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The Octocorals of Dongsha Atoll (South China Sea): An Iterative Approach to Species Identification Using Classical Taxonomy and Molecular Barcodes

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Yehuda Benayahu, Leendert Pieter van Ofwegen, Chang-feng Dai, Ming-Shiou Jeng, Keryea Soong, Alex Shlagman, Samuel W. Du, Prudence Hong, Nimrah H. Imam, Alice Chung, Tiana Wu, and Catherine S. McFadden (2018) Surveys of octocorals from Dongsha Atoll, Taiwan were conducted during 2011, 2013 and 2015 by SCUBA at a depth range of 6-25 m. The collections yielded ~540 specimens, encompassing the variety of taxa occurring in the explored sites; estimates of their abundances were also recorded. Dongsha features a highly diverse octocoral fauna, and octocorals are the dominant benthic organisms in the surveyed reef sites, often covering the majority of the hard substratum. Specimens were identified to the genus and species levels based on an iterative approach that integrates classical taxonomy with character-based molecular barcodes. A total of 51 nominal species representing 20 genera belonging to seven families were recorded, plus ~30 colonies that could only be assigned to a genus. Members of the family Alcyoniidae were the most abundant and diverse taxa, with 27 nominal species plus at least one potentially new, undescribed species of *Sinularia*, and 5-7 species each of *Cladiella*, *Lobophytum* and *Sarcophyton*. Problems with the taxonomic identification and phylogenetic relationships of species in these genera are discussed. The peculiarity of the Dongsha octocoral species composition is noted, and the composition is also compared to the other Taiwanese reef systems.

Key words: Alcyonacea, Coral reefs, DNA barcoding, Pure characteristic attributes, Taiwan, Species diversity, New records.

BACKGROUND

The Taiwanese reef systems at the junction of the Philippine-Japan islands arc include a variety of well-developed reef communities at the northern edge of the South China Sea and additionally

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around the adjacent Pacific offshore islands (*e.g.* Spalding et al. 2001; Ribas-Deulofeu et al. 2016). The octocoral fauna of these reef communities in Taiwan has been a subject of taxonomic research since the pioneering studies carried out by Utinomi (1950a) along the northeastern coast of Taiwan, as well as at its southern end (Utinomi 1950b 1951 1959). Later studies have addressed the octocoral diversity of the southern Taiwanese reefs at Kenting National Park, the Pacific Green Is. (*Lyudao*) (Benayahu and Perkol-Finkel 2004; Benayahu et al. 2004), the Penghu Archipelago (Benayahu and McFadden 2011; Benayahu and Ofwegen 2011; Ofwegen and Benayahu 2012; Benayahu et al. 2012), as well as the abundance and ecological significance of octocorals on the Taiwanese reefs (*e.g.* Dai 1990 1991a 1991b 1993; Fan et al. 2005). Of special interest is the reef-building function played by *Sinularia* octocorals in some coral reefs there (Jeng et al. 2011a). This record of publications from the region clearly indicates the high diversity and ecological importance of octocorals on the various reef systems in Taiwan, in both the East China Sea and Pacific Ocean.

Dongsha Atoll is located in the Pratas Islands at the edge of the continental shelf in the northern South China Sea (20°41'N, 116°48'E). It has a diameter of about 25 km, and its lagoon, reef flats and fore-reef cover ca. 500 km^2 in total area. The reef flats are ca. 1 m deep, and the lagoon is 12-21 m deep (Soong et al. 2002). These reefs are affected by the northeast monsoon during October-April, by the typhoon season between June-September, and by SW winds at other times of the year. The atoll experiences two contrasting physical phenomena: repetitive anomalies in the sea-surface temperature that exceed the coral bleaching threshold (DeCarlo et al. 2015); and regular effects of the world's strongest internal waves that result in the rhythmic upwelling of cold deep waters on the outer reef slopes of the atoll (Hsu and Liu 2000; Dai 2005; Liu et al. 2013; Wang 2016). This combination leads to a clear spatial separation between 'thermally-susceptible' stony coral genera, which mainly inhabit the fore-reef, and 'thermally-resistant' genera, which mainly reside in the lagoon. Consequently, it has been suggested that Dongsha Atoll constitutes a potential thermal refuge for reef-building corals in the northern South China Sea, facilitating the development of resilience and resistance to bleaching in coral communities of the lagoon (Tkachenko and Soong 2017).

Estimates of the number of species of stony corals found at Dongsha Atoll have steadily increased over time: 45 species were reported by Yang et al. (1975), 63 by Fang et al. (1990), and 137 by Dai et al. (1995). More recent surveys have revealed 257 stony coral species, 56 octocorals, six hydrozoans, and two antipatharians (Jeng et al. 2008 2011b). A comprehensive field guide to the octocorals of Dongsha Atoll was published recently and presents the diverse species composition there, comprising ten families (Dai and Chin 2017). These surveys have also indicated that fleshy octocorals, such as those of the families Alcyoniidae, Briareidae, Nephtheidae and Xeniidae, are abundant on the northern, eastern, and southern reef slopes of the atoll, but are relatively rare on the western reef slope (5-25 m) and almost absent in the lagoon.

The current study addresses the octocoral diversity at Dongsha based on the comprehensive collections conducted there. We use an iterative, integrative approach to identify species based on the reconciliation of morphological features with character-based molecular barcodes. In addition to a systematic list of the octocoral taxa found at Dongsha Atoll, we discuss aspects of their phylogeny and note their abundance and geographic distribution in relation to other Taiwanese reef systems.

MATERIALS AND METHODS

Material was collected, using SCUBA, during three field trips conducted in July 2011 (3 days, 6 dives), September 2013 (4 days, 7 dives), and June 2015 (6 days, 12 dives). All collections were made on the reef slope at a depth range of 6-25 m (Fig. 1). These collections yielded ~540 specimens of octocorals, encompassing the variety of taxa occurring in the explored sites. During the field work underwater abundance estimates of the different morphospecies were made visually and divided into four qualitative categories: rare, sporadic, abundant, and dominant (see also Benayahu et al. 2004). Most of the colonies were photographed *in situ* prior to collection, which assisted in determining the abundance of the identified species. All samples were preserved in 70% ethanol and subsamples were removed and preserved in absolute ethanol and salt-saturated DMSO buffer for molecular studies.

Specimens were identified at the species level based on an iterative approach that integrated classical taxonomy using morphological characters with molecular barcodes. Species identifications based on morphological characters were compared to identifications made independently by matching barcode sequences to an existing reference database (McFadden et al. 2006 2009 2014; Benayahu et al. 2012). When species identifications based on morphology vs. molecular barcodes were in disagreement we iteratively confirmed and reconsidered both sources of information and sought to resolve the discrepancy.

Morphological species identification

In order to identify morphospecies, sclerites from different parts of the studied colony were obtained by dissolving the tissues in 10% sodium hypochlorite, followed by careful rinsing in distilled water. Particular care was taken to examine polyp sclerites when applicable, as these play a major role in the taxonomy of the speciose genus *Sinularia* (*e.g.* McFadden et al. 2009; Ofwegen and Benayahu 2012). When necessary, sclerites were prepared for scanning electron microscopy as follows: they were carefully rinsed with double-distilled water, dried at room temperature, coated with gold, and examined with a Jeol 6480LV electron microscope operated at 10 kV. Identification of species was facilitated by comparisons with permanent sclerite preparations of type material (when available) kept in the Steinhardt Museum of Natural History, Tel Aviv University, Israel (SMNH) and the Netherlands Center for Biodiversity, Naturalis, Leiden (RMNH). The identified specimens are deposited at SMNH (collection numbers preceeded by ZMTAU) (Table 1).

