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Hydrolithon farinosum and *Lithophyllum epiphyticum* sp. nov. (Corallinaceae, Corallinales, Rhodophyta), Two Epiphytic Crustose Coralline Algae from the Abrolhos Archipelago, Brazil, Southwestern Atlantic

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Abstract: The aim of this study was to elucidate the taxonomy of the common but overlooked epiphytic coralline algae species from shallow reefs and seagrass meadows of the Abrolhos Archipelago, Brazil. Two thin (two vegetative cells thick) epiphytic coralline species were recorded: *Lithophyllum epiphyticum* sp. nov. and *Hydrolithon farinosum*. Molecular analysis from *psb*A genetic marker confirmed the position of *L. epiphyticum* into Lithophylloideae and revealed a phylogenetic relationship with an undescribed *Lithophyllum* from Italy. Thin thallus (2–3 cells thick) and cells lining the pore of tetrasporangial conceptacles protruding laterally occluding the canal, either partially or totally, are its main diagnostic characteristics. *Hydrolithon farinosum* is herein described in detail for Brazil, and its worldwide distribution is then discussed.

Keywords: CCA; Abrolhos bank; seagrass meadow; *psb*A; molecular analyses

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1. Introduction

Research efforts to provide a more accurate understanding of coralline algae taxonomy have steadily increased over the past decade [1–4]. This ongoing scientific interest on coralline algae can be mainly attributed to their ecological importance (reviewed by [5]), sensitivity to climate changes [6–10], as well as their increasing application as paleoecological proxies and paleoenvironmental recorders [11,12].

Coralline algae are distributed worldwide in a variety of marine habitats (only one freshwater species is known, [13]), occurring in areas as diverse as polar regions, tropical latitudes, intertidal shores, and the upper dysphotic zone, and can be encountered up to approximately 300 m deep [5]. They can be found attached to numerous substrates, including rocks, with epilithic forms encompassing the majority of coralline algae. They are also found attached to other algae or seagrasses (epiphytic forms); animals, such as mollusks, sponges, or echinoderms (epizoic forms); and glass, plastics, metal, and other artificial anthropogenic substrates (epigenous forms). Some species may also grow as unattached (free-living) rhodoliths, while others can grow wholly or partially inside another alga (parasitic or semi-endophytic forms) [14].

The Abrolhos Bank comprises much of the coralline algal diversity of the Brazilian marine area [15–17]. This region encompasses a mosaic of 8.844 km^2 biogenic reefs comprehending the largest and richest coral reefs of the South Atlantic and one of the world's

largest rhodolith beds (20.904 km^2) along the Southern Australian bed (>20.000 km^2) [18,19]. Non-geniculate coralline algae constitute one of the main reef builders on the Abrolhos Bank [18,20]. Fifteen rhodolith-forming non-geniculate coralline algae species are documented from the Abrolhos Bank [15,17,21], representing the world's richest rhodolith bed in terms of coralline algae species. Attached non-geniculate coralline algae are represented by 9–11 documented species (depending on taxonomic interpretation) recognized from the shallow coral reefs of Abrolhos [17,22], three of which are common to the Abrolhos' rhodolith beds.

Diving expeditions to Abrolhos Archipelago led us to note many thin, small crusts of coralline algae growing as epiphytes on seaweeds and seagrasses, a substrate that has been overlooked in previous studies of this region [17,22–24]. Thus, the aim of this study was to increase the knowledge about the diversity of common epiphytic coralline algae species, especially those found growing on algal host from shallow reefs and local seagrass meadows of the Abrolhos Archipelago.

2. Materials and Methods

Algal hosts with epiphytic coralline algae were photographed in situ and sampled through free diving and SCUBA at 3–5 m deep at the Abrolhos Archipelago, which is located within the Abrolhos Marine National Park, a No-Take Marine Protected Area in the Eastern Brazilian continental shelf, about 65 km from mainland. The hosts macroalgae were sampled from shallow reefs, adjacent soft-bottom communities and seagrass meadows (*Halodule wrightii*), and included chlorophyceans (*Caulerpa*, *Halimeda*, *Udotea*, *Valonia)* as well as the phaeophycean *Sargassum*. Samples were air dried, preserved in silica gel, and deposited in the Herbarium RB of the Rio de Janeiro Botanical Garden Research Institute.

For light microscopy, samples were prepared according to [25], with few modifications. The dry coralline algae crusts were decalcified in 10% nitric acid, rinsed in water, dehydrated in a sequence of 70%, 90%, and 100% ethanol solutions (60 min each), and immersed in Leica Historesin infiltration medium (12 h). After that, a hardening solution (Leica Historesin kit component) was added to the infiltration medium, and samples were placed in an oven at 60 °C for approximately 30 min for resin hardening.

Specimens were then sectioned (7 µm thickness) using a Reichert Jung 1130 rotary microtome. Sequential sections were removed from the microtome knife using a fine sable brush and transferred to a Petri dish containing toluidine blue (0.25 g borax 100 mL^{-1} and 0.06 g toluidine blue 100 mL^{-1}) for staining (2–5 min). The stained sections were transferred to another Petri dish containing distilled water, and they were subsequently opened in slides covered with distilled water drops. The slides were then kept in an electronic laboratory desiccator for at least 24 h, allowing the sections to adhere homogeneously to the slide. Finally, the slides were covered with coverslips using Entellan (Entellan; Merck, Darmstadt, Germany).

In cell measurements, length denotes the distance between primary pit connections and diameter, with the maximum width of the cell lumen at right angles to this. Conceptacle measurements follow [26], thallus anatomical terminology follows [27], and morphological (growth forms) terminology follows [28].

