrounding thallus surface	slightly raised	flush/slightly raised	flush	raised/ -	raised	raised	slightly raised	slightly raised/raised or flush
Tetra/bisporangial conceptacle chamber (height x diameter; µm)	180–290 x 320–780	110–180 x 150–360	160–280 x 300–430	104–156 x 180–250/ 135–180 x 178–315	90–140 x 143–442/- x 160–315	80–180 x 140–290	- x 300–600/ - x 222–389	200–320 x 375-755/150–200 x 280–750
Tetra/bisporangium (height x diameter; µm)	120–175 x 45–70	65–96 x 23–47	49–51 x 30–32	82–132 x 39–75/-	104–160 x 25–78/-	-	-	145–147 x 57–59/ 100–175 x 30–140
Tetra/bisporangial conceptacle roof forming cells (number)	6–7	-	3–4	-	up to 6/-	-	-/3–4	7–9/5–9
Tetra/bisporangial conceptacle roof thickness (µm)	50–65	5–40	25–35	13–30/-	13–26/10–25	18–47	-	66–80/30–70
Tetra/bisporangial conceptacle pore canal bounding cells x other roof cells	different in size and shape, basal cells	-	different in size and shape	same size and shape/-	same size and shape	-	-/same size and shape	same size and shape
Tetra/bisporangial conceptacle pore canal bounding cells shape	basal cell “baloon-like”	cylindrical to elongate/-	elongate to cylindrical	cylindrical/-	cylindrical/ cylindrical to elongate/-	-	-/cylindrical to elongate	cylindrical

Vegetative anatomical differences exist among these four genera. According to Gabrielson *et al.* (2023), *Lithothamnion* species display diverse morpho-anatomical epithallial cell types: a) quadratic cells with rounded lumens; b) flattened cells with elongate lumens; and c) flared (trapezoidal lumens). In contrast, *Meridiolithothamnion*, *Boreolithothamnion*, and *Roseolithon* have flattened, flared epithallial cells with trapezoidal lumens. The subepithallial initials (intercalary meristematic cells) of *Boreolithothamnion* and *Lithothamnion* have two reported character states: as long as or longer than the subtending cortical cells. However, the sub-epithallial initials of *Meridiolithothamnion* show a third character state, and can be as long, longer than, or shorter than subtending cortical cells (Richards *et al.* 2016, present study). Richards *et al.* (2016) described other specimens now in *Roseolithon,* from the Gulf of Mexico that show subepithallial initials as being as long as or shorter than the subtending cortical cells, which was also observed by Coutinho *et al.* (2021) in *Roseolithon* species from Brazil. Further work should be done to investigate the utility of using relative subepithallial initial size character states in these related genera. Lastly, trichocytes are absent or not observed in *Boreolithothamnion*, *Roseolithon*, and *Meridiolithothamnion* but are common to rare in *Lithothamnion*.

Molecular-based studies over the past decade have revealed a number of non-geniculate coralline algal species that are present in both Brazil and the Gulf of Mexico (Richards *et al.* 2019, Richards *et al.* 2020, Coutinho *et al.* 2021, Richards *et al.* 2022). The current known distribution of *Meridiolithothamnion atlanticum* in both Brazil and the Gulf of Mexico is another interesting example of a non-geniculate coralline species shared between both regions. Future floristic studies will likely reveal more species of non-geniculate coralline algae that are present in both regions. Regarding the distribution and intrageneric diversity of the genus, Richards *et al.* (2016) interestingly showed with *psb*A and COI sequences, that *Meridiolithothamnion* includes a species that is sister to *M. atlanticum* collected from Pacific Panama (as "*Lithothamnion* sp. J", see figs. 1 and 2). A future study will be done to formally describe this second species of *Meridiolithothamnion*. Additionally, ongoing global coralline algal research and DNA sequencing efforts may reveal additional species within *Meridiolithothamnion* from other parts of the world.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

TABLE S1. List of the other specimens used in the rbcL and psbA analyses with their GenBank accession and collection information.