Molecular species identification

Extraction of DNA from ethanol-preserved tissue samples, PCR amplification, and sequencing of the *mtMutS*, *COI* (including the adjacent intergenic region, *igr1*) and *28S* rDNA barcoding regions followed the protocols published in McFadden et al. (2011 2014). The

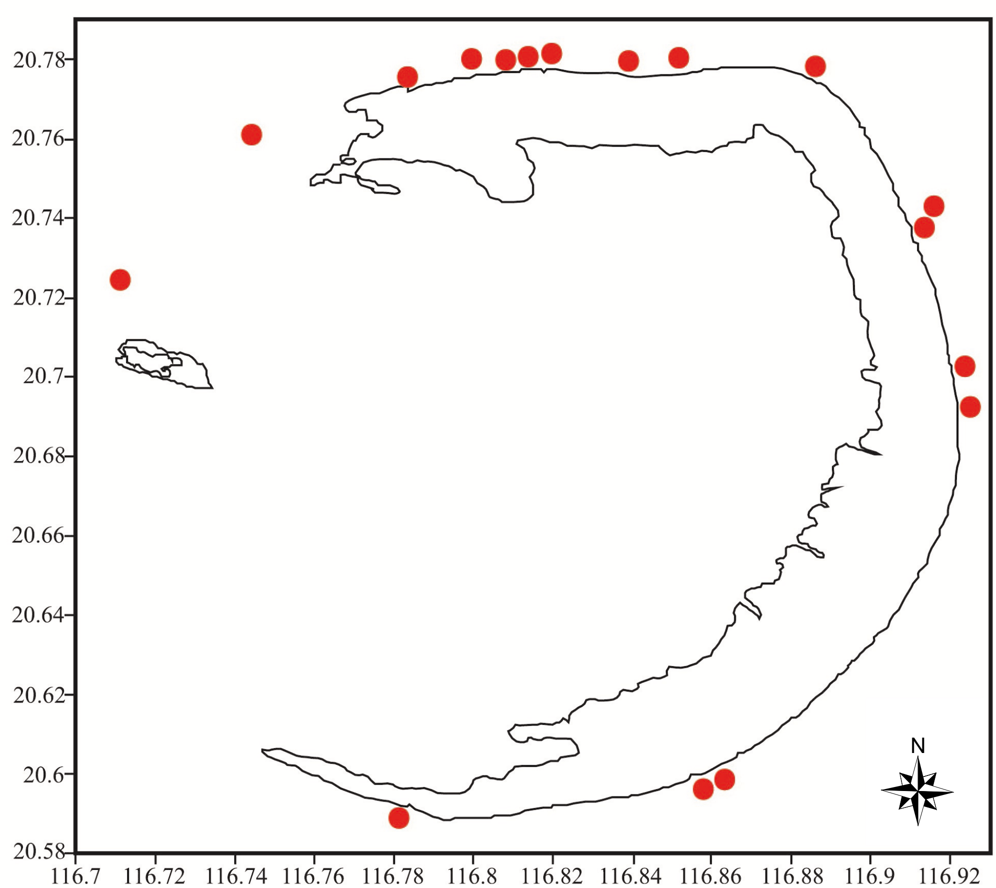

Fig. 1. Collection sites of octocorals at Dongsha Atoll.

Table 1. List of Octocorallia species of the orders Helioporacea Bock, 1938 and Alcyonacea (Lamouroux, 1816) from Dongsha Atoll with indication of the Museum inventory numbers (ZMTAU Co), their collection site, depth of occurrence, abundance estimate on the reef, and Distribution in Taiwan (southern Taiwan and Penghu Archipelago)

Classification
Family Helioporidae Moseley, 1876
Heliopora de Blainville, 1830
Heliopora coerulea (Pallas, 1766)
Occurrence: ZMTAU Co 36388, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013. Field notes: Rare. Distribution in Taiwan: Southern Taiwan.
Family Alcyoniidae Lamouroux, 1812
Aldersladum Benayahu & McFadden, 2011
Aldersladum jengi Benayahu & McFadden, 2011
Occurrence: ZMTAU Co 35392, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011. Field notes: Rare. Distribution in Taiwan: Penghu.
Cladiella Gray, 1869
Cladiella australis (Macfadyen, 1936)
Occurrence: ZMTAU Co 35324, Co 35333, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35344, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 35366, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011; ZMTAU Co 36277, Co 36279, Co 36284, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 6-10 m, 11 September 2013; ZMTAU Co 36313, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU Co 36344, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36912, Dongsha, (20°44.422'N; 116°54.865'E), 19-21 m, 12 June 2015; ZMTAU, Co 36987, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015. Field notes: Common. Distribution in Taiwan: Southern Taiwan and Penghu Archipelago.
Cladiella conifera (Tixier-Durivault, 1943)
Occurrence: ZMTAU Co 35376, Dongsha, (20°46.689'N; 116°47.932'E), 5m, 9 July 2011. Field notes: Rare. Distribution in Taiwan: New record.
Cladiella krempfi Hickson, 1919
Occurrence: ZMTAU Co 35347, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 35389, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 36289, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013. Field notes: Rare. Distribution in Taiwan: Penghu Archipelago.
Cladiella latissima (Tixier-Durivault, 1948)
Occurrence: MTAU Co 35320, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 36336, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013. Field notes: Rare. Distribution in Taiwan: Penghu Archipelago.
Cladiella pachyclados (Klunzinger, 1877)
Occurrence: MTAU Co 35377, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35409, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36314, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU 36352, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013. Field notes: Sporadic. Distribution in Taiwan: Southern Taiwan and Penghu Arcipelago.

Table 1. (Continued)

Cladiella sp.

Occurrence: ZMTAU Co 35323, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35425, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36901, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015; ZMTAU Co 36947, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015; ZMTAU Co 36963, Dongsha, (20°41.509'N; 116°55.379'E), 6-8 m, 14 June 2015; ZMTAU Co 37012, Dongsha, (20°35.859'N; 116°51.380'E), 5-8 m, 16 June 2015.
Field notes: Sporadic.

Klyxum Alderslade, 2000

Klyxum sp.

Occurrence: MTAU Co 35404, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36278, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 6-10 m, 11 September 2013; ZMTAU Co 36348, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36380, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36968, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015; ZMTAU Co 37008, Dongsha, (20°35.859'N; 116°51.380'E), 5-8 m, 16 June 2015.
Field notes: Sporadic.
Distribution in Taiwan: Southern Taiwan: *K. simplex* and Penghu: *K. utinomii*.

Lobophytum von Marenzeller, 1886

Lobophytum catalai Tixier-Durivault, 1957

Occurrence: ZMTAU Co 35340, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 35396, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36285, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 6-10 m, 11 September 2013.
Field notes: Rare.
Distribution in Taiwan: New record.

Lobophytum crassum von Marenzeller, 1886

Occurrence: ZMTAU, Co 35321, Co 35325, Co 35334 Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; Co 35354, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; Co 35370, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011; Co 35383, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; Co 35398, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36276, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 6-10 m, 11 September 2013; ZMTAU Co 36290, Co 36304, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36321, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU Co 36346, Co 36349, Co 36364, Co 36369, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013.
Field notes: Dominant.
Distribution in Taiwan: Southern Taiwan and Penghu Archipelago.

Lobophytum hirsutum Tixier-Durivault, 1956

Occurrence: ZMTAU Co 36385, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013.
Field notes: Rare.
Distribution in Taiwan: New record.

Lobophytum hsiehi Benayahu & Ofwegen, 2011

Occurrence: ZMTAU Co 35319, Co 35326, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35365, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011; ZMTAU Co 35399, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 35421, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36282, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 6-10 m, 11 September 2013; ZMTAU Co 36320, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 7-8 m, 14 September 2013; ZMTAU Co 36342, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36387, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013.
Field notes: Dominant.
Distribution in Taiwan: Penghu Archipelago.

Lobophytum legitimum Tixier-Durivault, 1970

Occurrence: ZMTAU Co 36311, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013.
Field notes: Rare.
Distribution in Taiwan: New record.

Lobophytum pauciflorum (Ehrenberg, 1834)

Occurrence: ZMTAU Co 35380, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011.

Table 1. (Continued)

Field notes: Rare.
Distribution in Taiwan: Southern Taiwan.