For SEM imaging, samples were prepared according to [29], and a JEOL JSM-6490LV scanning electron microscope was used (operated at 15 kV) from the Centro Brasileiro de Pesquisas Físicas (CBPF).

Molecular analysis were carried out at the Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Brazil. For DNA extraction, the thallus of the epiphytic algae was carefully scraped with a blade, removing only the surface layers in order to avoid host contamination. The DNA was extracted using Qiagen DNeasy Blood and Tissue Kit® (Qiagen, Crawley, UK), following the protocol of [30]. For *psb*A plastid-encoded markers, the stages of amplification and purification were performed following [30], including the pair of primers used. Purified products were sequenced by Macrogen Inc. (Seoul, South

Korea) in both directions, using the same PCR primers, through the traditional capillary sequencing method.

Consensus sequences were built using both BioEdith [31] and Sequencher® (v5.4.6, Gene Codes Corporation), chromatograms were visually checked for ambiguities, and the sequence generated was 888 base pairs. Alignment was performed first using MEGA6, and was then run through MAFFT Version 7 [32] and GBLOCKS to guarantee their quality. The extra sequences used were downloaded from GenBank, and only those with more than 750 bp and published were considered for the main tree (accession numbers in the phylogenetic tree—Figure 4). *Sporolithon* was picked out as an outgroup. The phylogenetic tree was inferred through the Maximum Likelihood method based on the General Time Reversible model (gamma distribution with invariant sites) at MEGA6 with 1000 bootstrap replicates [33], which were set as complete deletion. The analysis was counted with 71 sequences 751 bp in the final dataset. The intra and interspecific distance calculations were also conducted in MEGA6. The phylogenetic relationships were also examined using Bayesian inference (BI) with MrBayes 3.2.7 [34]. To sample across nucleotide substitution models, the command "lset nst = mixed" was used before running the analysis. Markov Chain Monte Carlo procedure consisted of four independent trials with four chains each. Each chain was run for 2000,000 generations. Posterior probability (PP) values for the resulting 50% majority rule consensus tree were estimated after discarding the first 20% of trees as burn-in.

3. Results

3.1. Morfoanatomical Results

Two species were identified and are described below. Additional illustrations are available in the Supplementary Material.

***Hydrolithon farinosum* (J.V. Lamouroux) Penrose & Y.M. Chamberlain 1993: 295.**

Basionym: *Melobesia farinosa* Lamouroux 1816: 315.

Lectotype: CN unnumbered (Mediterranean, unspecified locality, *Lamouroux*, epiphytic on *Sargassum linifolium*).

Specimens examined:

Brazil, Bahia State, Abrolhos Archipelago, Porto Norte (17°57′42″ S, 38°41′47″ W), at 3–5 m depth, with multiple specimens on *Halimeda* (*RG Bahia*, 03.iii.2016, RB 784872).

Observations:

Thalli attached ventrally by cell adhesion on a variety of algal hosts, including *Caulerpa*, *Halimeda*, *Sargassum*, and *Valonia* (Figure 1A,B). Colour of living thalli whitish or pink to dark red (Figure 1A–C) Growth-form encrusting with a flour-like, powdery covering appearance (Figure 1A–C). Thallus organization dorsiventral, vegetative thallus composed of a single layer of ventral filaments with cells measuring 5–15 µm in diameter and 10–20 µm high, and a single layer of flattened or rounded epithallial cells. Ventral filaments connected laterally by cell fusions. Secondary pit connections and trichocytes not found.

Tetrasporangial conceptacles protruding above surrounding thallus surface (Figure 1D–F). Conceptacle chambers measuring 130–180 µm in diameter and 50–90 µm high, and they usually contain two peripheral tetrasporangia (18–30 µm in diameter and 45–55 µm high) with zonately-divided tetraspores (Figure 1F). Central columella either present (Figure 1D) or absent (Figure 1E,F) within conceptacle chambers. Conceptacle floors were observed right above the surface of the surrounding vegetative thallus (Figure 1D–F). Roofs 2–3 cells thick (including epithallial cells) formed by filaments surrounding and interspersed within the fertile area (Figure 1F). Pore canals lined by a ring of conspicuous and enlarged cells, not protruding laterally into the canal, and oriented nearly perpendicularly to the roof surface (Figure 1D,E). Gametangial and carposporangial thalli not found.

***Lithophyllum epiphyticum* Lyra, Bahia & A.S.Harv. sp. nov.**

Holotype: RB 784870 collected 03 March 2016, *leg RG Bahia & FC Moraes*, *psb*A—GenBank OP186068.

Isotype: RB 784871, collected 03 March 2016, *leg RG Bahia & FC Moraes*.

