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New genus and species record of reef coral *Micromussa amakusensis* in the southern South China Sea



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Abstract

Background: Recent taxonomic revisions of zooxanthellate scleractinian coral taxa have inevitably resulted in confusion regarding the geographic ranges of even the most well-studied species. For example, the recorded distribution ranges of *Stylophora pistillata* and *Pocillopora damicornis*, two of the most intensely researched experimental subjects, have been restricted dramatically due to confounding cryptic species. *Micromussa* is an Indo-Pacific genus that has been revised recently. The revision incorporated five new members and led to substantial range restriction of its type species and only initial member *M. amakusensis* to Japan and the Coral Triangle. Here, we report the presence of *Micromussa amakusensis* in Singapore using phylogenetic methods.

Results: A total of seven *M. amakusensis* colonies were recorded via SCUBA surveys at four coral reef sites south of mainland Singapore, including two artificial seawall sites. Colonies were found encrusting on dead coral skeletons or bare rocky substrate between 2 and 5 m in depth. Morphological examination and phylogenetic analyses support the identity of these colonies as *M. amakusensis*, but the phylogeny reconstruction also shows that they form relatively distinct branches with unexpected lineage diversity.

Conclusions: Our results and verified geographic records of *M. amakusensis* illustrate that, outside the type locality in Japan, the species can also be found widely in the South China Sea. Moreover, our discovery provides a new genus and species record in Singapore and represents the southern-most occurrence of the species in the Indo-Pacific. Despite the extensive survey efforts in Singapore over the last three decades, taxonomic studies integrating morphological and molecular methods remain instrumental in quantifying the actual coral species diversity.

Keywords: Coral reef, Integrative taxonomy, Phylogenetics, Scleractinia, Singapore

Background

Reef-building corals are amongst the most extensively studied animals in the marine environment. At the turn of the millennium, the diversity and distribution of zooxanthellate stony coral species (Cnidaria: Anthozoa: Scleractinia) had appeared to be precisely characterised and resolved (Veron 1995, 2000, 2002). Yet, phylogenetic analyses performed in the last two decades have shown the need for a plethora of taxonomic revisions (Fukami et al. 2004, 2008; Budd et al. 2010;

Gittenberger et al. 2011; Benzoni et al. 2012, 2014; Arrigoni et al. 2016a; Kitahara et al. 2016). These changes are impacting our understanding of the distribution of even the most intensely researched species (Obura 2016).

Stylophora pistillata Esper, 1797 (Pocilloporidae), for instance, is considered a 'lab rat' for coral experimental studies (Keshavmurthy et al. 2013), owing to it being purportedly common and wide-ranging, both geographically and ecologically (Veron and Pichon 1976; Veron 2000). Comprehensive sampling throughout most of its range, from the Red Sea and Persian/Arabian Gulf to the western Pacific Ocean, has revealed that it comprises four distinct lineages, with two of them

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more closely related to *Seriatopora hystrix* Dana, 1846 than the remaining lineages of *S. pistillata sensu lato* (Keshavmurthy et al. 2013). The considerable genetic variation despite limited morphological distinction among these lineages (Stefani et al. 2011) means that biological and ecological inferences made at the species level have to be constrained within each of the four regions spanned by these lineages (Central Indo-Pacific, Chagos-Madagascar-South Africa, Gulf of Aden-Zanzibar-Madagascar, and Red Sea-Persian/Arabian Gulf-Kenya).

Similarly, for *Pocillopora* Lamarck, 1816 (Pocilloporidae), detailed taxonomic work on the genus has revealed that many colonies previously identified as the widespread and common *P. damicornis* Linnaeus, 1758, may actually be *P. acuta* Lamarck, 1816 (Schmidt-Roach et al. 2014). Also a well-studied 'lab rat' for experimental work in the Indo-Pacific (e.g. Ben-Haim et al. 2003; Cumbo et al. 2013; Poquita-Du et al. 2019a), many *P. damicornis*-like colonies have been confirmed to be *P. acuta* at multiple localities, including Japan (Kitano et al. 2015), Philippines (Torres and Ravago-Gotanco 2018), Singapore (Poquita-Du et al. 2017), American Sāmoa (Montgomery et al. 2019), Austral and Cook Islands (Mayfield et al. 2015), and Hawai'i (Johnston et al. 2018). These discoveries have wide-ranging impacts, even for the evaluation of species conservation status (see Agapow et al. 2004; Mace 2004; Ely et al. 2017). For example, a recent investigation of the identity of *Pocillopora* colonies in Singapore has shown that *P. acuta* is the only pocilloporid species remaining on its reefs following the historical loss of four species driven by habitat loss, coastal urbanisation and coral bleaching (Poquita-Du et al. 2019b). Due to the rapidly changing environment impacting corals locally and worldwide (Pandolfi et al. 2003; Hughes et al. 2014, 2017), the distribution of coral taxa ought to be assessed continually, particularly for those that have been revised taxonomically.