Lobophytum rigidum Benayahu, 1995
Occurrence: ZMTAU Co 35329, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 36306, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36934, Dongsha, (20°43.448'N; 116°42.520'E), 3-4 m, 13 June 2015; ZMTAU Co 37015, Dongsha, (20°35.859'N; 116°51.380'E), 5-8 m, 16 June 2015.
Field notes: Rare.
Distribution in Taiwan: New record.

Paraminabea Williams & Alderslade, 1999
Paraminabea aldersladei (Williams, 1992)
Occurrence: ZMTAU Co 36949, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015.
Field notes: Rare.
Distribution in Taiwan: Southern Taiwan.

Sarcophyton Lesson, 1834
Sarcophyton cinereum (Tixier-Durivault, 1946)
Occurrence: ZMTAU Co 35413, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36354, Co 36366, Co 36372, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013.ZMTAU Co 36275, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 6-10 m, 11 September 2013.
Field notes: Rare.
Distribution in Taiwan: New record.

Sarcophyton crassocaule Moser, 1919
Occurrence: ZMTAU Co 35330, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 36294, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013.
Field notes: Rare.
Distribution in Taiwan: Southern Taiwan.

Sarcophyton ehrenbergi von Marenzeller, 1886
Occurrence: ZMTAU Co 35313, Co 35337, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35356, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 35359, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011; ZMTAU Co 35382, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35403, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36280, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 6-10 m, 11 September 2013; ZMTAU Co 36293, Co 36295, Co 36299, Co 36303, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36308, Co 36317, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU Co 36331, Co 36338, Co 36339, Co 36340, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013; ZMTAU Co 36351, Co 36353, Co 36362, Co 36363, Co 36368, Co, Co 37370, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36382, Co 36398, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU Co 37020, Co 37022, Dongsha, (20°35.941'N; 116°51.632'E), 7-9 m, 16 June 2015.
Field notes: Dominant.
Distribution in Taiwan: Southern Taiwan and Penghu Archipelago.

Sarcophyton elegans Moser, 1919
Occurrence: ZMTAU Co 36318, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU Co 36966, Dongsha, (20°41.509'N; 116°55.379'E), 6-8 m, 14 June 2015.
Field notes: Rare.
Distribution in Taiwan: New record.

Sarcophyton nanwanensis Benayahu & Perkol-Finkel, 2004
Occurrence: ZMTAU Co 35346, Co 35350, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 35386, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35407, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 35415, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36310, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013.
Field notes: Common.
Distribution in Taiwan: Southern Taiwan.

Table 1. (Continued)

Sarcophyton trocheliophorum von Marenzeller, 1886

Occurrence: ZMTAU Co 35317, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35363, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011; ZMTAU Co 35379, Co 35388, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35418, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36302,Co 36291, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36335, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013; ZMTAU Co 36350, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36996, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015.

Field notes: Dominant.

Distribution in Taiwan: Southern Taiwan and Penghu Archipelago.

Sinularia May, 1898

Sinularia abrupta Tixier-Durivault, 1970

Occurrence: ZMTAU Co 35331, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 36305, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36332, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013; ZMTAU Co 36341, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013.

Field notes: Sporadic.

Distribution in Taiwan: Penghu Archipelago.

Sinularia acuta Manuputty & van Ofwegen, 2007

Occurrence: ZMTAU Co 35393, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36376, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36897, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015; ZMTAU Co 36943, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015; ZMTAU Co 36952, Co 36957, Dongsha, (20°41.509'N; 116°55.379'E), 6-8 m, 14 June 2015; ZMTAU Co 36984, Co 36988, Dongsha, (20°41.994'N; 116°55.370'E), 4-8 m, 15 June 2015; ZMTAU Co 36992, Co 36997, Co 37003, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015; ZMTAU Co 37009, Co 37016, Dongsha, (20°35.859'N; 116°51.380'E), 5-8 m, 16 June 2015; ZMTAU Co 37028, Dongsha, (20°35.941'N; 116°51.632'E), 7-9 m, 16 June 2015.

Field notes: Dominant.

Distribution in Taiwan: Penghu Archipelago.

Sinularia brassica May, 1898

Occurrence: ZMTAU Co 36328, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013; ZMTAU Co 35349,Co 35352, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 35360, Co 35368, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011; ZMTAU Co 35381, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35427, Co 35428, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36345, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36908, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015; ZMTAU Co 36911, Dongsha, (20°44.422'N; 116°54.865'E), 19-21 m, 12 June 2015; ZMTAU Co 37030, Dongsha, (20°35.941'N; 116°51.632'E), 7-9 m, 16 June 2015.

Field notes: Common.

Distribution in Taiwan: Southern Taiwan.

Sinularia capillosa Tixier-Durivault, 1970

Occurrence: ZMTAU Co 35410, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 35417, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011.

Field notes: Rare.

Distribution in Taiwan: New record.

Sinularia ceramensis Verseveldt, 1977

Occurrence: ZMTAU Co 35351, Co 35343, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 36326, Co 36334, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013; ZMTAU Co 36355, Co 36357, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 35390, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 36333, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013; ZMTAU Co 36379, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36938, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015; ZMTAU Co 37429, Dongsha, (20°43.448'N; 116°42.520'E), 3-4 m, 13 June 2015; ZMTAU Co 37001, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015; ZMTAU Co 37010, Dongsha, (20°35.859'N; 116°51.380'E), 5-8 m, 16 June 2015.

Field notes: Dominant.

Distribution in Taiwan: New record.

Table 1. (Continued)

Sinularia curvata Manuputty & van Ofwegen, 2007
Occurrence: ZMTAU Co 35338, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35367, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011.
Field notes: Rare.
Distribution in Taiwan: New record.

Sinularia densa (Whitelegge, 1897)
Occurrence: ZMTAU Co 35373, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 36902, Co 36907, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015; ZMTAU Co 36935, Dongsha, (20°43.448'N; 116°42.520'E), 3-4 m, 13 June 2015; ZMTAU Co 36965, Dongsha, (20°41.509'N; 116°55.379'E), 6-8 m, 14 June 2015; ZMTAU Co 36977, Co 36985, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015; ZMTAU Co 37005, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015.
Field notes: Sporadic.
Distribution in Taiwan: Southern Taiwan.

Sinularia erecta Tixier-Durivault, 1945
Occurrence: ZMTAU Co 36329, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013.
Field notes: Rare.
Distribution in Taiwan: Southern Taiwan and Penghu Archipelago.

Sinularia exilis Tixier-Durivault, 1970
Occurrence: ZMTAU Co 36360, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36898, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015; ZMTAU Co 36940, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015; ZMTAU Co 36994, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015; ZMTAU Co 37006, Dongsha, (20°35.859'N; 116°51.380'E), 5-8 m, 16 June 2015.
Field notes: Common.
Distribution in Taiwan: Southern Taiwan.

Sinularia flexibilis (Quoy & Gaimard, 1833)
Occurrence: ZMTAU Co 35405, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36301, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36325, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013.
Field notes: Common.
Distribution in Taiwan: Southern Taiwan.

Sinularia heterospiculata Verseveldt, 1970
Occurrence: ZMTAU Co 36281, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 6-10 m, 11 September 2013.
Field notes: Rare.
Distribution in Taiwan: New record.

Sinularia hirta (Pratt, 1903)
Occurrence: ZMTAU Co 36298, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36392, Co 36383, Co 36394, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36941, Co 36945, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015.
Field notes: Rare.
Distribution in Taiwan: Penghu Archipelago.

Sinularia humesi Verseveldt, 1971
Occurrence: ZMTAU Co 36309, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU Co 36395, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36917, Dongsha, (20°44.422'N; 116°54.865'E), 19-21 m, 12 June 2015; ZMTAU Co 36899, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015.
Field notes: Sporadic.
Distribution in Taiwan: Southern Taiwan.