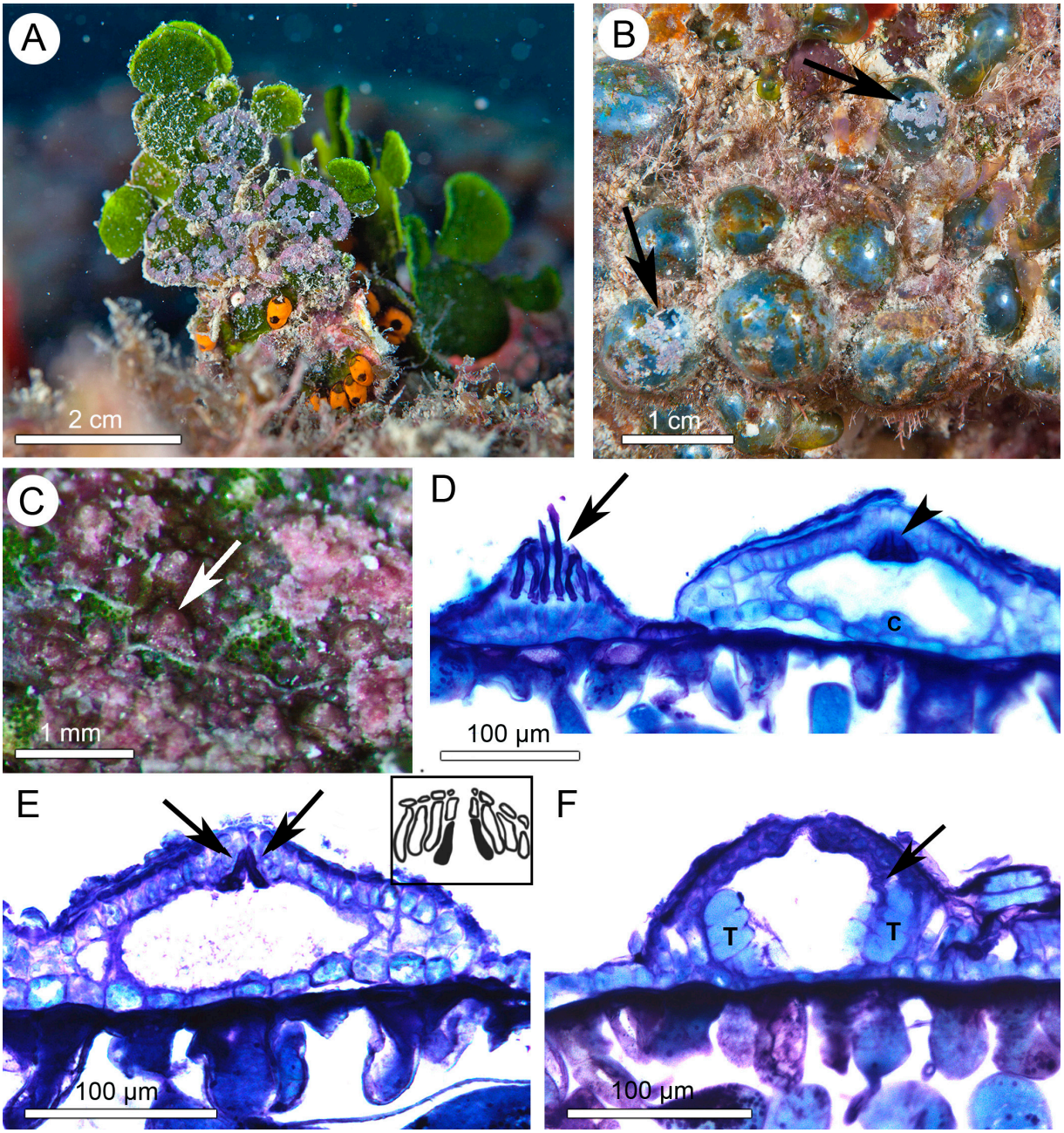


Figure 1. (**A**–**F**) Vegetative and reproductive features of *Hydrolithon farinosum*. (**A**) Crusts attached on the host *Halimeda*. (**B**) Crusts attached on the host *Valonia.* (**C**) Magnified view of an encrusting specimen showing uniporate tetrasporangial conceptacles (arrow). (**D**) Section through a young (left) and mature (right) uniporate tetrasporangial conceptacle. Note the ring of developing elongate cells (arrow) that will line the pore canal when the conceptacle is mature. These corresponding cells (arrowhead) are smaller in a mature conceptacle and more or less perpendicularly positioned in relation to the roof surface. Note, also, the vestiges of the central columella (c) in a mature conceptacle. (**E**) Section through a tetrasporangial conceptacle showing the pore canal lined by elongate cells that do not protrude into the canal, and that are oriented more or less perpendicularly to the roof surface (in the upper right corner, a schematic drawing of this characteristic is depicted). Note that the chamber floor is located above the surrounding vegetative thallus surface. (**F**) Section through a tetrasporangial conceptacle, showing two peripherally tetrasporangia (t) with zonately-divided tetraspores. (Underwater photographs by Áthila Bertoncini).

Type Locality: Porto Norte, Abrolhos Archipelago, Bahia State, Brazil (17°57′42″ S, 38°41′37″ W), subtidal (3–5 m deep), epiphytic on *Udotea flabellum* (J. Ellis & Solander) M. Howe 1904: 94.

Etymology: 'epiphyticum' (from Latin, meaning epiphyte), referring to the epiphytic habit of the species.

Additional specimens examined: Brazil, Bahia State, Abrolhos Archipelago, Porto Norte (17°57′42″ S, 38°41′37″ W), at 5 m depth, specimens on *Udotea flabellum* (J. Ellis & Solander) M. Howe 1904: 94 (*FC Moraes*, 08.v.2016, RB 784871).

Distribution: Northeast Brazil, Bahia State (present study).

Observations:

Thalli attached ventrally by cell adhesion forming disk-like crusts, mostly on *Udotea flabellum* (Figure 2A), with growth-form encrusting, colour whitish to pink (Figure 2A,B). Thallus organization dorsiventral, construction dimerous (Figure 2C). Vegetative thallus composed of a single basal layer of sinuate palisade cells measuring 10–15 µm in diameter and 55–90 µm high and a single layer of flattened or rounded epithallial cells (Figure 2C). Basal filament connected laterally by secondary pit connections (Figure 2C). Cell fusions and trichocytes not found.