Micromussa Veron, 2000 (Lobophylliidae), is an Indo-Pacific genus with type species *Acanthastrea amakusensis* Veron, 1990, from Amakusa Island, Japan. Possessing gross morphological characteristics similar to the Indo-Pacific genus *Acanthastrea* Milne Edwards & Haime, 1848, it was initially recognised as a separate genus due to the smaller corallite diameter of ≤ 8 mm for its first members—*M. minuta* (Moll & Best, 1984), *M. amakusensis*, and *M. diminuta* Veron, 2000 (Veron 2000). The genus was later said to be established 'to include species of *Acanthastrea* with corallites less than 5 mm diameter' (Veron 2002: 127). Based on more recent analyses integrating molecular and morphological data by Arrigoni et al. (2016a) and Huang et al. (2016), *M. minuta* was reverted to *Acanthastrea minuta*, *M. diminuta* moved to *Goniopora*, and three existing species

transferred into *Micromussa*, namely *A. lordhowensis* Veron & Pichon, 1982, *Montastrea multipunctata* Hodgson, 1985, and *A. regularis* Veron, 2000. Two new species, *Micromussa indiana* Benzoni & Arrigoni, 2016 and *M. pacifica* Benzoni & Arrigoni, 2016, were also described (Arrigoni et al. 2016a).

Following these extensive revisions, the type species of *Micromussa* and its only initial member *M. amakusensis* had its recorded range reduced to Japan and the Coral Triangle, while the genus remained widespread in the Indo-Pacific, ranging from the southern Red Sea to French Polynesia. Past records from the disjointed range in the southern Red Sea and western Indian Ocean (Veron 2000) have been attributed to the new species *M. indiana* (Arrigoni et al. 2016a).

In this study we reassess the distribution range of *M. amakusensis* based on records in the northern and eastern South China Sea, as well as introduce a new genus and species record in Singapore.