Sinularia humilis van Ofwegen, 2008
Occurrence: ZMTAU Co 35316, Co 35328, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 36330, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013; ZMTAU Co 36390, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16

Table 1. (Continued)

September 2013; ZMTAU Co 36900, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015; ZMTAU Co 36916, Dongsha, (20°44.422'N; 116°54.865'E), 19-21 m, 12 June 2015; ZMTAU Co 36920, Co 36930, Dongsha, (20°43.448'N; 116°42.520'E), 3-4 m, 13 June 2015; ZMTAU Co 36942, Co 36944, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015; ZMTAU Co 36986, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015.
Field notes: Common.
Distribution in Taiwan: New record.

Sinularia lochmodes Kolonko, 1926
Occurrence: ZMTAU Co 35318, Co 35332, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35391, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35423, Co 35426, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36292, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36356, Co 36375, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36377, Co 36386, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36903, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015; ZMTAU Co 36936, Co 36937, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015.
Field notes: Dominant.
Distribution in Taiwan: Southern Taiwan and Penghu Archipelago.

Sinularia maxima Verseveldt, 1971
Occurrence: ZMTAU Co 35384, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35414, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36283, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 6-10 m, 11 September 2013; ZMTAU Co 36300, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36381, Co 36384, Co 36391, Co 36399, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36924, Dongsha, (20°43.448'N; 116°42.520'E), 3-4 m, 13 June 2015.
Field notes: Dominant.
Distribution in Taiwan: Southern Taiwan and Penghu Archipelago.

Sinularia ovispiculata Tixier-Durivault, 1970
Occurrence: ZMTAU Co 35353, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 37584, Dongsha, (20°46.767'N; 116°48.393'E), 10 m, coll. Ming-Shion Jeng, 29 May 2015; ZMTAU Co 36995, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015.
Field notes: Rare.
Distribution in Taiwan: Southern Taiwan.

Sinularia pavida Tixier-Durivault, 1970
Occurrence: ZMTAU Co 35374, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35408, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36946, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015.
Field notes: Rare.
Distribution in Taiwan: Penghu Archipelago.

Sinularia penghuensis van Ofwegen & Benayahu, 2012
Occurrence: ZMTAU Co 35322, Co 35314, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35387, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35422, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36287, Co 36296, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36343, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36914, Dongsha, (20°44.422'N; 116°54.865'E), 19-21 m, 12 June 2015; ZMTAU Co 36919, Co 36921, Dongsha, (20°43.448'N; 116°42.520'E), 3-4 m, 13 June 2015; ZMTAU Co 36974, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015; ZMTAU Co 37000, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015; ZMTAU Co 37025, Dongsha, (20°35.941'N; 116°51.632'E), 7-9 m, 16 June 2015.
Field notes: Dominant.
Distribution in Taiwan: Penghu Archipelago.

Sinularia querciformis (Pratt, 1903)
Occurrence: ZMTAU Co 36297, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36928, Dongsha, (20°43.448'N; 116°42.520'E), 3-4 m, 13 June 2015.
Field notes: Rare.
Distribution in Taiwan: Southern Taiwan.

Table 1. (Continued)

Sinularia scabra Tixier-Durivault, 1970

Occurrence: ZMTAU Co 36367, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013.
Field notes: Rare.
Distribution in Taiwan: Southern Taiwan.

Sinularia slieringsi van Ofwegen & Vennam, 1994

Occurrence: ZMTAU Co 35394, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36307, Co 36315, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU Co 36397, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36913, Co 36918, Dongsha, (20°44.422'N; 116°54.865'E), 19-21 m, 12 June 2015; ZMTAU Co 36923, Co 36925, Co 36926, Co 36927, Co 36931, Co 36933, Dongsha, (20°43.448'N; 116°42.520'E), 3-4 m, 13 June 2015; ZMTAU Co 36948, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015; ZMTAU Co 36971, Co 36979, Co 36981, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015; ZMTAU Co 36999, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015; ZMTAU Co 37007, Dongsha, (20°35.859'N; 116°51.380'E), 5-8 m, 16 June 2015; Co 37019, Dongsha, (20°35.859'N; 116°51.380'E), 5-8 m, 16 June 2015; ZMTAU Co 37021, Co 37023, Co 37031, Dongsha, (20°35.941'N; 116°51.632'E), 7-9 m, 16 June 2015.
Field notes: Dominant.
Distribution in Taiwan: Penghu Archipelago.

Sinularia soongi Benayahu & van Ofwegen, 2011

Occurrence: ZMTAU Co 36359, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013.
Field notes: Rare.
Distribution in Taiwan: Penghu

Sinularia tumulosa van Ofwegen, 2008

Occurrence: ZMTAU Co 35372, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35401, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 35416, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36288, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 12-17 m, 11 September 2013; ZMTAU Co 36319, Co 36327, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU Co 36361, Co 36371, Co 36373, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36389, Co 36400, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36909, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015; ZMTAU Co 36929, Co 36932, Dongsha, (20°43.448'N; 116°42.520'E), 3-4 m, 13 June 2015; ZMTAU Co 36950, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015; ZMTAU Co 36953, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015; ZMTAU Co 37018, Dongsha, (20°35.859'N; 116°51.380'E), 5-8 m, 16 June 2015; ZMTAU Co 37027, Dongsha, (20°35.941'N; 116°51.632'E), 7-9 m, 16 June 2015.
Field notes: Dominant.
Distribution in Taiwan: New record.

Sinularia variabilis Tixier-Durivault, 1945

Occurrence: ZMTAU Co 35397, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36323, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013; ZMTAU Co 36365, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36378, Co 36396, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36939, Dongsha, (20°43.448'N; 116°42.520'E), 4-5 m, 13 June 2015.
Field notes: Common.
Distribution in Taiwan: Southern Taiwan.

Sinularia wanannensis van Ofwegen & Benayahu, 2012

Occurrence: ZMTAU Co 35345, Co 35355, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 35361, Co 35358, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011; ZMTAU Co 35400, Co 35395, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36895, Co 36905, Co 36906, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015; ZMTAU Co 36910, Co 36915, Dongsha, (20°44.422'N; 116°54.865'E), 19-21 m, 12 June 2015; ZMTAU Co 36991, Co 36993, Co 36998, Co 37004, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015; ZMTAU Co 37011, Co 37013, Co 37014, Co 37017, Dongsha, (20°35.859'N; 116°51.380'E), 5-8 m, 16 June 2015; ZMTAU Co 37026, Co 37029, Dongsha, (20°35.941'N; 116°51.632'E), 7-9 m, 16 June 2015.
Field notes: Dominant.
Distribution in Taiwan: Penghu Archipelago.

Sinularia yamazatoi Benayahu, 1995

Occurrence: ZMTAU Co 35369, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011.

Table 1. (Continued)

Field notes: Rare.
Distribution in Taiwan: New record.

Sinularia n. sp.
Occurrence: ZMTAU Co 36337, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013.
Field notes: Rare.

Family Briareidae Gray, 1859

Briareum Blainville, 1830
Briareum stechei (Kukenthal, 1908)
Occurrence: ZMTAU Co 35348, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 35385, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 36286, Dongsha, (20°35'23.5"N; 116°46'52.1"E), 6-10 m, 11 September 2013; ZMTAU Co 36347, Co 36374, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36983, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015.
Field notes: Common.
Distribution in Taiwan: Southern Taiwan.

Family Tubiporidae Ehrenberg, 1828

Tubipora Linnaeus, 1758
Tubipora musica Linnaeus, 1758
Occurrence: ZMTAU Co 35339, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35378, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 36324, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013.
Field notes: Rare.
Distribution in Taiwan: Southern Taiwan.

Family Nephtheidae Gray, 1862

Capnella Gray, 1869
Capnella imbricata (Quoy & Gaimard, 1833)
Occurrence: ZMTAU Co 35336, Co 35611, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 36358, Dongsha, (20°46'50.2"N; 116°48'38.5"E), 7-8 m, 15 September 2013; ZMTAU Co 36961, Co 36964, Dongsha, (20°41.509'N; 116°55.379'E), 6-8 m, 14 June 2015; ZMTAU Co 36989, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015; ZMTAU Co 37024, Dongsha, (20°35.941'N; 116°51.632'E), 7-9 m, 16 June 2015.
Field notes: Common.
Distribution in Taiwan: New record.