Tetrasporangial conceptacles viewed protruding above the surrounding surface of the thallus (Figure 2D–F). Conceptacle chambers measuring 240–300 µm in diameter and 100–140 µm high. Central columella either present or absent within the conceptacle chambers. Conceptacle chamber floor located one or two cells below the adjacent surface of the vegetative thallus (Figure 2D,E). Conceptacle roofs 2–4 cells (including epithallials) thick (Figure 2D,E). Cells lining the pore canals protrude laterally (Figure 2E,F) found either completely occluding the canal pore (Figure 2F,G,I) and unobstructed (Figure 2E,H). Pore measures are 4–7 µm in diameter and 6–10 µm high. Tetrasporangia (35–60 µm in diameter and 80–100 µm high) with four zonately divided tetraspores (Figure 2E).

Gametangial thalli are apparently monoecious, as male and carpogonial conceptacles seen forming the same crust. Whether these corresponded to only one individual or two fused ones, however, is uncertain. Male conceptacles protruding above the surrounding surface of the thallus; chambers measuring 135–285 µm in diameter and 45–75 µm high; floor located at the same level as the surrounding thallus surface; roofs composed of 2–3 layers of cells (Figure 3A,B). Spermatangial filaments unbranched and confined to the chamber floor (Figure 3B–D). Carpogonial conceptacles protruding above the surrounding surface of the thallus; floor located at same level as the surrounding thallus surface; chambers with 200–230 µm in diameter and 85–105 µm high; roofs composed of 2–3 layers of cells (Figure 3E). Carpogonial filaments arising from chamber floor, usually 2 cells long and bearing carpogonia with elongate trichogyne (Figure 3E). Carposporangial conceptacles larger than carpogonial ones, chambers with 265–340 µm in diameter and 100–165 µm high (Figure 3F). Carposporophytes comprises a central fusion cell (Figure 3E,F), and several-celled gonimoblast filaments arise peripherally with terminal orbicular carposporangia, 40–90 µm in diameter (Figure 3F).

3.2. Molecular Results

DNA sequences were successfully obtained only for *Lithophyllum epiphyticum*. Exhaustive attempts at DNA extractions were made for *H. farinosum*, but all were unfruitful. The phylogenetic tree (Figure 4) shows that *L. epiphyticum* was resolved in a clade sister to undetermined deep water (54–80 m) *Titanoderma* (=*Lithophyllum*) specimens from the USA (Gulf of Mexico). *L. epiphyticum* formed a clade with three different species, two of which are not yet described in the literature, including the closest one, *Lithophyllum* sp. (MZ438453) from Italy [10], which diverges 5.3%. The second sequence in the clade is *L.* cf. *pustutatum* with 5.7%, and the most distant one is *Lithophyllum.* sp. (MZ438322) from Japan [10] with 8.7% of divergence.