Results

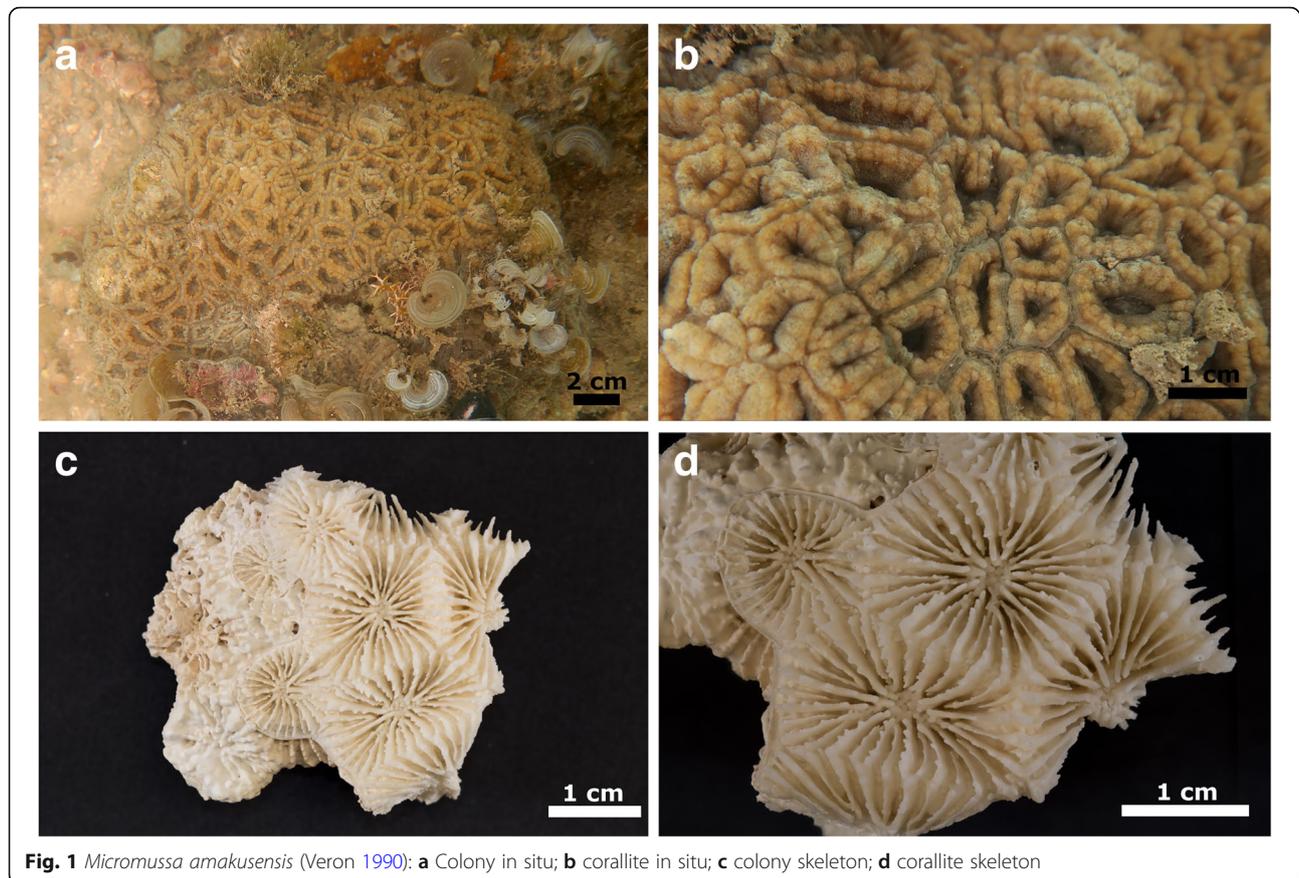
Field observations

A total of seven colonies were observed via SCUBA surveys at four sites among the southern islands of Singapore. Two of the sites were fringing reefs at Kusu Island (1°13'31.57"N, 103°51'35.71"E) and Sultan Shoal (1°14'21.48"N, 103°38'52.89"E). The other two sites were on granite rock seawalls on the eastern (1°13'42.71"N, 103°51'18.90"E) and western (1°13'47.87"N, 103°50'55.65"E) shores of Lazarus Island. Colonies, seen at depths of 2–5 m below chart datum, encrusted on dead coral skeletons or bare rocky substrate. The average size of the colonies at Kusu and Lazarus Islands was 19.7 ± 4.3 cm (geometric mean diameter \pm SD, $n = 5$).

Morphological identification

Colonies of *Micromussa amakusensis* are encrusting, with a thick fleshy mantle, and are light brown to mottled red-yellow in colour. Both intra- and extracalicular budding modes are observed. Corallites are mostly ceroid with a variable diameter ranging from 7 to 15 mm, and a relief of 3–6 mm. Corallite shapes range considerably, with some corallites having regular outlines and others being more elongate. The few widely-spaced corallites are separated by a groove filled with sediment and algae when alive. Septa are in 3–4 cycles (24–36 septa), each with 3–5 large septal teeth, and granules are scattered on the septal face. Free septa are irregularly arranged. The columella, 1–3 mm in diameter, is spongy (Fig. 1).

Species similar to *M. amakusensis* include *M. multipunctata*, which is distinctly plocoid and has less variable, smaller corallites (up to 9 mm in diameter) (Hodgson 1985); and *M. lordhowensis*, which has larger



and more angular corallites (up to 20 mm in diameter) (Veron and Pichon 1980; Turak and DeVantier 2011; Arrigoni et al. 2016a).

Phylogenetic analysis

Our phylogeny reconstruction recovers the same genus clades as Arrigoni et al. (2016a) and Huang et al. (2016) (Fig. 2; see also Arrigoni et al. 2016b, 2019). In particular, *Micromussa* forms a sister clade to *Homophyllia* (bootstrap support or BS = 71, posterior probability or PP = 1), and both are a strong sister group to *Australophyllia wilsoni* (BS = 100, PP = 1). The five *Micromussa* spp. included here form a well-supported clade (BS = 100, PP = 1). Both specimens from Singapore are in a clade comprising *M. amakusensis* and *M. multipunctata* with moderate support (BS = 66, PP = 1). Interestingly, while *M. multipunctata* is a well-supported clade (BS = 93, PP = 1), *M. amakusensis* sequences form a paraphyly. The distinct lineages represent previously unreported species-level diversity, but the limited sampling in terms of specimens (seven) and geography (Japan and Singapore) suggests that a more comprehensive collection is needed to characterise this species precisely.