Dendronephthya Kuekenthal, 1905
Dendronephthya sp.
Occurrence: ZMTAU Co 36393, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 35362, Co 35364, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011; ZMTAU Co 35411, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011.
Field notes: Common.
Distribution in Taiwan: Southern Taiwan and Penghu Archipelago.

Lemnalia Gray, 1868
Lemnalia sp.
Occurrence: Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013; ZMTAU Co 36955, Co 36960.
Field notes: Rare.
Distribution in Taiwan: New record.

Litophyton Forskål, 1775
Litophyton sp.
Occurrence: ZMTAU Co 35342, Dongsha, (20°46.697'N; 116°51.051'E), 7-10 m, 8 July 2011; ZMTAU Co 35315, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35371, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35420,

Table 1. (Continued)

Co 35424, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36316, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU Co 36322, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-13 m, 14 September 2013; ZMTAU Co 36962, Dongsha, (20°41.509'N; 116°55.379'E), 6-8 m, 14 June 2015; ZMTAU Co 36969, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015; ZMTAU Co 37002, Dongsha, (20°41.994'N; 116°55.370'E), 5-7 m, 15 June 2015.
Field notes: Dominant.
Distribution in Taiwan: New record.

Paralemnalia Kükenthal, 1913
Paralemnalia thyrsoides (Ehrenberg, 1834)
Occurrence: ZMTAU Co 36401, Dongsha, (20°43'23.6"N; 116°42'31.5"E), 7-8 m, 16 September 2013; ZMTAU Co 36976, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015.
Field notes: Rare.
Distribution in Taiwan: Southern Taiwan.

Stereonephthya Kükenthal, 1905
Stereonephthya sp.
Occurrence: ZMTAU Co 35327, Dongsha, (20°46.703'N; 116°50.324'E), 8-10 m, 8 July 2011; ZMTAU Co 35357, Dongsha, (20°46.700'N; 116°53.137'E), 10-11 m, 9 July 2011; ZMTAU Co 35375, Dongsha, (20°46.689'N; 116°47.932'E), 5 m, 9 July 2011; ZMTAU Co 35406, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 36312, Dongsha, (20°46'25.8"N; 116°46'52.1"E), 10-12 m, 14 September 2013; ZMTAU Co 36954, Co 36958, Dongsha, (20°41.509'N; 116°55.379'E), 6-8 m, 14 June 2015; ZMTAU Co 36970, Co 36972, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015.
Field notes: Common.
Distribution in Taiwan: New record.

Family Xeniidae Ehrenberg, 1828

Anthelia Lamarck, 1816
Anthelia philippinense (Roxas, 1933)
Occurrence: ZMTAU Co 36967, Co 36973, East side of atoll, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015; ZMTAU Co 36951, Co 36956, Dongsha, (20°41.509'N; 116°55.379'E), 6-8 m, 14 June 2015.
Field notes: Rare.
Distribution in Taiwan: New record.

Heteroxenia Kölliker, 1874
Heteroxenia medioensis Roxas, 1933
Occurrence: ZMTAU Co 35402, Co 35412, Dongsha, (20°45.609'N; 116°44.525'E), 7-11 m, 10 July 2011; ZMTAU Co 35419, Dongsha, (20°46.778'N; 116°48.533'E), 5-6 m, 10 July 2011; ZMTAU Co 36896, Dongsha, (20°44.316'N; 116°54.827'E), 12-14 m, 12 June 2015; ZMTAU Co 36982, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015; ZMTAU Co 36959, Dongsha, (20°41.509'N; 116°55.379'E), 6-8 m, 14 June 2015.
Field notes: Rare.
Distribution in Taiwan: New record.

Xenia Lamarck, 1816
Xenia lillieae Roxas, 1933
Occurrence: ZMTAU Co 36975, Co 36980, Co 36990, Dongsha, (20°41.994'N; 116°55.370'E), 4-6 m, 15 June 2015.
Field notes: Rare.
Distribution in Taiwan: New record.

Family Melithaeidae Gray, 1870

Melithaea Milne Edwards, 1857
Melithaea ochracea (Linnaeus, 1758)
Occurrence: ZMTAU Co 36922, Dongsha, (20°43.448'N; 116°42.520'E), 3-4 m, 13 June 2015.
Field notes: Rare.
Distribution in Taiwan: Southern Taiwan.

L-INS-i method in MAFFT (Katoh et al. 2005) was used to align sequences to reference datasets consisting of previously published sequences for the relevant genera (*e.g.* McFadden et al. 2006 2009 2014; Benayahu et al. 2012). Pairwise measures of genetic distance (Kimura 2-parameter) among sequences were computed using MEGA v.5 (Tamura et al. 2011). jModelTest2 (Darriba et al. 2012) was used to select appropriate models of evolution for maximum likelihood (ML) analyses that were run using GARLI 2.0 (Zwickl 2006). Analyses were run using *mtMutS* alone (*Sinularia*), *mtMutS* concatenated with *igr1* + *COI* (all taxa), and *28S rDNA* alone [*Cladiella*, *Klyxum*, Nephtheidae, Xeniidae (for list of genera of these families see Table 1)]. Bayesian analyses used MrBayes v. 3.2.1 (Ronquist et al. 2012) with the same evolutionary models as ML, run for 5,000,000 generations (or until standard deviation of split partitions < 0.01) with a burn-in of 25% and default Metropolis coupling parameters.

Identification of characteristic attributes in *Sinularia*

To resolve discrepancies between morphological vs. molecular species identifications in the speciose genus *Sinularia*, we identified sets of characteristic attributes within the *mtMutS* sequence to use as species-specific barcodes. All *mtMutS* sequences obtained for *Sinularia* were aligned and viewed using MacClade (Maddison and Maddison 2005). Each nucleotide position within the 735 bp alignment was then categorized as invariant or variant, and variant positions were further scrutinized to identify pure characteristic attributes (simple PuCAs *sensu* Rach et al. 2008) of (1) clades and (2) species within clades. Clade-specific PuCAs occurred when all of the species belonging to a clade (clades 1-5 as defined in McFadden et al. 2009) shared the same nucleotide at a particular position within the *mtMutS* sequence and no species of any other clade shared that nucleotide identity. Species-specific PuCAs were defined as nucleotide positions at which all of the individuals of a morphospecies shared the same nucleotide at a particular position, and no other morphospecies belonging to that clade shared that nucleotide identity. Compound PuCAs consisting of unique combinations of nucleotide identities at more than one nucleotide position were also identified for some taxa that lacked diagnostic simple PuCAs. Considered together, the clade-specific and species-specific PuCAs represent a compound PuCA (*i.e.* a diagnostic character set) that can be used as a unique sequence barcode to identify most species of *Sinularia* unequivocally.

RESULTS

The study yielded species in the families Alcyoniidae, Nephtheidae, Xeniidae, Briareidae, Tubiporidae, Helioporidae, and Melithaeidae (Table 1). Members of the family Alcyoniidae were the most abundant on Dongsha reefs, represented by eight genera and 46 species plus some additional colonies that were assigned only to genera: *Aldersladum* (1 species), *Cladiella* (5 species + sp.), *Klyxum* spp., *Lobophytum* (7), *Paraminabea* (1), *Sarcophyton* (6) and *Sinularia* (27 + sp.). The family Nephtheidae was represented by *Capnella* (1 species), *Dendronephthya* spp., *Lemnalia* (sp.), *Litophyton* spp., *Paralemnalia* (1 species), and *Stereonephthya* spp.; and the family Xeniidae by three genera, *Anthelia*, *Heteroxenia* and *Xenia*, each with a single species. The families Briareidae, Helioporidae, Melithaeidae, and Tubiporidae were similarly represented each by a single species. In total, the collection yielded 51 nominal species plus ~30 colonies that could not be identified to the species level, but were assigned to the genera *Cladiella*, *Klyxum*, *Sinularia*, *Dendronephthya*, *Lemnalia*, *Litophyton* and *Stereonephthya*. Molecular barcode sequences (*mtMutS*, *igr1* + *COI* and *28S rDNA*) for all specimens have been deposited in GenBank (accession numbers MH516349-MH516914).

