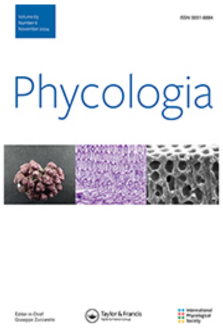

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Molecular diversity of reef-associated crustose coralline algae (Corallinophycidae, Rhodophyta) of the Spermonde Archipelago, Indonesia

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ABSTRACT

Although important consolidators and settlement inducers of organisms such as corals, echinoderms, and molluscs on coral reefs, crustose coralline algae (CCA) have been some of the least studied organisms in the megadiverse Coral Triangle in the tropical Indo-Pacific Ocean. CCA were sampled from reefs across different ecological zones of the Spermonde Archipelago within the Coral Triangle through diver collections along 10 X 1 m transects on coral reefs and deployment of Autonomous Reef Monitoring Structures (ARMS). Using DNA sequences of *psb*A, COI-5P, and *rbc*L barcodes, we re-assessed the diversity of the reef-associated CCA of this region, previously studied only using morpho-anatomy. Species delimitation methods resulted in 63 molecular operational taxonomic units (OTUs) representing 11 genera from three orders. This tripled the species richness previously reported, with cryptic diversity observed in all genera except *Porolithon* (order Corallinales) and *Melyvonnea*, (order Hapalidiales) represented by one OTU each. Distinct communities of CCA OTUs were recorded from reef surveys and the ARMS collections that targeted the external and internal reef environments, respectively. Thirty-five OTUs appeared to be endemic to the Spermonde Archipelago. The rich phylogenetic diversity exhibited in the Spermonde Archipelago, as in studies on other Pacific areas, revealed that a significant amount of biodiversity has been overlooked in Indo-Pacific reefs, especially in the Coral Triangle. These findings emphasize the need for more research before losses are incurred due to their vulnerability to climatic and anthropogenic threats.

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INTRODUCTION

The term coralline algae refers to calcifying red algae of the subclass Corallinophycidae (Le Gall & Saunders, 2007). Non-geniculate corallines, more commonly known as crustose coralline algae (CCA) in coral reef studies, lack uncalcified joints and they are present in the four calcified orders recognized in this subclass (Bailey & Chapman, 1998). We utilize CCA *sensu* Adey & Macintyre (1973) from here on to include attached and free-living (i.e. rhodoliths) forms. CCA fulfil important roles in: (1) strengthening the overall reef structure by binding loose substrate and different coral colonies together (Björk *et al*., 1995), (2) helping reduce the growth of leafy macroalgae (Johnson & Mann, 1986), (3) being food sources for organisms such as parrotfish, chiton, or sea urchins (Steneck, 1985), and (4) creating new surfaces for colonization (Nelson, 2009). Some species not only provide a physical substrate, but also actively induce or inhibit the settlement and metamorphosis of various reef organisms including reef-building corals (Harrington *et al*., 2004; Morse & Morse, 1996; O'Leary *et al*., 2012; Ritson-Williams *et al*., 2010). This may be an important factor in the maintenance of coral reefs and recovery after disturbances (Teichert *et al*., 2020).

Despite the important ecological role of CCA, they are often lumped together as a single group in coral reef studies (Dean *et al*., 2015). This stems from the taxonomic challenges inherent in the group. Species identification in CCA

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traditionally required the examination of vegetative and reproductive anatomical characters which is impossible to do *in situ*. Furthermore, the external morphology of a single species can take on various forms, while different species can also assume convergent morphologies (Caragnano *et al*., 2018; Gabrielson *et al*., 2018). DNA barcoding of coralline algae has greatly contributed to our understanding of their systematics, resulting in considerable changes in their taxonomy and classification across several systematic levels. These include the circumscriptions of the subclass Corallinophycidae that is characterized by the presence of calcite in their cell walls, new orders (Le Gall *et al*., 2010; Jeong *et al*., 2021; Nelson *et al*., 2015), and numerous new genera and species in the last 15 years, i.e. *Crusticorallina* (Hind *et al*., 2016), *Crustaphytum* (Liu *et al*., 2018), *Roseolithon* (Coutinho *et al*., 2021; Min-Khant-Kyaw, Kato *et al*., 2024), and *Adeylithon* (Peña *et al*., 2019). Additionally, species that were once considered cosmopolitan were shown to consist of numerous, genetically distinct (pseudo-)cryptic species (Gabrielson *et al*., 2018; Kato *et al*., 2013; Pezzolesi *et al*., 2019; Sissini *et al*., 2014). While molecular taxonomic research on CCA has progressed, especially in certain areas such as the European coasts, New Zealand, Brazil and South Africa (Peña *et al*., 2018; Puckree-Padua *et al*., 2022; Sissini *et al*., 2022; Twist *et al*., 2019), there are still places where CCA assemblages remain largely unknown or have been neglected for decades. This includes the region with the world's highest concentration of coral reefs, the Coral Triangle (Fig. 1; Veron *et al*., 2009) in the tropical Indo-Pacific Ocean (Keats *et al*., 2009; Rösler *et al*., 2016; Verheij, 1994). Using occurrence reports as a proxy for research effort (Fig. 1), the entire Coral Triangle has far less data than neighbouring countries (Corallinales in GBIF Secretariat, 2023). Since taxonomy is the foundation for understanding, managing, and conserving natural resources, it is important to fill in this gap especially with the increasing threat of biodiversity loss (Wheeler *et al*., 2004).

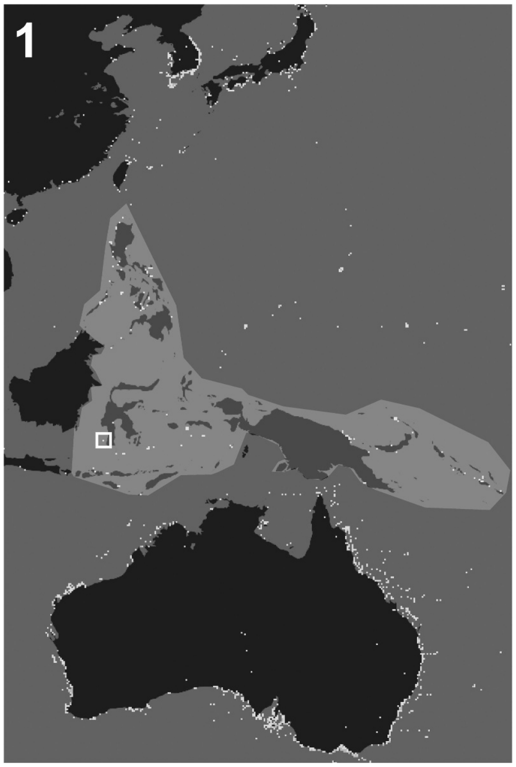

Fig. 1. Global Biodiversity Information Facility (GBIF) observation records (white points) of coralline algae in the Coral Triangle (lighter outline; Veron *et al*., 2009) and neighbouring areas. The location of the Spermonde Archipelago in South Sulawesi, Indonesia is indicated by the white box.