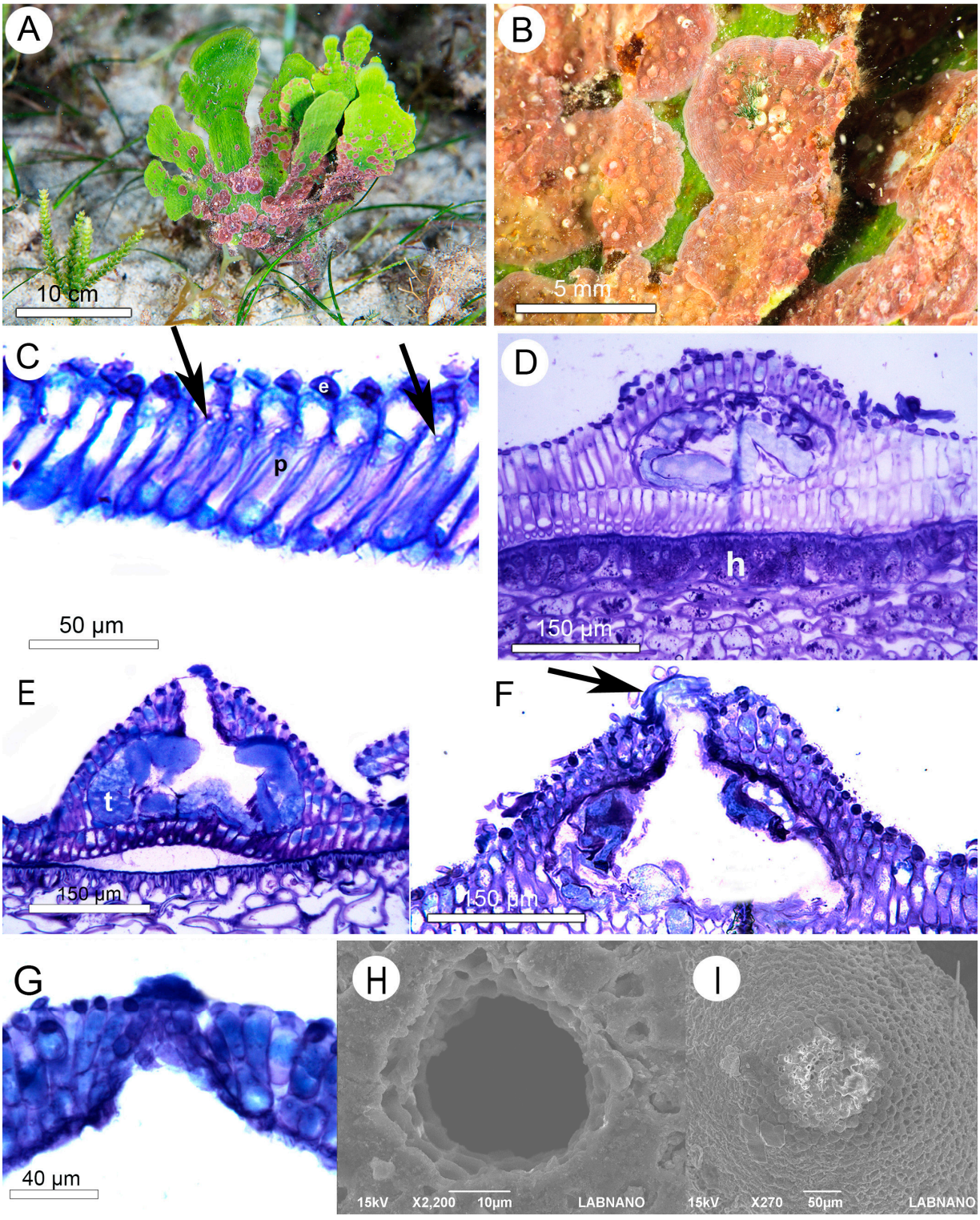


Figure 2. (**A**–**I**) Vegetative and reproductive features of *Lithophyllum epiphyticum*. (**A**) Crusts attached on the host *Udotea flabellum*. (**B**) Magnified view of discoid encrusting specimens showing uniporate tetrasporangial conceptacles. (**C**) Section through the two-cell layered vegetative thallus showing sinuate palisade cells (p), rounded epithallial cells (e), and secondary pit connections (arrows) linking the basal filament. (**D**) Section through an immature tetrasporangial conceptacle chamber showing its floor located only one cell below the surrounding thallus surface. Note the host thallus (h) below

the sectioned specimen. (**E**) Longitudinal section through an uniporate tetrasporangial conceptacle showing a partially covered pore canal, and a tetrasporangia with four zonately arranged tetraspores (t). (**F**) Tetrasporangial conceptacle showing a pore plug (arrow) blocking the canal. (**G**) Approximate view of a conceptacle pore completely occluded. (**H**,**I**) SEM imaging. (**H**) Approximate view of a tetrasporangial conceptacle with the pore entirely open. (**I**) Another mature conceptacle with whitish cells blocking the canal. (Underwater photograph by Áthila Bertoncini).