Identification of *Sinularia* species using pure characteristic attributes (PuCAs)

A total of 27 nominal species of *Sinularia* plus at least one potentially new, undescribed species were identified based on the reconciliation of morphological with molecular data (Table 1). Phylogenetic analyses of *mtMutS* plus *igr1* + *COI* identified *Sinularia* specimens to clade and sub-clade (see McFadden et al. 2009) with high support (data not shown). Within sub-clades, however, distinct morphospecies often shared identical or nearly identical *mtMutS* sequences. Minimum pairwise genetic distances (Kimura 2-parameter) among morphospecies ranged from 0.5-1.1% among five species in sub-clade 4D, and from 0-1.8% among eleven species belonging to sub-clade 5C. Intraspecific genetic distances as high as 0.8% were observed in several morphospecies. As a result of this substantial overlap between intra- and interspecific genetic distances, there was no barcoding gap that could be used as a threshold value for delimiting species reliably. Morphospecies whose *mtMutS* sequences differed by just a single nucleotide (genetic distance ~0.1%) could, however, be distinguished unequivocally if that difference represented a pure characteristic attribute (PuCA). All 12 species belonging to clade 4 and 9 of 13 species belonging to clade 5 had simple or compound PuCAs that distinguished them from all other species (Fig. 2). For example, the presence of a C at nucleotide position 245 of *mtMutS* is a simple PuCA that distinguished *S. lochmodes* (Fig. 3A) from all other species belonging to clade 5. Within sub-clade 5C, however, individuals of four morphospecies (*S. abrupta*: Fig. 3B, *S. acuta*: Fig. 3C, *S. penghuensis*: Fig 3D and *S. slieringsi*) could not be distinguished reliably using PuCAs as they often shared identical *mtMutS* haplotypes. In addition, some colonies identified morphologically as *S. exilis* had *mtMutS* haplotypes that were identical to those of *S. erecta* (Figs. 2; 3E). For those morphospecies that lacked diagnostic PuCAs or for which there was an unresolved incongruence between morphology and molecular barcode, the barcode nonetheless narrowed the initial identification to a small subset of species within a clade, after which we relied on morphological characters for the final species identification.

Phylogenetic relationship between *Sarcophyton* and *Lobophytum*

The second-most speciose genera of soft corals found at Dongsha Atoll were the alcyoniids *Lobophytum* (7 species) and *Sarcophyton* (6

Clade 4	**N**	**075**	**081**	**093**	**096**	**124**	**128**	**140**	**165**	**179**	**182**	**187**	**204**	**207**	**252**	**253**	**286**	**294**	**303**	**343**	**358**	**365**	**384**	**389**	**444**	**451**	**474**	**504**	**544**	**561**	**576**	**583**	**595**	**631**	**642**	**651**	**663**	**666**	**668**	**716**	**722**
S. flexibilis	3	A	C	G	T	C	G	C	G	A	A	C	C	C	C	G	A	T	C	G	G	G	A	T	C	T	T	C	G	C	T	A	G	T	G	C	T	G	G	T	C
S. yamazatoi	1	A	C	G	T	C	G	C	A	A	A	C	C	C	C	G	A	T	C	G	G	G	A	T	C	T	T	C	G	C	T	A	G	T	G	C	G	G	G	T	C
S. querciformis	2	G	C	A	C	T	A	C	G	G	A	C	Y	C	T	R	A	T	C	G	G	G	A	C	C	T	C	C	G	C	C	A	G	T	G	C	T	G	A	T	C
S. variabilis	4	G	C	G	C	T	G	C	G	G	A	C	C	T	C	G	A	T	T	G	G	G	G	C	C	T	C	C	G	C	T	A	A	T	G	C	T	G	A	T	T
S. heterospiculata	1	G	T	G	C	T	G	C	G	G	A	C	C	C	C	G	G	T	C	G	G	G	A	C	C	T	C	C	G	T	T	G	G	T	G	C	T	G	A	T	C
S. curvata	2	G	C	G	C	T	G	C	G	G	A	C	C	C	C	A	A	T	T	G	G	G	A	C	C	T	C	C	G	C	T	A	G	T	G	C	T	A	A	T	C
S. humilis	9	G	C	G	C	T	G	C	G	G	A	C	C	C	C	A	A	T	C	G	G	G	A	C	C	T	C	C	G	C	T	A	G	T	G	C	T	A	A	T	C
S. ceramensis	13	G	C	G	C	T	G	C	G	R	A	C	T	C	C	G	A	C	C	G	G	G	A	C	C	T	C	C	G	C	T	A	G	T	G	C	T	G	A	T	C
S. ovispiculata	2	G	C	G	C	T	G	C	G	G	A	C	C	C	C	G	A	T	C	G	G	G	A	C	C	C	C	C	A	C	T	A	G	T	G	C	T	G	A	T	C
S. pavida	3	G	C	G	C	T	G	C	G	G	A	C	C	C	C	G	A	T	C	G	G	A	A	C	C	T	C	T	G	C	T	A	G	C	G	C	T	G	A	T	C
S. scabra	1	G	C	G	C	T	G	C	G	G	A	T	C	C	C	G	A	T	C	G	A	G	A	C	T	T	C	C	G	C	T	A	G	T	A	C	T	G	A	T	C
S. tumulosa1	8	G	C	G	C	T	G	C	G	G	A	C	C	C	C	G	A	T	C	G	G	G	A	C	C	T	C	C	G	C	T	A	G	T	G	C	T	G	A	C	C
S. tumulosa2	8	G	C	G	C	T	G	C	G	G	A	C	C	C	C	G	A	T	C	A	G	G	A	C	C	T	C	C	G	C	T	A	G	T	G	C	T	G	A	T	C

Clade 5	**N**	**060**	**117**	**143**	**144**	**176**	**188**	**224**	**245**	**249**	**279**	**282**	**285**	**310**	**311**	**315**	**322**	**340**	**358**	**400**	**438**	**475**	**540**	**547**	**549**	**559**	**561**	**571**	**612**	**618**	**620**	**628**	**690**	**711**
S. humesi	4	G	T	A	C	C	C	C	T	A	A	T	A	A	C	C	A	G	G	G	A	A	A	A	G	A	T	G	G	C	A	G	T	A
S. hirta	5	G	C	G	C	C	C	C	T	A	A	T	A	A	C	T	G	G	G	G	A	A	A	A	G	A	C	G	G	A	G	G	T	G
S. capillosa	2	G	C	A	C	C	T	C	T	T	A	T	A	G	C	C	G	G	G	G	A	A	A	A	G	A	C	G	G	C	G	G	T	A
S. densa	9	G	C	A	C	C	C	C	T	T	A	T	A	A	C	C	G	G	G	G	A	A	A	T	G	A	C	G	G	C	G	G	T	A
S. erecta	3	G	C	A	C	C	C	C	T	C	A	C	A	A	C	C	G	G	A	A	G	A	A	A	A	A	C	G	A	C	G	G	T	A
S. exilis	2	G	C	A	T	C	C	C	T	T	A	T	A	A	C	C	G	G	G	G	A	A	A	A	G	A	C	G	G	C	G	G	T	A
S. lochmodes	10	G	C	A	C	C	C	C	C	T	A	T	A	A	C	C	G	G	G	G	A	A	A	T	G	A	C	G	G	C	G	G	T	A
S. maxima	8	G	C	A	C	C	C	T	T	T	A	T	C	A	C	C	G	G	G	G	A	A	A	A	G	A	C	G	G	T	G	G	C	A
S. abrupta	3	G	C	A	C	C	C	C	T	Y	A	T	A	A	C	C	G	G	G	G	A	A	A	A	G	A	C	G	G	C	G	G	T	A
S. acuta	14	G	C	A	C	C	C	C	T	T	A	T	A	A	C	C	G	G	R	G	A	A	A	A	G	A	C	G	G	C	G	G	T	A
S. penghuensis	11	G	C	A	C	C	C	C	T	T	A	T	A	A	C	C	G	G	G	G	A	A	A	A	G	A	C	G	G	C	G	G	T	A
S. slieringsi	22	G	C	A	C	C	C	C	T	T	A	T	A	A	C	C	G	G	G	G	A	A	A	A	G	A	C	G	G	C	G	G	T	A
S. wannanensis	15	G	C	A	C	C	C	C	T	C	A	T	A	A	C	C	G	G	G	G	A	A	A	A	G	A	C	G	G	C	G	G	T	A