Checklists (Atmadja & Prud'homme van Reine, 2010; Lastimoso & Santiañez, 2021; N'Yeurt & Payri, 2004; Titlyanov *et al*., 2015; Tsuda, 2004) provide information on the historical records of CCA in some Pacific Ocean localities but these lists need verification using molecular methodologies. Since detailed taxonomic studies supply more information (e.g. morpho-anatomy, environmental preference, or molecular data in recent publications) on samples observed in specific regions (Adey *et al*., 1982; Baba & Kato, 2023; Nelson *et al*., 2015; Townsend & Huisman, 2018; Wang, 2023), these are particularly useful for comparison with recent collections analysed using modern methods. Only two of the CCA diversity studies have been published in the Coral Triangle, one from the Philippines (Trono *et al*., 1985) and another from the Spermonde Archipelago (Verheij, 1993b, 1994). Considering the known high tropical marine diversity in the Coral Triangle, these studies based only on morpho-anatomical identifications likely underestimate the diversity of CCA revealed by sequence data. Our study aims to assess the diversity of reef-associated CCA in the Spermonde Archipelago using DNA barcodes from new collections.

MATERIAL AND METHODS

Study site descriptions

The Spermonde Archipelago covers a ~16,000 km^2 area in southwest Sulawesi, Indonesia and consists of ~120 islands in addition to submerged reefs on a carbonate platform with a maximum depth of ~60 m (Kench & Mann, 2017). A barrier reef forms the western edge along the Makassar Strait with a steep drop-off to ~200 m. It has been partitioned into different ecological zones according to environmental characteristics and biological communities (Renema & Troelstra, 2001). CCA samples were collected from nine reefs (Table S1) with representatives from each ecological zone (Fig. 2). Living coral cover was highest on the reef slope, from the crest down to ~10 m depth, except for the islands nearest to Makassar (Lae Lae and Gusung Tallang) which were characterized by heavy sedimentation and patchy coral reefs.

Sample collection

REEF SURVEYS

Field work was conducted from 31 July 2022 to 29 August 2022. A permit was obtained for this study from the Badan Riset dan Inovasi Nasional (BRIN), the National Research and Innovation Agency of Indonesia (Permit number 96/SIP/IV/FR/7/2022). Samples were collected using a dive knife and hammer in reef surveys. A targeted search for CCA along 1 × 10 m belt transects

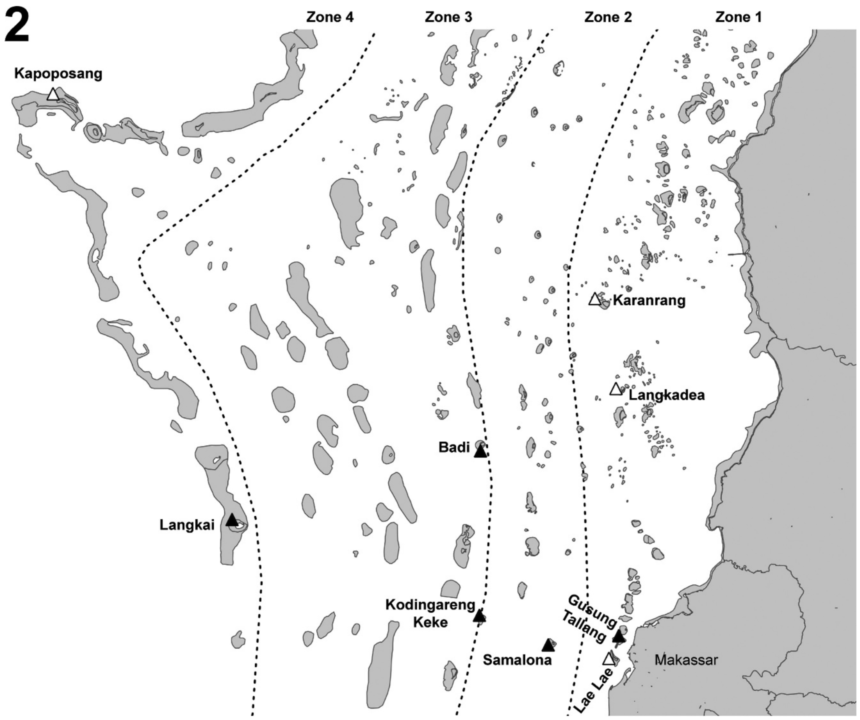

Fig. 2. Reef survey locations (triangles) in the Spermonde Archipelago. Autonomous Reef Monitoring Structures (ARMS) deployment sites are black. Ecological zones are separated by dashed lines.

was conducted for approximately 25 minutes. Photographs were taken of each sample before collection. No collections were made in cases where it would cause damage to living coral substrate. Transects were laid on the reef flat (3 reefs, 9 transects) and the reef slope at 6 m (9 reefs, 20 transects) and 10 m depth (6 reefs, 14 transects). Samples were air-dried and stored in silica gel away from sunlight. Opportunistic collections by other researchers were also included. Samples were transferred to the University of Granada in accordance with the Materials Transfer Agreement (MTA) between the European Institutions of the 4D-REEF Project and Universitas Hasanuddin (UNHAS) in Makassar, Indonesia. Sequenced samples were fragmented with one part deposited at the University of Granada Herbarium (GDA) and the other sent to the Naturalis Biodiversity Center, Leiden, Netherlands (L) which will arrange for its transfer to a permanent repository in Indonesia as stated in the MTA.

AUTONOMOUS REEF MONITORING STRUCTURES

Three Autonomous Reef Monitoring Structures (ARMS) were installed in April 2021 at the reef slopes (8–10 m depth) of five sites (black triangles; Fig. 2). ARMS are passive samplers consisting of a stack of PVC plates separated by spacers, which creates small niches for colonization (Ip *et al.*, 2023). These standardized structures were designed to capture organisms that reside in cryptic habitats, which were not sampled in past surveys (Verheij, 1993b, 1994; Verheij & Erftemeijer, 1993). ARMS units were deployed for 16 months by the time of retrieval (1 unit lost from Langkai). Samples of distinct CCA communities were collected from the plates and dried. The entire thallus fragment was pulverized for DNA extraction.

In addition to the Spermonde Archipelago samples, recent collections from another reef system in Pangasinan, Philippines were loaned from the Gregorio T. Velasquez Phycological Herbarium (MSI) of the Marine Science Institute, University of the Philippines, Diliman, Quezon City, Philippines for comparison and to increase the sequence availability from Coral Triangle localities.

DNA extraction, amplification and sequencing

A cleaned area of the thallus surface was pulverized for DNA extraction using the NucleoSpin® 96 Tissue Core Kit (Macherey-Nagel, GmbH and Co. KG, Germany) following the manufacturer's instructions. DNA extraction and PCR amplification were done at the Service de Systématique Moléculaire (SSM) of the Muséum National d'Histoire Naturelle, Paris, France.

Primer pairs used to amplify and sequence barcoding markers were as follows: (1) *psb*A: psbA-F1/psbA-R1 (~851 bp product) or psbA-F1/psbA600R (~540 bp product; Yoon *et al.*, 2002); (2) COI-5P: GazF1/GazR1 or GazF1/GCorR3 primer pairs (~664 bp product; Peña *et al.*, 2015; Saunders, 2005); (3) *rbc*L: F1150Cor/R-rbcS start (~529 bp product; Freshwater & Rueness, 1994; Sissini *et al.*, 2014). PCR conditions followed Peña *et al.* (2015) for amplifying *psb*A and COI-5P markers and Ramos *et al.* (2024) for *rbc*L. The PCR products were purified and sequenced commercially (Macrogen Europe, Spain and Eurofins Scientific, France).