Taken together, the morphological observations and phylogenetic analyses support the new genus and species record of *M. amakusensis* in Singapore.

Discussion

Micromussa amakusensis has been documented widely from the Indo-Pacific, but is poorly studied and considered globally rare (Arrigoni et al. 2016a; Veron et al. 2016). The species was first recorded in western Thailand, Tanegashima Island and mainland Japan (including Amakusa Island after which the species was named), and Vanuatu (Veron 1990). Its known distribution range was then expanded to include the Central Indo-Pacific, western Pacific, Gulf of Aden and the southern Red Sea (Veron 2000).

Two studies following the above range characterisation have led to increasing restriction of the range of *M. amakusensis*. First, a treatise of all scleractinian corals in Moreton Bay, eastern Australia, suggests that a species there recognised as *M. amakusensis* may be distinct from the holotype of Amakusa Island due to the more abundant septa (Wallace et al. 2009). Second, according to Veron (2000), records from the central Pacific appear to be doubtful, and furthermore, no examination of



Fig. 2 Maximum likelihood phylogeny of Lobophylliidae with Merulinidae outgroups *Orbicella annularis*, *Goniastrea retiformis* and *Merulina ampliata*. Dataset combines Lobophylliidae sequences from Huang et al. (2016) and *Micromussa* sequences from Arrigoni et al. (2016a) and this study. *Micromussa amakusensis* sampled from Singapore indicated in bold (REL0471 = ZRC.CNI.1392; REL0473 = ZRC.CNI.1393). Filled circles represent maximum likelihood bootstrap support of ≥ 80 and Bayesian posterior probability of 1, while unfilled circles represent bootstrap support of ≥ 50 and posterior probability ≥ 0.8

specimens have been reported. This casts doubt on the *M. amakusensis* records in central and western Pacific (Veron 2000), including one from Papua New Guinea (Turak and DeVantier 2007). The Red Sea and western Indian Ocean records have also been affirmed as *M. indiana* based on an integrative morpho-molecular analysis (Arrigoni et al. 2016a). Consequently, *M. amakusensis*' distribution range has been limited to Japan and the western part of the Coral Triangle *sensu* Hoeksema (2007) (see also Arrigoni et al. 2016a).

Our consolidated records of *M. amakusensis* from published literature show that the species is known to occur outside the type locality in Japan. In particular, published records are known in the northern and eastern South China Sea—in Vietnam (Vo et al. 2002), Hong Kong (Ang et al. 2003; Chan et al. 2005), Brunei (Turak and DeVantier 2011), and Calamian Islands, Philippines (Veron 2000) (Fig. 3). The new record of this species in Singapore suggests that there is evidence of its dispersal range along the coasts of South China Sea and Sunda Shelf.