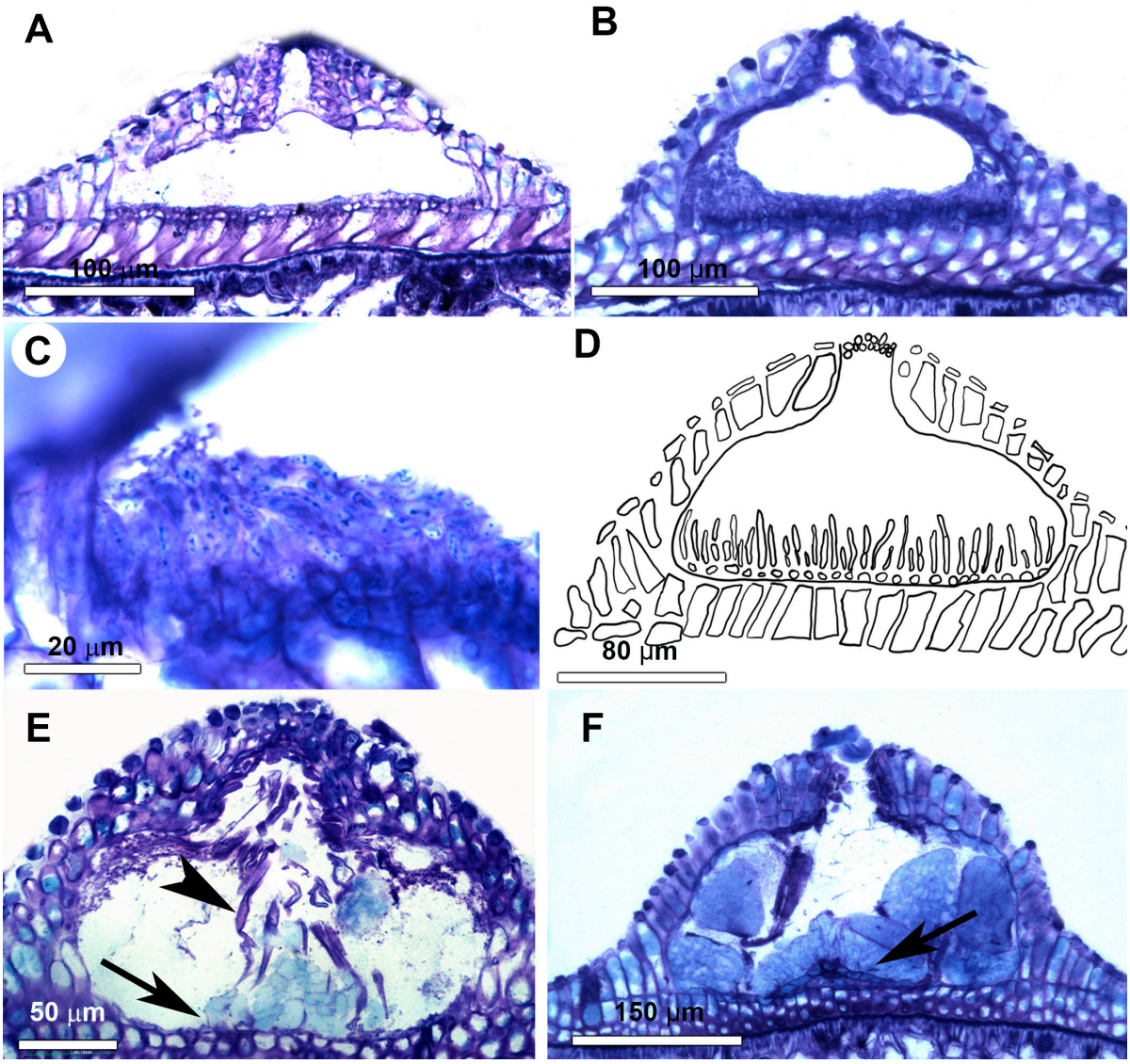


Figure 3. (**A**–**F**) Gametangial and carposporangial features of *Lithophyllum epiphyticum*. (**A**) Section through an empty male conceptacle with a roof composed of three layers of cells. (**B**) Section through a male conceptacle chamber showing numerous spermatangial filaments confined to its floor. (**C**) Magnified view of spermatangial filaments. (**D**) Diagrammatic drawing of a male conceptacle containing unbranched spermatangial filaments confined to its floor. (**E**) Carpogonial conceptacle containing branches in the center of the chamber. Note a basal carpogonium (arrow) that extends into a narrow upper trichogyne (arrowhead). (**F**) Section through a carposporangial conceptacle showing a columella formed by a cluster of fused cells (arrow).

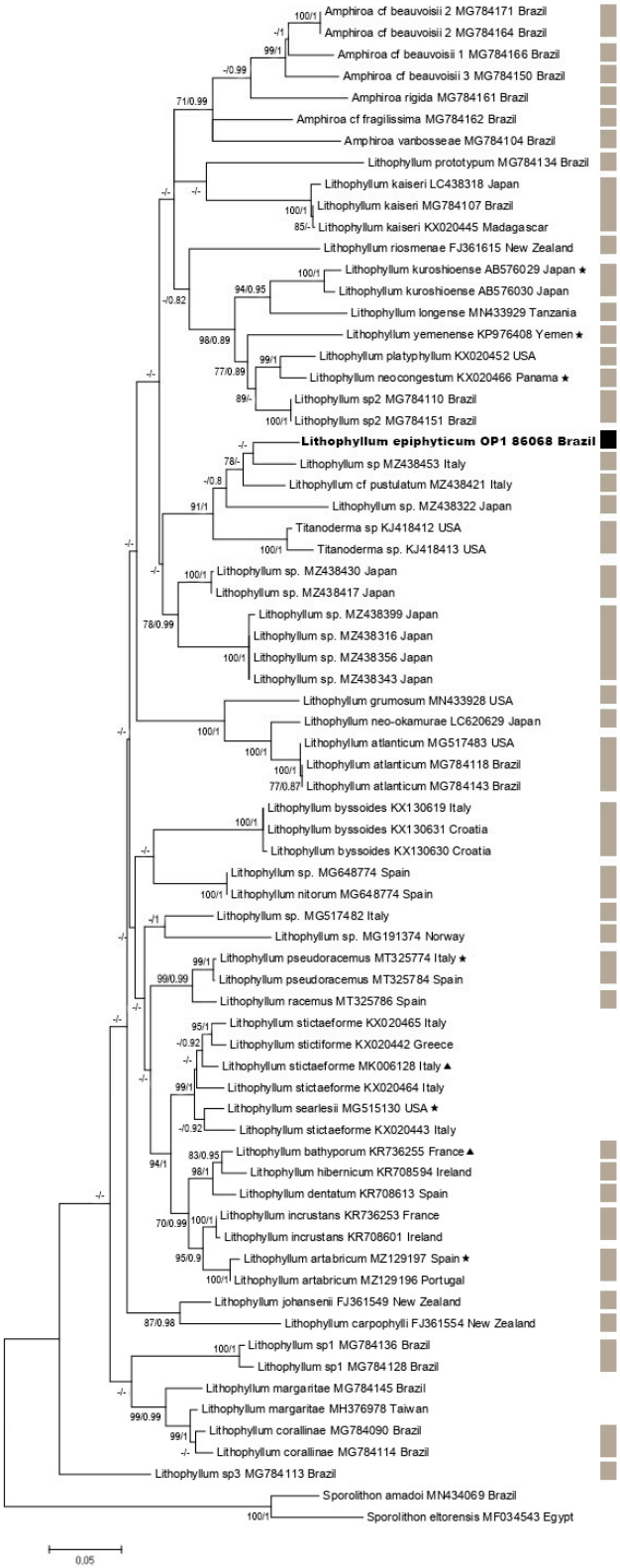


Figure 4. Phylogenetic tree inferred from ML and BI analyses of the *psb*A dataset. Bootstrap support (1000 replicates) and Bayesian posterior probabilities (PP) indicated at the nodes. Bootstrap values lower than 70% and PP values lower than 0.8 or inconsistent with the original tree are not shown. In bold, *Lithophyllum epiphyticum*. Type sequences are shown with a star on the side, and lectotypes with a triangle. Gray bars on the side indicate divided sequence groups used to calculate mean distance within and between groups. (*) Divided according to [3].