Raw sequence reads were evaluated, assembled, edited, and aligned using the Clustal implementation in CodonCode Aligner 10.0.3 (CodonCode Corporation, n.d.). Novel sequences (Table S2) were compared with selected sequences of Pacific CCA and coralline type sequences (Table S3) downloaded from GenBank. Newly generated *psb*A sequences <500 bp were excluded from the final phylogenies presented. COI-5P sequences had similar lengths while *rbc*L sequence lengths varied the most because of the shorter sequences typically obtained for type specimens (from 225 bp). Manual adjustments to the alignment were made when necessary. Separate alignments were assembled for each marker. The final assemblies were trimmed to 851 bp for *psb*A, 664 bp for COI-5P, and 1388 bp for *rbc*L. Outgroups selected for all datasets include representatives from subclass Rhodymeniophycidae and subclass Nemaliophycidae (Table S3). Percent sequence divergences (*p*-distances) were calculated with MEGA 11 (Tamura *et al*., 2021).

In total, 382 CCA collections from reef survey and opportunistic sampling and 127 CCA collections from the ARMS were processed for DNA extraction and amplification. We successfully obtained 203 sequences (126 *psb*A, 48 COI-5P, 29 *rbc*L) from 145 unique specimens collected. An additional 18 *psb*A sequences were obtained from Pangasinan (Philippines) collections. Multiple markers were sequenced for only 49 samples (see Table S2), so a concatenated dataset was not made.

Molecular analyses and species delimitation

Phylogenies were inferred through maximum likelihood (ML) and Bayesian Inference (BI) methods. The ML tree was generated in IQ-TREE 2.2.2.7 (Minh *et al*., 2020) using the best model selected by ModelFinder (Kalyaanamoorthy *et al*., 2017). Support for each node was calculated through 1000 non-parametric bootstrap replications. The BI consensus tree was inferred using MrBayes 3.2.7 running a GTR+I +Γ model for 3,000,000 (COI-5P and *rbc*L) or 65,000,000 (*psb*A) runs until the average standard deviation of split frequencies <0.01, the Effective Sample Size (ESS) 100, and the Potential Scale Reduction Factor (PSRF) ~ 1.0 for all parameters (Ronquist *et al*., 2012). A 25% burn-in was set before calculating posterior probability consensus trees.

Species delimitation algorithms were applied to provide an estimate of species richness represented by the number of molecular operational taxonomic units (OTUs). Two algorithms were used for all datasets, (1) Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al*., 2021) and (2) Bayesian implementation of Poisson tree process (bPTP; Zhang *et al*., 2013) through their respective web servers. The two highest ranked scenarios of ASAP and the Bayesian bPTP solution using the rooted ML tree as input (MCMC for 500,000 generations with 10% burn-in) are presented. The OTUs of our sequences were based on the agreement between two or more of the delimitation results. The *psb*A tree is presented since it was the largest dataset but OTUs were determined by considering the COI-5P and *rbc*L trees (Figs. S1–S2). When delimitation discrepancies were observed between different genes, the delimitation of the more variable marker was used (COI-5P or *rbc*L), which resulted in several OTUs not corresponding to the delimitations shown in Fig. 3. In cases where all delimitation results were different, the OTU was assigned by clade membership.

Morpho-anatomical observations

Sample fragments were processed for the scanning electron microscopes FEG-ESEM QemScan650F (Centro de Instrumentación Científica, Universidad de Granada) or JEOL JSM-6400 (Universidade da Coruña) and measured using ImageJ (Schneider *et al*., 2012). The congruence of molecular genus identifications with the anatomy observed from SEM images was compared for each sequenced sample except for ARMS samples which were completely pulverized. Nine sequences were excluded from the final alignments because molecular identifications did not match the expected morpho-anatomy for the identified genus. The ambiguity between the sequence and morpho-anatomy of the sample removed their utility for comparisons with the morpho-anatomical observations of previous CCA collections from the Spermonde Archipelago (Verheij, 1992, 1993a, 1993b, 1994). Supplementary Figs. S3–S14 show images of representative morpho-anatomical structures compared in the discussion.

RESULTS

The orders Corallinales (134 samples), Sporolithales (7 samples), and Hapalidiales (4 samples) were represented in the Spermonde Archipelago. Species delimitations ranged from 37–84 OTUs for *psb*A sequences (Fig. 3), 25–31 OTUs for COI-5P sequences (Fig. S1), and 19–25 OTUs for *rbc*L sequences (Fig. S2) depending on the method used. Evaluating the results from the three barcoding markers resulted in 63 OTUs in 11 genera, 2 unidentified Hapalidiales, and 1 unidentified Corallinales for all sampled reefs. Thirteen OTUs were assigned based on clade membership because there were no agreements among the species delimitation results. Three genera recorded previously, *Mesophyllum, Lithothamnion*, and *Mastophora*, were not detected (Table 1). We report four genera, *Parvicellularium, Harveylithon, Dawsoniolithon*, and *Lithoporella* for the first time from the Spermonde Archipelago. *Parvicellularium* was the most diverse genus in the Spermonde Archipelago (12 OTUs) followed by *Neogoniolithon* (10 OTUs), *Dawsoniolithon* and *Lithophyllum* (7 OTUs each). *Parvicellularium* was also identified in all sampling sites except Lae Lae. Forty-nine OTUs were from reef surveys and 18 were from ARMS, with only four OTUs shared between both collection methods. We encountered the same genera previously reported by Verheij (1993b, 1994) from the following sites: Samalona (*Spongites*), Kodingareng Keke (*Hydrolithon, Porolithon, Lithophyllum, Neogoniolithon, Spongites, Sporolithon*), and Langkai (*Hydrolithon, Neogoniolithon, Sporolithon*). Our sequences did not match the any of the seven previously reported species with *psb*A, COI-5P, or *rbc*L type sequences (last column of Table 1). Outside of Indonesia, sequences from the Spermonde Archipelago were most similar to those from western Pacific Ocean localities such as Guam, Taiwan, and the Philippines.

Table 1. Collection details (including depth of collection) and type sequence availability of species records in the Spermonde Archipelago, Indonesia.