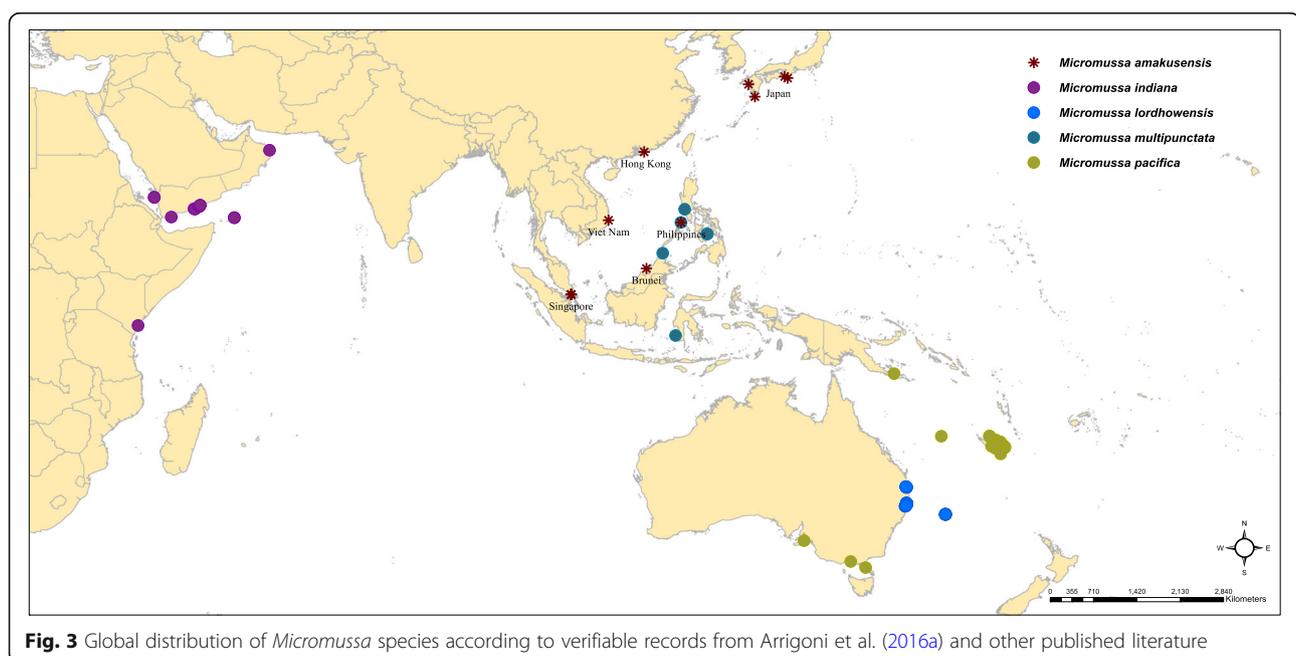
In Singapore, the genus *Micromussa* and in particular *M. amakusensis* have not been documented from historical or contemporary records (Huang et al. 2009; Guest et al. 2016; Wong et al. 2018; Chow et al. 2019), so our discovery represents the southern-most record of this species in the South China Sea region (Huang et al. 2015). The present finding is remarkable given that species losses have occurred over the last five decades as a consequence of coastal urbanisation in Singapore (Hoeksema and Koh 2009; Poquita-Du et al. 2019b). Growth rates of encrusting lobophyllids have rarely

been reported in the literature (Madin et al. 2016). Nevertheless, based on the approximate age of the seawalls at Lazarus Island that were constructed in the early 2000s, and a conservative growth estimate of 0.5–1 cm per year for encrusting or massive corals, we suggest that the colonies observed are at least 10–18 years old. Despite the chronic anthropogenic impacts and habitat degradation (Chou et al. 2019), it is evident that coral recruitment is active not only on Singapore's reefs, but also in non-reefal areas such as the seawalls of Lazarus Island on which *M. amakusensis* has been observed (see also Lee et al. 2009; Ng et al. 2012).

Micromussa amakusensis appears to be widespread in Singapore, spanning the western (Sultan Shoal) and eastern (Kusu Island) limits of the established reefs here. However, it has only been detected after more than three decades of coral reef monitoring (Guest et al. 2016). It is likely that some colonies were either misidentified as similar-looking, fleshy taxa such as *Dipsastraea* spp. or *Acanthastrea* spp., or that their encrusting growth form and drab colouration rendered them less noticeable by surveyors. Regardless, as in the case of *Pocillopora acuta* described above, *M. amakusensis* may be found in other areas of its newly-expanded range and, following our record, be recognised more readily in the future.

Conclusions

Through field observations, morphological identification based on skeleton morphology, molecular phylogenetics and species mapping, we have here better established the geographic range of *Micromussa*, with particular



focus on *M. amakusensis* (Fig. 3). Our record of the species in Singapore represents a new genus and species record of *M. amakusensis* in the southern South China Sea. This follows a recent taxonomic revision along with two new species described that have overhauled the species ranges of existing species (Arrigoni et al. 2016a). Our phylogenetic inference is broadly congruent with the results of the revision (Arrigoni et al. 2016a; see also Arrigoni et al. 2016b, 2019; Huang et al. 2016), though it also reveals a paraphyletic *M. amakusensis* and may foreshadow further taxonomic changes.

In light of plans to develop Singapore's coastal areas in the coming decade, there is an even greater urgency to understand and manage the city-state's natural heritage (Chou et al. 2019). Increased survey efforts and taxonomic expertise, encompassing both morphological and molecular methods, will be necessary to shed light on the identities of species that have been hiding in plain sight.