4. Discussion

4.1. Ecological and Taxonomical Aspects

The epiphytic coralline algae identified in the present study were collected from large meadows of seagrass *Halodule wrightii* Ascherson intermixed with macroalgal communities at the Abrolhos Archipelago (see the description of these communities in [24]). Calcareous epibionts, such as coralline algae, have been demonstrated to be of paramount importance in the carbon cycle of seagrass ecosystems, as they are major contributors to CO_2 fluxes through their high $CaCO_3$ production and dissolution [35]. In addition, they make a significant contribution to calcareous sediment accumulation over geological timescales [36,37]. In respect to their ecological importance, calcareous epibionts may play an indirect role on host growth and proliferation once they reduce host photosynthetic capacity, increase the chance of host frond loss (breakage), increase the boundary layer at the host surface, and produce allelopathic substances that suppress the development of algal sporelings [38]. These corallines, however, are threatened by the global environmental changes that are expected in this century. Results obtained by [39] suggest that $CaCO_3$ production by epiphytic coralline algae may decrease by more than 50% by the year 2100 due to anthropogenic ocean acidification. Specifically in Brazil, these algae are in extreme danger due to acidification, which has a higher % Mg substitution in the calcite crystals lattice that makes them more prone to dissolution in the near future [40].

Prior to this study, the published knowledge of *Hydrolithon farinosum* in Brazil was limited to isolated records without anatomical evidence (e.g., [41], as *Fosliella farinosa*). The subfamilial and generic position of *H. farinosum* remain unclear as long as no DNA sequences are available for this taxon. DNA sequencing of thin laminar thalli similar to our epiphytic species is challenging, as it is difficult to avoid DNA contamination from the algal host underneath. Therefore, the ascription of this species into Hydrolithoideae, with its single genus *Hydrolithon*, was based on morpho-anatomical features. According to [1], Hydrolithoideae is circumscribed by the following combination of features: (1) an outline of cell filaments entirely lost in large portions of the thallus due to pervasive and extensive cell fusions, giving it a distinctive and unique appearance in cross-section; (2) its primarily dimerous thallus construction; (3) its tetra/bisporangial conceptacle roof, formed by filaments surrounding and interspersed among tetrasporangial initials; and (4) its pore canals of uniporate tetra/bisporangial conceptacles, which are lined by a ring of elongate cells that do not protrude into the canal and are oriented more or less perpendicularly to the roof surface. All of these features were observed in *H. farinosum* from Abrolhos Archipelago, with exception of the first, which can only be observed in species with a thicker thallus [1].

Hydrolithon farinosum from the Abrolhos Archipelago closely matched the lectotype description provided by [42], with two notable exceptions: in the majority of cases, only two sporangia per chamber, and the absence of trichocytes. For the type material [42], a range of 3–8 sporangia is typically observed per chamber, however, the number of sporangia per chamber seen in the Australian specimens are similar to observed here. This feature is still somewhat variable, depending on the moment of life of the individual. As pointed out by [42,43], temperature and light may represent key environmental factors influencing the production or lack of trichocytes in coralline algae individuals, making both characteristics unreliable for taxa diagnosis. For this reason, we have decided to maintain the present determination as *H. farinosum* until molecular data are available to ensure a definitive identification.

In addition to *H. farinosum*, *Hydrolithon boergesenii* (Foslie) Foslie (1909: 56) is the only other species from the subfamily Hydrolithoideae that has been recorded in Brazil [17]. *Hydrolithon farinosum* can be distinguished from this species mainly by the presence of two features: (1) thalli that is exclusively epiphytic, and (2) vegetative thalli that is composed of only two cells. Taking into account these aspects, our specimen also resembles the alga *Porolithon improcerum* whose generic position is still unresolved [1]. *P. improcerum* also possess two layered thalli that can be epiphytic [44,45], but it is composed of several

applanate branches that overgrowth one another and display trichocytes in large tightly packed horizontal fields [44,45], which have not been observed in the present samples identified as *H. farinosum*.

Lithophyllum epiphyticum Lyra, Bahia & A. S. Harv. sp. nov. is herein described as a new species for the Brazilian coast based on molecular data and phylogenetic analyses. Regarding the existent literature for this genus, the intraspecific divergence for *Lithophyllum* is considered lower than 2% for the *psb*A marker [46,47]. Here, the interspecific divergence with the most similar sequence, *Lithophyllum* sp. 9 [10], is 5.3%, and is significantly distinct.

L. epiphyticum resembles *Lithophyllum chamberlainianum* [48–50] in almost every morphoanatomical aspect but lacks an important diagnostic characteristic: completely occluded conceptacle pores by a cluster of overlapping tubular cells that usually project above the surrounding roof filaments. Due to the absence of molecular information regarding *L. chamberlainianum*, owing to the difficulty to obtain DNA sequences of type material being stored in formaldehyde, we can only confirm if they are different species when DNA data from topotypes become available.

Lithophyllum epiphyticum can be distinguished from the other five *Lithophyllum* species confirmed to occur in Brazil based on morpho-anatomical and molecular data [3], but mainly by the following combination of features: (1) an epiphytic habitat, and (2) a thin mature thallus (<10 layers of cells) (Table 1). [3] reported the occurrence of other four cryptic, as yet unnamed, *Lithophyllum* species from Brazil based on molecular data, but none correspond to epiphytic algae.

Based on morpho-anatomical data presented in Table 1, *L. epiphyticum* most closely resembles *L. prototypum* (Foslie) Foslie (1905:129) in Brazil. Both species exhibit a vegetative thallus composed only of palisade basal cells covered by a layer of epithallial cells in addition to other shared features related to tetrasporangial conceptacles. However, *L. prototypum* is commonly found in imbricate and numerous applanate branches with swirled margins in surface view [17,48], which have not been observed in *L. epiphyticum* from Abrolhos Archipelago, Brazil. In addition, the position of *L. epiphyticum* in *psb*A phylogram was in a distinct clade from *L. prototypum*.

Table 1. Comparison of the main features that distinguish *Lithophyllum* species.