Species	Collection sites [1,2]	Type Locality[3]	Type Sequence Availability
Lithophyllum bamleri (Heydrich) Heydrich	KK (5–10 m), LG (1–10 m), LY (0–5 m), BT (2 m), GU (1 m)	Tami Island, Huon Gulf, Papua New Guinea	
Lithophyllum kotschyanum Unger	BT (2m)	Gulf of Bahrain	LSU[4]: KP696794
Lithophyllum okamurae Foslie	LG (10–15 m)	Misaki, Japan	*psb*A[5]: MZ128805 LSU[5]: MZ129208
Lithophyllum pygmaeum (Heydrich) Heydrich = *L. tamiense* (Heydrich) Verheij	KK (2–5 m), LG (5–10 m), LY (1–5 m), GU (1–2 m), BT (1–2 m), KP (2 m)	Tami Island, Huon Gulf, Papua New Guinea	
Hydroltithon boergesenii (Foslie) Foslie = *Hydrolithon reinboldii* (Weber Bosse & Foslie) Foslie	BL (1–25 m), KK (1–2 m), SA (1 m), LG (1–15 m), LY (1–5 m), LL (1 m), BT (2–15 m), KP (2 m)	St Croix, U.S. Virgin Islands (*H. boergesenii*); Muaras Reef, East Kalimantan, Indonesia (*H. reinboldii*)	
Porolithon gardineri (Weber-Bosse & Foslie) Foslie = *Hydrolithon gardineri* (Foslie) Verheij & Prud'homme	LY (5–10 m)	Coetivy Reef, Seychelles	*rbc*L[6]: MZ419562
Porolithon onkodes (Heydrich) Foslie = *Hydrolithon onkodes* (Heydrich) Penrose & Woelkerling	KK (0–5 m), BB (0–5 m), LG (1–15 m), LY (0–5 m), SA (1 m), BL (1 m)	Tami Island, Gulf of Huon, Papua New Guinea	mitogenome[7]: KY212106 chloroplastid genome[7]: KY212107 nuclear genome[7]: KY212108
Mastophora pacifica (Heydrich) Foslie	KK (30 m)	Hawaiian Islands	
M. rosea (C.Agardh) Setchell	BL (2 m)	Guam, Mariana Islands	Several *psb*A and COI-5P from topotype specimens[8]
Neogoniolithon brassica-florida (Harvey) Setchell & L.R. Mason	BL (2–10 m), KK (1–25 m), SA (1m), LG (1–15 m), BT (2–35 m), LY (5 m)	Algoa Bay, Cape Province, South Africa	
Spongites sulawesiensis Verheij	BL (2–20 m holotype), BT (20 m), KK (5–25 m), SA (5 m)	Kodingareng Keke, Spermonde Archipelago, Sulawesi	
Lithothamnion proliferum Foslie	BL (1–5m), BT (2 m), LG (10 m)	Lumu-Lumu shoal (Pulau Lumulumu), Borneo Bank, Indonesia	
Melyvonnea madagascariensis (Foslie) Athanasiadis & D.L.Ballantine = *Mesophyllum erubescens* (Foslie) Me.Lemoine	BL (5–25 m), KL (25–35 m), SA (20–30 m)	Fort Dauphin (Taolagnaro), south Madagascar (*Mel. madagascariensis*); Fernando de Noronha, Brazil (*Mes. erubescens*)	
Mesophyllum funafutiense (Foslie) Verheij*	KK (15–35 m), BL (5 m), SA (5 m)	Tutange, Funafuti, Tuvalu	
Mesophyllum syrphetodes W.H.Adey, R.A.Townsend & Boykins*	KK (30–35 m), BT (35 m)	Southwest Molokai, Hawaii	
Sporolithon episoredion (W.H.Adey, R.A.Townsend & Boykins) Verheij	KK (15–20 m), LG (15–65 m)	St Rogatien Bank, Hawaii	*rbc*L[9]: OQ290685
Sporolithon episporum (M.Howe) E.Y.Dawson	KK (20 m), SA (1 m)	Point Toro, near Colón, Panama	*rbc*L[10]: KY994125
Sporolithon molle (Heydrich) Heydrich	SA (1–5 m), KK (5–15 m), LG (5–20 m), LY (1 m), BL (1 m), LL (1 m)	El Tor, Egypt	*rbc*L[10]: KY994121
Sporolithon ptychoides Heydrich	KK (5–30 m), BL (5–25 m), LL (1–2 m), SA (10–30 m), BT (15–30 m), LG (10 m)	El Tor, Egypt	*rbc*L[10]: KY994119

Only *psb*A, COI-5P, and *rbc*L sequences were used in this study. Type localities for heterotypic synonyms are included. Asterisks (*) indicate taxa with uncertain taxonomic status[3]. KK: Kodingareng Keke; LG: Langkai; LY: Lanyukang; BT: Bone Tambung; GU: Gusung; KP: Kapoposang; BL: Barang Lompo; SA: Samalona; LL: Lae Lae; BB: Bone Baku; KL: Kodingareng Lompo[1]Verheij, 1993b; [2]Verheij, 1994; [3]Guiry & Guiry, 2023; [4]Basso *et al.*, 2023; [5]Kato *et al.*, 2022; [6]Richards, Saunders *et al.*, 2021; [7]Gabrielson *et al.*, 2018; [8]Mills *et al.*, 2023; [9]Gabrielson, Hughey *et al.*, 2023; [10]Richards *et al.*, 2017

Fig. 3. Maximum Likelihood tree of *psb*A sequences from the Spermonde Archipelago (Indonesia) and Pangasinan (Philippines). Novel sequences are in boldface. Type-linked samples are underlined. Vertical black bars illustrate the species delimitations for our sequences (top 2 delimitations of ASAP and the Bayesian delimitation of bPTP). The OTU labels reflect species delimitation results of the COI-5P or *rbc*L phylogenies if they do not match the proposed delimitations indicated. Node support values ≥95/0.95 (bootstrap/posterior probabilities) are indicated by an asterisk (*) and values 70/0.90 were excluded.