Fig. 2. Pure characteristic attributes (PuCAs) diagnostic of species in *Sinularia* clades 4 and 5 from Dongsha Atoll. Number above each column indicates nucleotide position in 735-nt *mtMutS* sequence relative to the start codon (ATG = positions 1-3). Nucleotides highlighted in gray represent species-diagnostic PuCAs; nucleotides highlighted in blue represent clade-diagnostic PuCAs. N = number of specimens sequenced. IUPAC ambiguity codes (*e.g.* Y, R) denote intraspecific polymorphisms.

species). The phylogenetic relationship between these two genera is currently unclear, as previous molecular analyses have divided their species among three distinct clades, each supported by diagnostic morphological characters (McFadden et al. 2006). A combined analysis of *mtMutS* and *COI* sequences obtained for specimens from Dongsha unequivocally assigned individuals to each of these three previously designated clades ('*Sarcophyton*', '*Lobophytum*' and 'mixed') (Fig. 4).

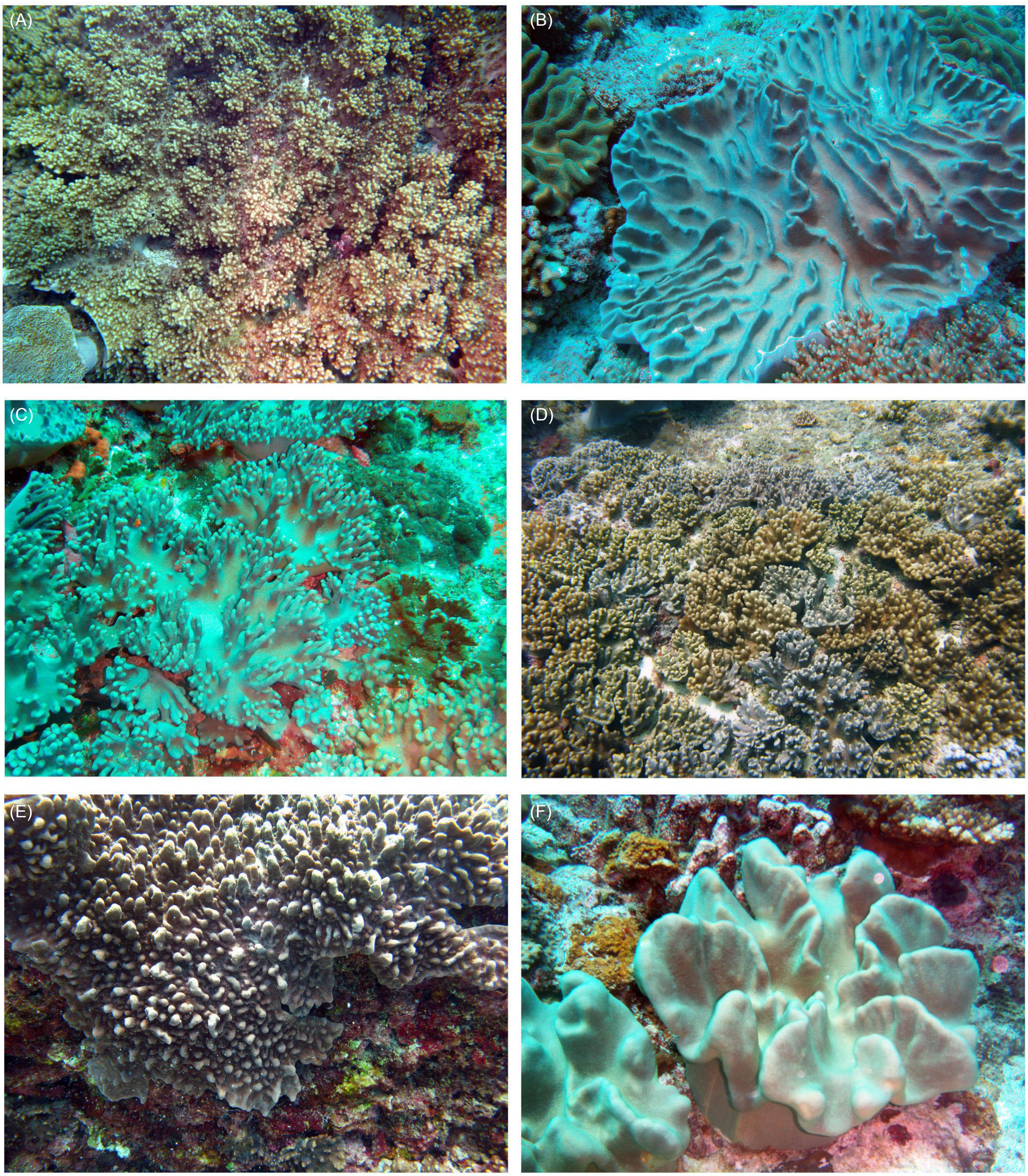

Fig. 3. Underwater photographs of Dongsha Atoll octocorals: (A) *Sinularia lochmodes*, (B) *S. abrupta*, (C) *S. acuta*, (D) *S. penghuensis*, (E) *S. erecta* and (F) *Lobophytum rigidum*.

However, six colonies identified as *S. crassocaule* and *L. rigidum* (Fig. 3F) belonged to a well-supported, genetically distinct fourth clade that was sister to the [‘*Sarcophyton*’ + ‘*Lobophytum*’] clade; a reference specimen of *S. crassocaule* from Indonesia also belonged to this fourth clade,