Methods

SCUBA was used to access four coral reef sites at the three islands in southern Singapore from 2015 to 2019. Fragments from two colonies at Kusu Island were collected between February and March 2019 for morphological examination and molecular phylogenetic analyses. An approximately 4 cm² piece of tissue from each colony was preserved in 100% molecular grade ethanol and stored at -80 °C until further analysis. The remaining coral fragments were placed in freshwater for 24 h and 15% household bleach for one week, cleaned and dried. Specimens were examined and compared against the holotype of *Micromussa amakusensis* (G32485, Museum of Tropical Queensland) before depositing at the Zoological Reference Collection (ZRC.CNI.1392 and ZRC.CNI.1393), Lee Kong Chian Natural History Museum.

DNA was isolated from the ethanol-preserved subsamples using the DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. Mitochondrial cytochrome c oxidase subunit 1 (COI) gene, nuclear internal transcribed spacers (ITS) and histone H3 (HH3) were amplified using the following primers respectively: MCOIF (5'-TCT ACA AAT CAT AAA GAC ATA GG-3') and MCOIR (5'-GAG AAA TTA TAC CAA AAC CAG G-3') (Fukami et al. 2004); A18S (5'-GAT CGA ACG GTT TAG TGA GG-3') and ITS4 (5'-TCC TCC GCT TAT TGA TAT GC-3') (Takabayashi et al. 1998); H3F (5'-ATG GCT CGT ACC AAG CAG ACV GC-3') and H3R (5'-ATA TCC TTR GGC ATR ATR GTG AC-3') (Colgan et al. 1998). PCRs were performed in 25- μ l reaction mixes comprising 2 μ l of template DNA, 12.5 μ l of GoTaq Green Master Mix (Promega, Wisconsin, USA), 1 μ l of each forward and reverse primer (10 μ M), and

8.5 μ l of molecular grade water. The thermal cycling profile used for COI and ITS was as follows: initial denaturation at 94 °C for 1 min, 35 cycles of 94 °C for 45 s, 48 °C for 45 s, 72 °C for 90 s, and a final extension at 72 °C for 3 min. The thermal cycling profile used for HH3 was as follows: initial denaturation at 95 °C for 3 min, 40 cycles of 95 °C for 30 s, 53 °C for 45 s, 72 °C for 45 s, and a final extension at 72 °C for 5 min.

Successfully amplified products were purified using SureClean Plus (Bioline Inc., London, UK), and sequenced with the BigDye Terminator v3.1 (Applied Biosystems) in a 3730xl DNA Analyzer (Thermo Fisher Scientific), following manufacturers' protocols. Gene sequences were assembled and checked using Geneious v10.1.3.

Combining data from Arrigoni et al. (2016a) and Huang et al. (2016), sequences were organised by gene in Mesquite v3.6 (Maddison and Maddison 2016), aligned using the E-INS-i option with default parameters in MAFFT v7.205 (Katoh et al. 2002; Katoh and Toh 2008; Katoh and Standley 2013), and concatenated. Maximum likelihood analysis was performed in RAxML v8.0.9 (Stamatakis 2014) with 50 alternate runs from distinct parsimony starting trees under the default GTRGAMMA model and 1000 bootstrap replicates. Bayesian analysis was carried out in MrBayes v3.2.6 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Ronquist et al. 2012) using the most suitable evolutionary model for each partition assessed via jModelTest 2.1.4 (Guindon and Gascuel 2003; Posada 2008; Darriba et al. 2012) under the Akaike information criterion. Four Markov chains of 12 million generations were implemented in two Markov chain Monte Carlo runs, saving a tree every 100th generation. The first 20,001 trees were discarded as burn-in following convergence assessment in Tracer v1.7 (Rambaut et al. 2018).

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Authors' contributions

DH, CSLN conceived the project. CSLN, YPK, SQS performed the field work. SSJ performed the laboratory work. DH, NTHN analysed the data. All authors drafted the manuscript and gave final approval for publication.

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Availability of data and materials

DNA sequences are available at GenBank (accession numbers MN235859–MN235860, MN249394–MN249397).

Ethics approval

Approval to collect coral specimens was issued under the National Parks Board Singapore (research permit NP/RP16–156).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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