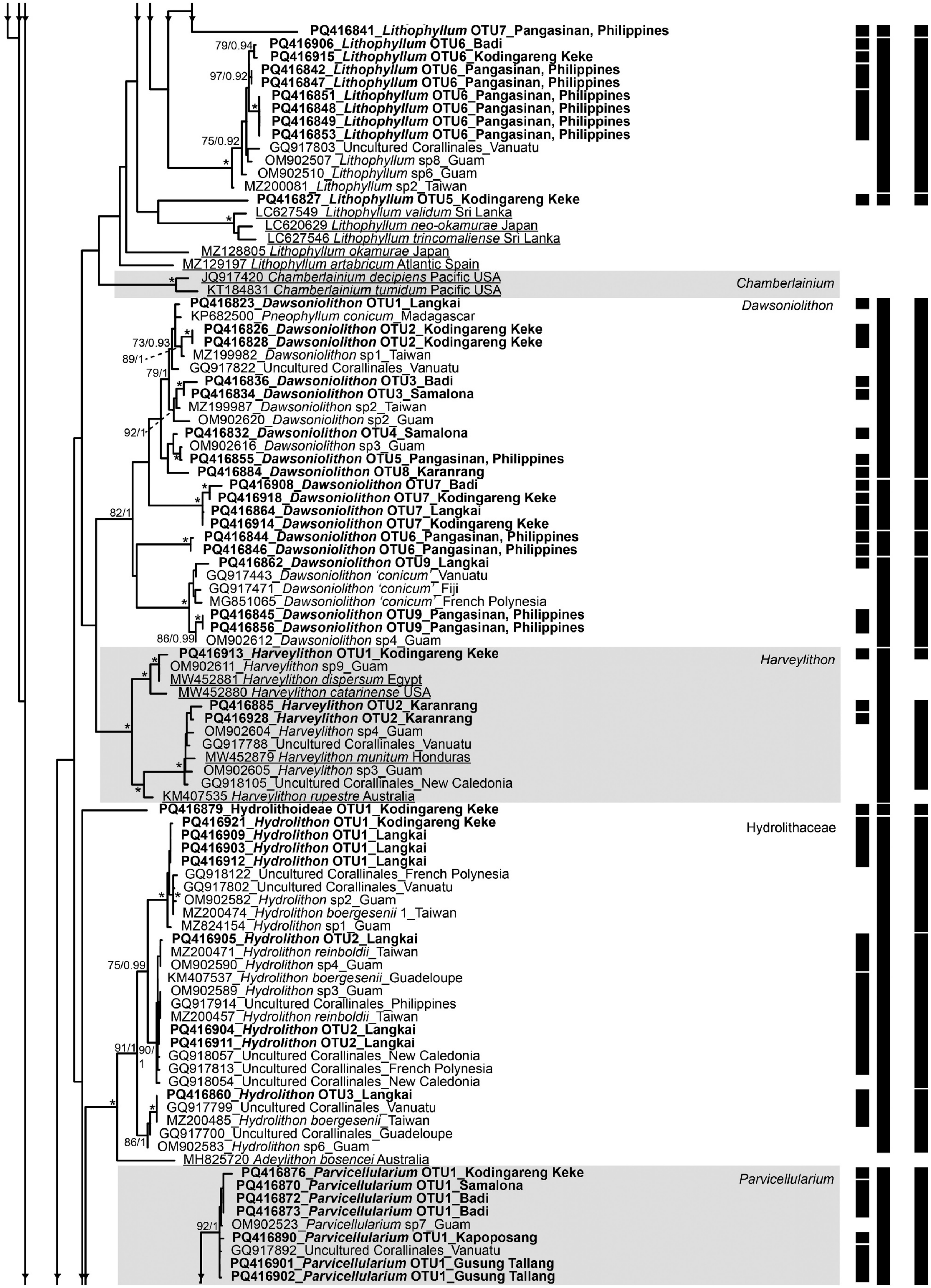

Fig. 3. (Continued).

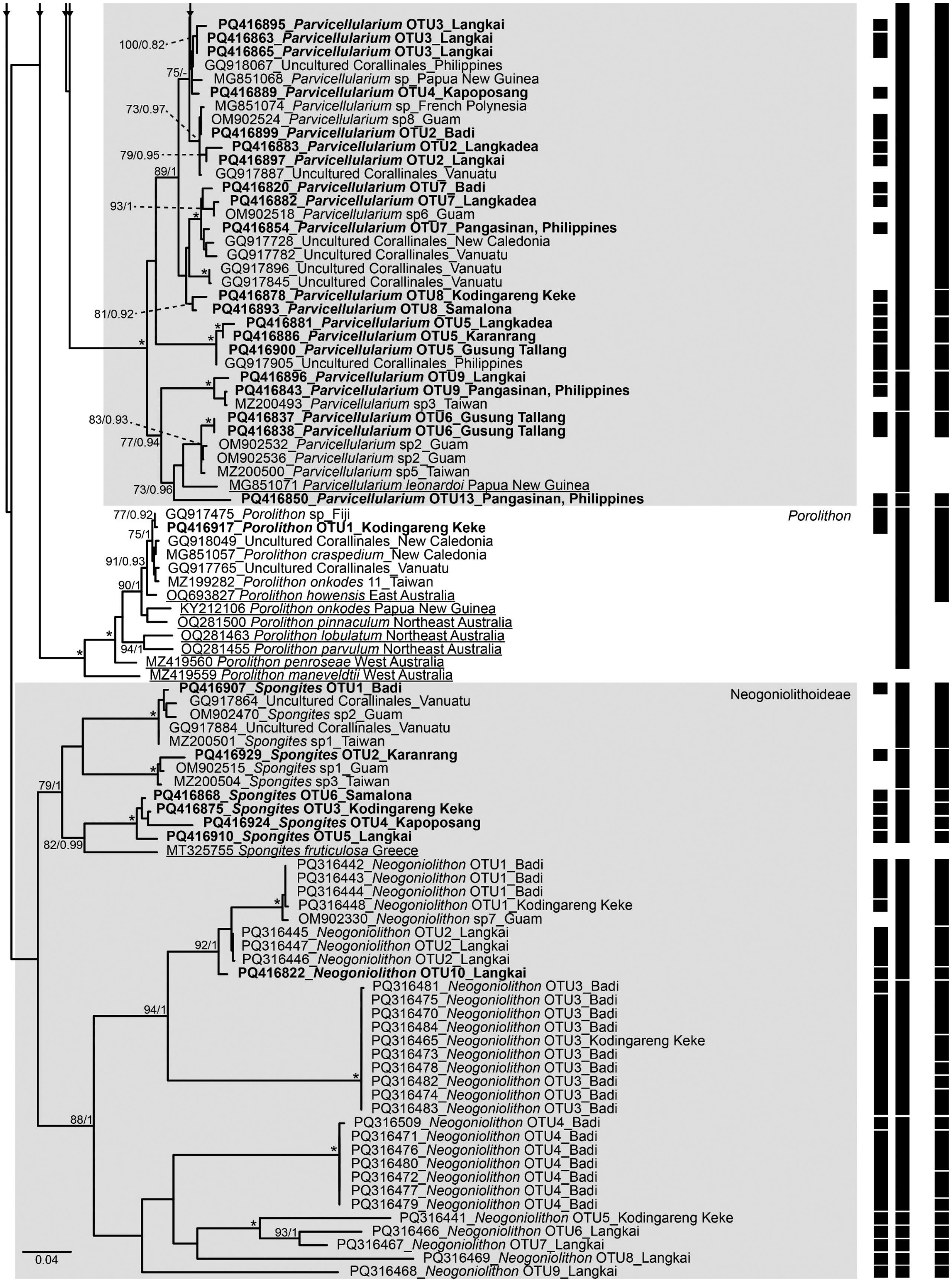

Fig. 3. (Continued).

Eleven OTUs from Pangasinan (Philippines) were delimited from 18 specimens. These OTUs represented the genera *Lithoporella* (1 OTU), *Lithophyllum, Dawsoniolithon* and *Parvicellularium* (3 OTUs each) in order Corallinales and *Crustaphytum* (1 OTU) in order Hapalidiales. The latter three genera are reported for the first time from the Philippines and only *Lithophyllum* was previously known from Pangasinan. Four of the eleven OTUs were unique to Pangasinan, while five were also found in the Spermonde Archipelago.

DISCUSSION

Comparisons of past and present CCA records in the Spermonde Archipelago

Molecular systematics introduced significant changes to the classification of CCA, and morpho-anatomical characters have been deemed unreliable resulting in several groups (subfamilies, genera, species) only differentiated with the use of sequence information (Caragnano *et al.*, 2018; Hind *et al.*, 2016; Rösler *et al.*, 2016). To reassess the CCA diversity in the Spermonde Archipelago, we sequenced samples from six of the 11 sites previously surveyed (Verheij, 1992, 1993a, 1993b, 1994; Verheij & Erftemeijer, 1993) and added three more, albeit from shallower depth ranges and focused primarily on reef-associated samples. Seven of the 11 genera of sequenced samples were consistent with the updated generic status of existing records in the Spermonde Archipelago (Guiry & Guiry, 2023). Three of the new generic records, [i.e. *Dawsoniolithon, Parvicellularium* (Caragnano *et al.*, 2018), and *Harveylithon* (Rösler *et al.*, 2016)], were described after molecular methods were incorporated into taxonomic research.