	L. epiphytica [1]	*L. irvineanum* [2]	*L. chamberlainianum* (Type Collection) [2]	*L. prototypum* (Type Collection) [2]	*L. pustulatum* [2,3,4]	*L. cystoseirae* [5]	*L. laminariae* [6]
Distribution [7]	Abrolhos Archipelago (Brazil)	South and Western Australia	South Pacific	Caribbean, Western Atlantic, Arabian Gulf, Indo-Pacific	Mediterranean, Indo-Pacific, Eastern and Western Atlantic, Red Sea, Arabian Gulf, Caribbean, Arctic Ocean	Adriatic Sea, Mediterranean, Eastern Atlantic	Eastern Atlantic
Habit	Epiphytic	Epiphytic	Epiphytic	Epilithic/epiphytic/free-living as rhodolith	Epilithic/free-living as rhodolith	Epiphytic	Epiphytic
Growth form	Encrusting	Encrusting	Encrusting	Encrusting	Encrusting/warty to lumpy	Encrusting	Encrusting
Thalli structured in several applanate branches with swirled margins in surface view	Absent	Present	Absent	Present	Absent	Absent	Absent
Basal layer of palisade or sinuate cells	Present	Present	Present	Present	Present	Present	Present
Mature thallus thickness (number of cell layers)	<10	<10	<10	<10	>10	>10	>10
Trichocytes	Absent	Absent	Absent	Absent	Absent	Present	Absent
Tetra/bisporangial conceptacle chamber diameter (μm)	240–300	180–263	145–252	330–415	420–465/328–556	288–475/307–324	312–364
Tetra/bisporangial conceptacle chamber height (μm)	100–140	82–125	60–135	100–190	300–320/110–180	80–172/80–124	104–156
Pore canals of tetra/bisporangial conceptacles occluded by cells	Absent/present	Present	Present	Absent	Absent	Present	Absent
Number of cell layers in tetra/bisporangial roof filaments	2–4	2–4	2–5	2–3	2–4	3–6	ND
Position of tetra/bisporangial chamber floor below thallus surface (number of cells)	1	1–3	1	1	1–5	ND	6-+
Conceptacle position in the thallus	Superficial	Superficial/immersed	Superficial/immersed	Superficial/immersed	Superficial/immersed	Superficial/immersed	superficial/immersed
Columella	Present	Present	Present	Present	Present	Present	Present

[1] [Present study]; [2] [48]; [3] [51]; [4] [16]; [5] [52]; [6] [53]; [7] [50]; ND = Not disclosed.

4.2. Biogeographic Aspects

Hydrolithon farinosum is a cosmopolitan species (pending molecular confirmation) found on various seaweeds and seagrasses in tropical and temperate regions of the Pacific, Atlantic, and Indian Oceans [54]. Some of the common hosts of *H. farinosum*, such as *Sargassum* and *Zostera* [55], could function as dispersal vectors during algal rafting. The broad geographical distribution of *H. farinosum*, if confirmed through DNA analyses, could be related to rafting opportunities provided by its hosts, as observed for some invertebrates [56].

Ref. [57] demonstrated that debris containing benthic marine algae from the Great Tohoku Earthquake and Tsunami of March 2011 in Japan arrived on the coasts of Oregon and Washington, USA in June 2012, proving that dispersion over long distances can occur in a short period of time. In particular, smaller species may disperse more easily, and they might be more widespread globally. This feature was investigated by [58] in their search for traits that might predict introductions of species, concluding that size was influential for some taxonomic groups. Considering that coralline algae have been reported as having negative buoyancy and non-motile spores, which indicates short dispersal distances per generation [59], transoceanic dispersion through spores is unlikely.

4.3. Perspectives Biogeography x Taxonomy

Recent DNA sequence data is forcing taxonomists to question the practice of placing into synonymy specimens of coralline red algae that are widely geographically separated [60]. For example, [61] demonstrated that specimens labelled *Mesophyllum erubescens* (Foslie) Me.Lemoine (1928:252) based on morpho-anatomical characters in the Pacific Ocean are not the same molecular species as those reported from the Western Atlantic Ocean (including type locality), and it has been hypothesized that numerous cryptic species are apparently posing under that one name. On the other hand, there are increasing instances where morpho-anatomically related specimens from different ocean basins do belong to the same species. For example, DNA sequences of specimens of *Hydrolithon boergesenii* from the Caribbean and the Indo-Pacific (as *H. reinboldii*) could not be delimited by any single marker or combination of markers in the encompassing phylogenetic molecular analysis of the Corallinaceae provided by [1]. Similarly, [62] found identical *rbc*L and *psb*A sequences of *Lithophyllum kaiseri* (Heydrich) Heydrich (1897:412) from the Red Sea, the Caribbean, and Indo-West Pacific, while [17] also confirmed its occurrence through *psb*A sequence data in the Abrolhos Bank, Brazil.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15091013/s1. Figure S1: Illustrative diagrams depicting features of *H. farinosum* and *L. epiphyticum*, providing a more comprehensive visual representation of both species. (A,B) *H. farinosum.* (C,D) *L. epiphyticum*. (A) Tetrasporangial conceptacle with vestigial filaments (black) resulting in enlarged, domed cells lining the base of the pore canal. Note that the pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. (B) Tetrasporangial conceptacle showing roof structure and two peripherally tetrasporangia with zonately divided tetraspores. (C) Vegetative thallus showing sinuate palisade cells with secondary pit connections. (D) Tetrasporangial conceptacle showing roof structure, with pore entirely open, two peripherally tetrasporangia with zonately divided tetraspores and a central columella (black cell).

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