The abundance of cryptic species in CCA highlighted the importance of type sequences for species identification (Gabrielson *et al.*, 2018; Gabrielson, Hughey, *et al.*, 2023; Puckree-Padua *et al.*, 2021). Nine species reported from the Spermonde Archipelago already have type or topotype sequences (Table 1), one of which was an LSU sequence and could not be compared with our data. With some exceptions, genetic studies support the restricted range of coralline red algae (De Jode *et al.*, 2019; Maneveldt *et al.*, 2019; Yan *et al.*, 2024); therefore, the absence of type-sequenced species described from localities outside the Pacific Ocean (Table 1) was not surprising; however, none of the species from the Pacific Ocean were detected either. Given the observed lack of similarities between published type sequences (Table 1) and the species identified from the Spermonde Archipelago, we discuss below possible affinities between the previous species records and the delimited OTUs.

A phylogenetic study including the generitype sequence of *Spongites* resulted in the transfer of some species to either *Chamberlainium* or *Dawsoniolithon* (Caragnano *et al.*, 2018). We can confirm the presence of *Spongites* and *Dawsoniolithon* in the Spermonde Archipelago but *Chamberlainium* was not detected, having only been documented from temperate regions (Caragnano *et al.*, 2018; Zhan *et al.*, 2022). *Dawsoniolithon* OTU9 resolved with the reference sequences for the selected generitype, *Dawsoniolithon conicum* (E.Y.Dawson) Caragnano, Foetisch, Maneveldt & Payri (Caragnano *et al.*, 2018), but these were not from the type specimen so the correct assignation of this name remains doubtful.

Having been recognized earlier as the same genus, *Spongites* and *Dawsoniolithon* OTUs were compared with *Spongites sulawesiensis* Verheij, and an unidentified *Spongites* were described from the Spermonde Archipelago (Verheij, 1993a, 1994). These *Spongites* specimens exhibited monomerous thallus construction similar to the *Dawsoniolithon* OTUs but unlike the dimerous construction of our *Spongites* OTUs. Our specimens of *Spongites* and *Dawsoniolithon* OTUs bore conceptacles that were much smaller than *S. sulawesiensis* (Verheij, 1993a). Instead, *S. sulawesiensis* more closely resembled several of our *Parvicellularium* OTUs, a resemblance also noted in the circumscription of the genus (Caragnano *et al.*, 2018). However, *S. sulawesiensis* possesses a non-coaxial hypothallus in contrast to our *Parvicellularium* samples, where coaxial hypothallial arrangement was predominant. Unfortunately, we could not locate the type specimen of *S. sulawesiensis* in the Naturalis Biodiversity Center (L) for DNA extraction or more extensive morpho-anatomical comparisons. Since our samples did not sufficiently conform to the species' morpho-anatomical description, we cannot select a suitable topotype specimen to represent it in molecular phylogenies.

Verheij (1994) used the name *Neogoniolithon brassica-florida* (Harvey) Setchell & L.R.Mason for all *Neogoniolithon* collections from the Spermonde Archipelago but recognized three growth forms (i.e. crustose – '*ecad fosliei*', warty – '*ecad laccadivicum*', and branching – '*ecad frutescens*') and intermediate forms. The *Neogoniolithon* OTUs include encrusting (9 OTUs) and warty (1 OTU) forms. Several studies of *Neogoniolithon* show high diversity, crypsis and endemism in the genus, including in the Spermonde Archipelago (Bittner *et al.*, 2011; Kato *et al.*, 2013; Mateo-Cid *et al.*, 2014; Ramos *et al.*, 2024). It is unlikely that the widely reported *N. brassica-florida* described from South Africa is present in the Spermonde Archipelago. Unfortunately, attempts to obtain sequences from type specimens have been unsuccessful so the correct assignment of specimens to older names remains difficult. The 10 *Neogoniolithon* OTUs found in just three islands in the Spermonde Archipelago show the high diversity of this genus in our study area, exceeding the species richness currently known from the Coral Triangle (6 spp.; Atmadja & Prud'homme van Reine, 2010; Fabricius *et al.*, 2015; Lastimoso & Santiañez, 2021; Trono *et al.*, 1985; Verheij, 1994; Womersley & Bailey, 1970).

Four *Lithophyllum* species were reported in the Spermonde Archipelago: *L. bamleri* (Heydrich) Heydrich, *L. kotschyanum* Unger, *L. pygmaeum* (Heydrich) Heydrich (as *L. tamiense* (Heydrich) Verheij) and *L. okamurae* Foslie (Atmadja & Prud'homme van Reine, 2010; Verheij, 1994). The fruticose *L. bamleri* and *L. tamiense* were some of the more dominant coralline algae of the reef crests of the southeastern Spermonde Archipelago (Verheij, 1994). We were unable to collect samples from the reef crest but can confirm the abundance of branching *Lithophyllum* species in the adjacent reef flat, growing on the branch axes of subdichotomous forms of the coral *Acropora*. Three *Lithophyllum* OTUs were delimited possessing flattened or plate-like (OTUs 1 and 8) and more cylindrical (OTU6) branches described for *L. bamleri* and *L. tamiense*, respectively (Verheij, 1994). Both species were described from Papua New Guinea but their types are not yet sequenced. Unlike other *Lithophyllum* species reported from the Spermonde Archipelago, OTUs 2 and 3 have a dimerous thallus construction. *Lithophyllum* OTUs 4 and 5 were only sequenced from ARMS samples (no SEM images produced) and will need further collections for morpho-anatomical examinations. None of the OTUs conformed to morpho-anatomical descriptions of *L. kotschyanum* or *L. okamurae* (Verheij, 1994) nor were they similar to the type sequence for the latter (Kato *et al.*, 2022).

Samples anatomically referable to *Titanoderma* included GDA 73871 (OTU3; PQ416919) and MSI 30808 (OTU7; PQ416841; Pangasinan, Philippines). These and *Lithophyllum* OTU4 sequences were also genetically similar to sequences belonging to clades identified as *Titanoderma* (Yan *et al.*, 2024). The phylogenetic relationships between these sequences and the other *Lithophyllum* sequences were not clear in our results (low support). We retain these under *Lithophyllum* until generitype sequences of *Titanoderma* are available, but it should be noted that the tropical clades of *Lithophyllum* might correspond to different genera since the *Lithophyllum* generitype clade was restricted to temperate Europe (Yan *et al.*, 2024).

Porolithon OTU1 samples were morpho-anatomically similar to *Porolithon onkodes* (Heydrich) Foslie depicted by Verheij (1994). Even though the *psb*A delimitation for our sample was unclear, *Porolithon* OTU1 was distinct from the *P. onkodes* lectotype in both ASAP1 and bPTP for the *psb*A data as well as all COI-5P delimitations. The name *P. onkodes* is known to represent several cryptic species (Gabrielson *et al.*, 2018) and our samples seem to be part of this species complex. Our *Porolithon* OTU1 *psb*A sequence was more similar to *Porolithon howensis* S.Y.Jeong & G.Diaz-Pulido than *P. onkodes* but we suspect our samples to be a different species because *P. howensis* produces a lumpy thallus with short, robust branches. Obtaining rbcL sequences from *Porolithon* OTU1 is needed for comparison with the *P. howensis* holotype to check if there is additional support for this hypothesis. Without *Porolithon rbc*L sequences, we were also unable to confirm the presence of the other species reported from the Spermonde Archipelago, *P. gardineri* (Foslie) Foslie (Richards, Saunders, *et al.*, 2021; Verheij, 1994).

Hydrolithon reinboldii (Weber Bosse & Foslie) Foslie, the generitype, was reported as one of the most common species on the reef flat of the Spermonde Archipelago (Verheij, 1994). It was synonymized under *H. boergeseni* (Foslie) Foslie (Rösler *et al.*, 2016) but this synonymy has been questioned since no type sequences were available and even sequences of *H. boergeseni*/*H. reinboldii* samples collected near the type locality of *H. boergesenii* in the Caribbean segregated into different phylogenetic clades (Richards, Saunders, *et al.*, 2021). *Hydrolithon reinboldii* was described from Muaras Reef, East Kalimantan, across the Makassar Strait from the Spermonde Archipelago so its presence in our sites is possible. *Hydrolithon* OTU2 exhibited a lumpy growth form similar to the *H. reinboldii* lectotype (Penrose & Woelkerling, 1988, Fig. 1) and the sample from the Spermonde Archipelago (Verheij, 1994, Fig. 36). Sequencing the lectotype and additional samples with this morphology will determine if it is characteristic for the species. Other *Hydrolithon* and Hydrolithoideae OTUs were encrusting and did not form protuberances. The anatomical similarities of the different *Hydrolithon* OTUs suggests that several species may have been lumped under *H. reinboldii*.

Harveylithon was established to accommodate *Hydrolithon* species with plumose hypothallial arrangement (Rösler *et al.*, 2016). While *Harveylithon* OTU1 was delimited as a separate species in ASAP1 and bPTP, OTU2 delimitations were not congruent at all. The *psb*A sequence of *Harveylithon* OTU2 diverged from a type-matched sample of *H. munitum* A. Rösler, Perfectti, V.Peña & J.C.Braga (NCU 673213) by 1.13–1.91%, falling between the reported intraspecific (up to 0.79%) and interspecific (2.5%9.34%) ranges of some *Harveylithon* species (Costa *et al.*, 2019). The different delimitations obtained may be a result of the smaller variability of *psb*A compared to COI or *rbc*L. Richards *et al.* (2021) recommended these two latter markers for species delimitation in *Harveylithon*. Since only *psb*A sequences were obtained from our samples, we could not verify the conspecificity of OTU2 with *H. munitum*.

Even though it was reported from the Spermonde Archipelago (Verheij, 1994), we could not genetically confirm the presence of *Mastophora*. Sequences of samples morpho-anatomically resembling *Mastophora* formed a clade that was designated as *Lithoporella* and distinct from other sequences identified as *Mastophora* (Fig. 3) including samples from the locality of the generitype, *M. rosea* (C.Agardh) Setchell (Mills *et al.*, 2022). *Lithoporella* is vegetatively indistinguishable from *Mastophora* but differs in tetrasporangial conceptacle development (Turner & Woelkerling, 1982a, 1982b). Although we were unable to observe their development, tetrasporangial conceptacles of the *Lithoporella* OTUs had roof filaments that appear to be derived from Type 2 development and lacked a columella. *Lithoporella* OTUs 1,2, 3 and 5 exhibited a high degree of overgrowth by applanate branches to produce a thicker, compact thallus similar to *M. multistrata* Keats (Keats *et al.*, 2009). Applanate branching was also observed in *M. pacifica* (Heydrich) Foslie from the Spermonde Archipelago but did not appear to generate thicker thalli (Verheij, 1994, Fig. 39). Our molecular phylogenies support the recognition of what we considered *Lithoporella* and *Mastophora* as distinct genera but type or topotype sequences of the *Lithoporella* generitype are needed to confirm this identification since these genera were differentiated based only on morpho-anatomy (Turner & Woelkerling, 1982a, 1982b).

Athanasiadis & Ballantine (2014) reassigned specimens identified as *Mesophyllum erubescens* from the Spermonde Archipelago to *Melyvonnea madagascariensis* (Foslie) Athanasiadis & D.L.Ballantine. Our *Melyvonnea* samples belonged to the same clade as *M. erubescens* but diverged by 7.50–7.73% (*psb*A) and 8.78% (*rbc*L) from the holotype, supporting its separation from this species. With the absence of sequences from the generitype *M. canariensis* (Foslie) Athanasiadis & D.L.Ballantine, *M. erubescens* (Foslie) Athanasiadis & D.L. Ballantine has represented the genus due to its type sequence availability but the species name has also been applied to multiple cryptic species (Gabrielson, Maneveldt, *et al.*, 2023; Richards *et al.*, 2020; Sissini *et al.*, 2014). Our samples conformed to the description of *M. madagascariensis* by Verheij (1994) and exhibited the sunken rosette cells described for the genus (Athanasiadis & Ballantine, 2014). Despite the discovery of cryptic species under this genus (Sissini *et al.*, 2014; Zhan *et al.*, 2022), no additional species has been described since its circumscription. *Crustaphytum* is another genus genetically distinct but superficially similar to *Mesophyllum*/*Melyvonnea* (Liu *et al.*, 2023) and is reported here for the first time in the Philippines, based on a *psb*A sequence of a sample from Bolinao, Pangasinan.

Lithothamnion proliferum Foslie was reported from the Spermonde Archipelago (Verheij, 1994) but we were unable to confirm this genus from our data. Instead of *Lithothamnion*, we obtained two Hapalidiales OTUs that did not resolve with any other sequenced Hapalidiales genera. Our OTUs resolved as a sister group to the *Boreolithothamnion* clade with low bootstrap support (*psb*A and *rbc*L). *Boreolithothamnion* species were formerly under *Lithothamnion* until it was split up into several genera (Coutinho *et al.*, 2021; Gabrielson, Maneveldt, *et al.*, 2023). Based on their separation from other Hapalidiales, our OTUs could represent an undescribed genus.

Five *Sporolithon* OTUs were delimited as distinct species by ASAP1 and bPTP but OTU2 was resolved with *S. ptychoides* Heydrich by bPTP. It is unclear if OTU2 is conspecific with *S. ptychoides* from the *psb*A data, so additional markers from OTU2 are needed to assess their relationship. *Sporolithon rbc*L sequences (OTUs 1, 4, 5) were distinct from the four species reported (Verheij, 1994) and other Indonesian species, *S. sibogae* (Weber Bosse & Foslie) P.C. Silva and *S. timorense* (Foslie) P.C.Silva (Gabrielson, Hughey, *et al.*, 2023). *Sporolithon* OTUs 1–4 were morpho-anatomically similar to the *S. ptychoides* or *S. molle* which are difficult to distinguish from one another (Richards *et al.*, 2017), while OTU5 lacked reproductive structures for comparison. None of the *Sporolithon* OTUs shed their sori, typical to *S. episporum* (M.Howe) E.Y.Dawson, nor had large (>180 μm long) tetrasporangia as in *S. episoredion* (W.H. Adey, R.A.Townsend & Boykins) Verheij. We did not attempt to sequence Verheij´s samples because of their formalin preservation. Apart from *S. ptychoides*, it is unlikely that the species names he applied would be confirmed by sequence data considering the large geographic distances between the type localities and the Spermonde Archipelago (Table 1).

CCA in cryptic habitats

ARMS sampling complements reef survey collections by targeting different communities. Where CCA cover is often underestimated in visual reef surveys (Dean *et al.*, 2015; Fabricius *et al.*, 2015), it is one of the dominant organisms on ARMS plates (Lee *et al.*, 2024; Sembiring *et al.*, 2023). Our results demonstrated that the CCA in our ARMS survey is very different from those in exposed reef, sharing only four OTUs. CCA in ARMS could represent primary colonizers, species that tolerate darker conditions, or species that are outcompeted in more exposed environments. Questions regarding the environmental preferences of CCA species and how the communities occupying the internal structure affect the natural reef, such as in inducing settlement of reef organisms, and more broadly how it shapes biodiversity patterns and ecosystem services are interesting avenues for research.

As availability of genetic data increases, ARMS will become more useful for monitoring CCA communities. We recommend that taxonomic vouchers also be collected, if possible, before they undergo the usual protocol (i.e. scraping the plates clean and homogenizing the scrapings); otherwise, the sequence data would remain unlinked to physical specimens. For taxonomic purposes, it may be better to conduct targeted sampling for these communities using stacked settlement plates rather than complete ARMS units. Lee *et al.* (2024) noted that universal COI metabarcoding markers produced poor DNA yield for CCA relative to the abundance observed on the ARMS plates. Development of CCA-specific metabarcoding markers are needed to increase yield of CCA sequence reads which might improve taxonomic resolution, and overall enhance the efficacy of the process for monitoring CCA diversity (Govender *et al.*, 2022).

Biogeographic relationships of OTUs in the Spermonde Archipelago

Molecular analyses revealed that few species of non-geniculate coralline algae were distributed over wide geographic ranges (Maneveldt *et al.*, 2019) and some species, despite small genetic divergence, have been kept distinct due to large geographic distances (Jeong *et al.*, 2023; Jesionek *et al.*, 2020). Our results supported this pattern as sequences of an OTU were more similar the closer they were geographically. The number of OTUs shared with other Western Pacific Ocean localities also far exceeds those shared with areas farther out (i.e. Vanuatu, French Polynesia, and Egypt). Although possibly an artefact of limited sampling, ~56% of OTUs were only found in the Spermonde Archipelago. These results in turn highlight the few cases of species such as *Lithophyllum longense* Hernández-Kantún, P.W.Gabrielson & R.A.Townsend (Maneveldt *et al.*, 2019) or *N.* '*brassica-florida*' (Clade 2A in Ramos *et al.*, 2024) with seemingly extensive ranges. Long range dispersal would have to depend on water movement directly carrying the spores or a vector, such as grazers or substrates of the algae, or rafting on more mobile animals or man-made structures (Santelices, 1990). Large spatial gaps in species occurrences and lack of population genetics research hinder our understanding of CCA distributions and the extent of genetic exchange from which dispersal ranges might be indirectly inferred.

CCA of the coral triangle

The Coral Triangle situated in the tropical Pacific Ocean is recognized as a biodiversity hotspot (Veron *et al.*, 2009), especially for coral reefs, but updated information on CCA diversity is lacking. Extensive barcoding studies conducted in other areas of the Pacific Ocean such as in Guam (106 OTUs) and New Zealand (122 OTUs) resulted in CCA diversities that were several times higher than previous morpho-anatomical records (Gordon *et al*., 1976; Mills *et al*., 2022; Twist *et al*., 2019; Woelkerling & Nelson, 2004) while the first molecular surveys of subtropical algal reefs in Taiwan revealed the highest CCA diversity (151 OTUs) in the Pacific Ocean to date (Liu *et al*., 2018; Zhan *et al*., 2022). In comparison, 79 OTUs of coralline red algae (63 non-geniculate coralline algae OTUs) were delimited from biogenic reef surveys in Brazil (Sissini *et al*., 2022).

The linear relationship between the abundance and diversity of reef-associated CCA and the development of tropical coral reefs (Teichert *et al*., 2020) implies that we can expect a high diversity of CCA in the Coral Triangle, where corals have diversified to at least 500 species (Veron *et al*., 2009). Our study is the first molecular survey of CCA in the Coral Triangle and the 63 OTUs delimited from the Spermonde Archipelago already exceeds the species richness known from Indonesia. Morpho-anatomical identifications in previous studies reported the highest CCA richness in Indonesia (53 spp.; Atmadja & Prud'homme van Reine, 2010; Verheij, 1994) and the Philippines (35 spp.; Lastimoso & Santiañez, 2021; Trono *et al*., 1985) while fewer species were known from other constituent territories of the region, such as in Papua New Guinea (15 spp.; Fabricius *et al*., 2015; Millar *et al*., 1999), Solomon Islands (12 spp.; Womersley & Bailey, 1970), and Malaysia (4 spp.; Phang *et al*., 2016). Given the general lack of taxonomic research on CCA in these areas, there is a high likelihood for discovering taxa unknown to science using modern methods. The large gap in taxonomic knowledge that currently exists between corals and coralline algae in the Coral Triangle should be addressed to better understand the interactions between these two reef builders to aid in the management and conservation of reef systems and the diversity they support.

Including this study, 23 genera of non-geniculate coralline algae have been reported in the Coral Triangle (Table S4). Our sequences represented nine of the 11 genera under order Corallinales, and *Sporolithon*, the only genus of order Sporalithales reported. Order Hapalidiales was poorly represented in our data (2/11 genera). Like other barcoding studies in the Pacific Ocean (Mills *et al*., 2022; Twist *et al*., 2019), only a small proportion of our OTUs were genetically similar to sequences of confirmed species, reflecting the lack of sequenced type specimens while also suggesting an abundance of taxa that are putatively new to science.

Conclusions

The first molecular analysis of CCA from the Coral Triangle revealed high phylogenetic diversity at least three times richer than previously known in the Spermonde Archipelago, Indonesia, and Pangasinan, the Philippines. Cryptic diversity was evident in all genera from initial observations of the morpho-anatomy of different OTUs. We expect the true diversity to be even higher since sequences were successfully obtained from roughly a third of the samples collected, and study sites were restricted to a narrow depth range and from a small number of the ~120 islands in the archipelago. Our results echo similar studies in the Pacific Ocean that demonstrate the incredibly high diversity in this region. This study provides much needed information about the CCA diversity in the Coral Triangle where modern taxonomic research on these organisms is very limited.

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