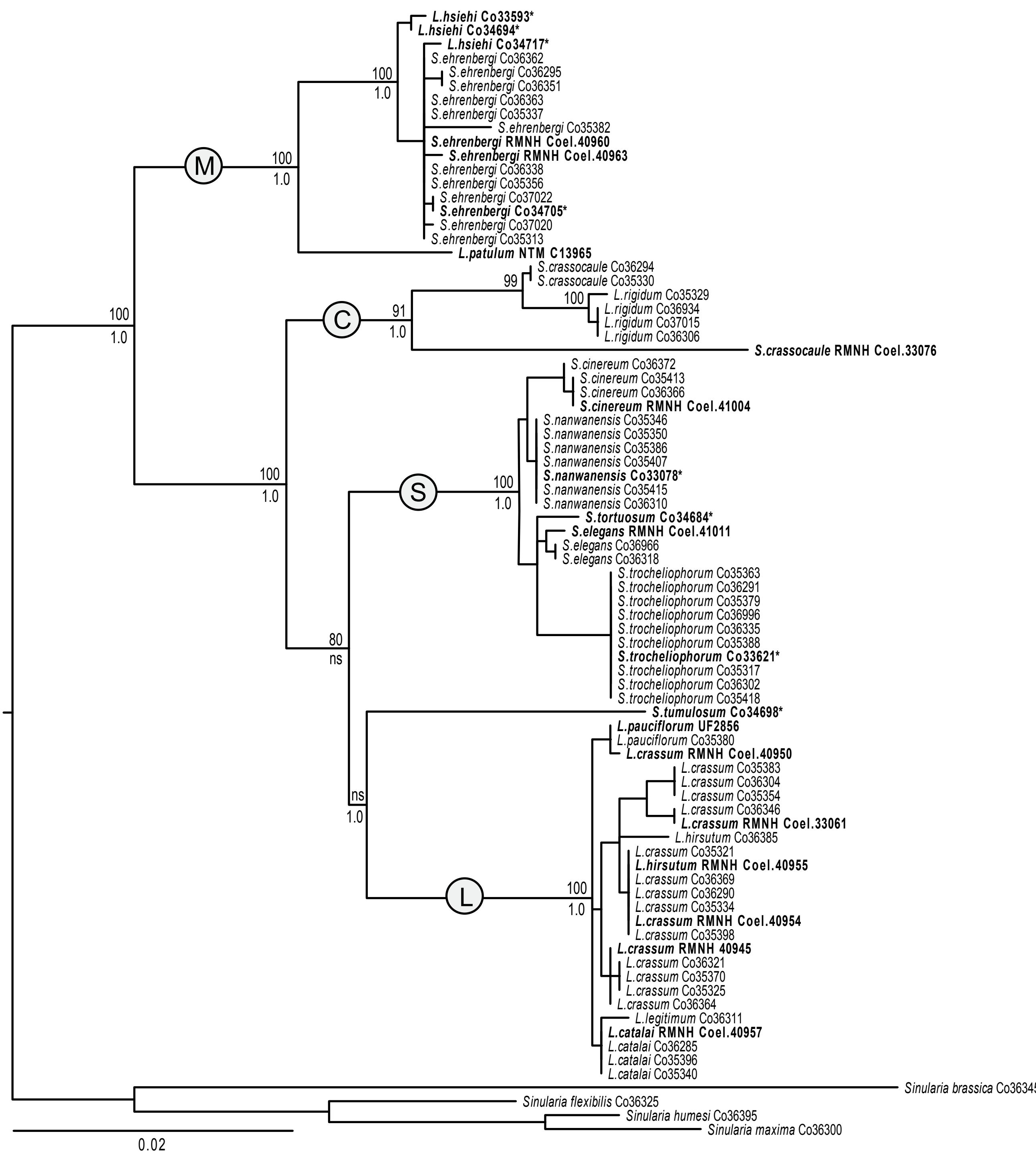

Fig. 4. Maximum likelihood tree based on concatenated *mtMutS* and *igr1* + *COI* sequences (1552 bp) for the soft coral genera *Lobophytum* and *Sarcophyton*. Circled letters indicate clades: M, “mixed” clade; C, “*Crassocaule*” clade; S, “*Sarcophyton*” clade; L, “*Lobophytum*” clade (see McFadden et al. 2006). Numbers above nodes: ML bootstrap values; below nodes: Bayesian posterior probabilities. Boldface taxon labels: reference sequences from other studies; *specimen from Penghu Archipelago (Benayahu et al. 2012). Co: ZMTAU accession number.

although it was genetically distinct from the *S. crassocaule* in Dongsha. Four species belonging to the '*Sarcophyton*' clade (*S. cinereum*: Fig. 5A, *S. elegans*, *S. nanwanensis*: Fig. 5B, *S. trocheliophorum*: Fig. 5C, D) were morphologically and phylogenetically distinct from one another and had unique barcode sequences that closely matched reference material of those species. Within the '*Lobophytum*' clade, five species were identified based on morphology: *L. catalai*, *L.*

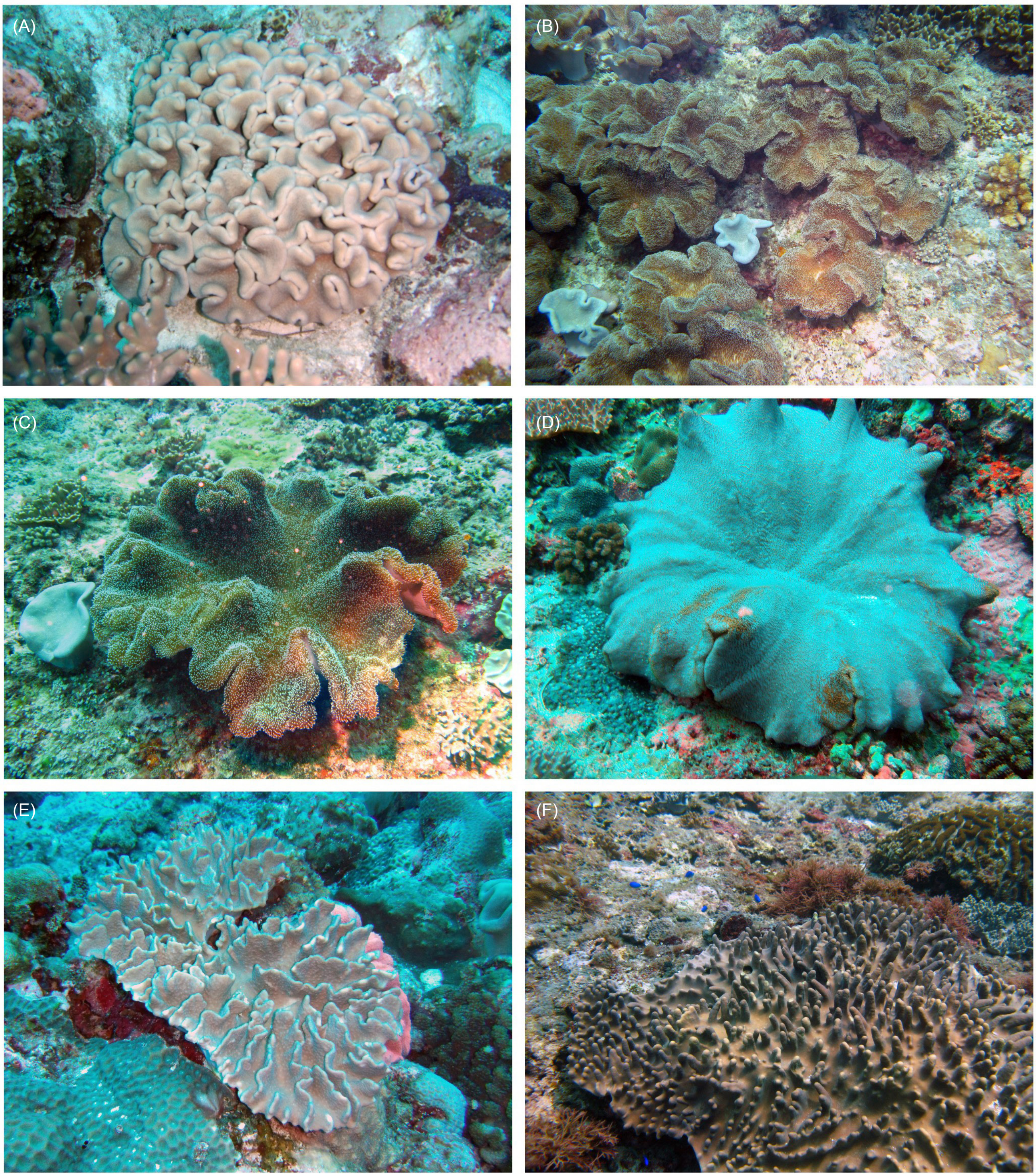

Fig. 5. Underwater photographs of Dongsha Atoll octocorals: (A) *Sarcophyton cinereum*, (B) *S. nanwanensis*, (C) *S. trocheliophorum*, (D) *S. trocheliophorum*, (E) *Lobophytum crassum* and (F) *L. pauciflorum*.

crassum: Fig. 5E, *L. hirsutum*, *L. legitimum*, and *L. pauciflorum*: Fig. 5F. Colonies identified as *L. crassum*, however, belonged to four genetically distinct sub-clades, each of which also included reference material previously identified as *L. crassum* as well as some other species (Fig. 4). Two 'mixed' clade species were identified, *S. ehrenbergi* (Fig. 6A) and *L. hsiehi* (Fig. 6B). Barcode sequences for *S. ehrenbergi* varied slightly among individuals but most haplotypes

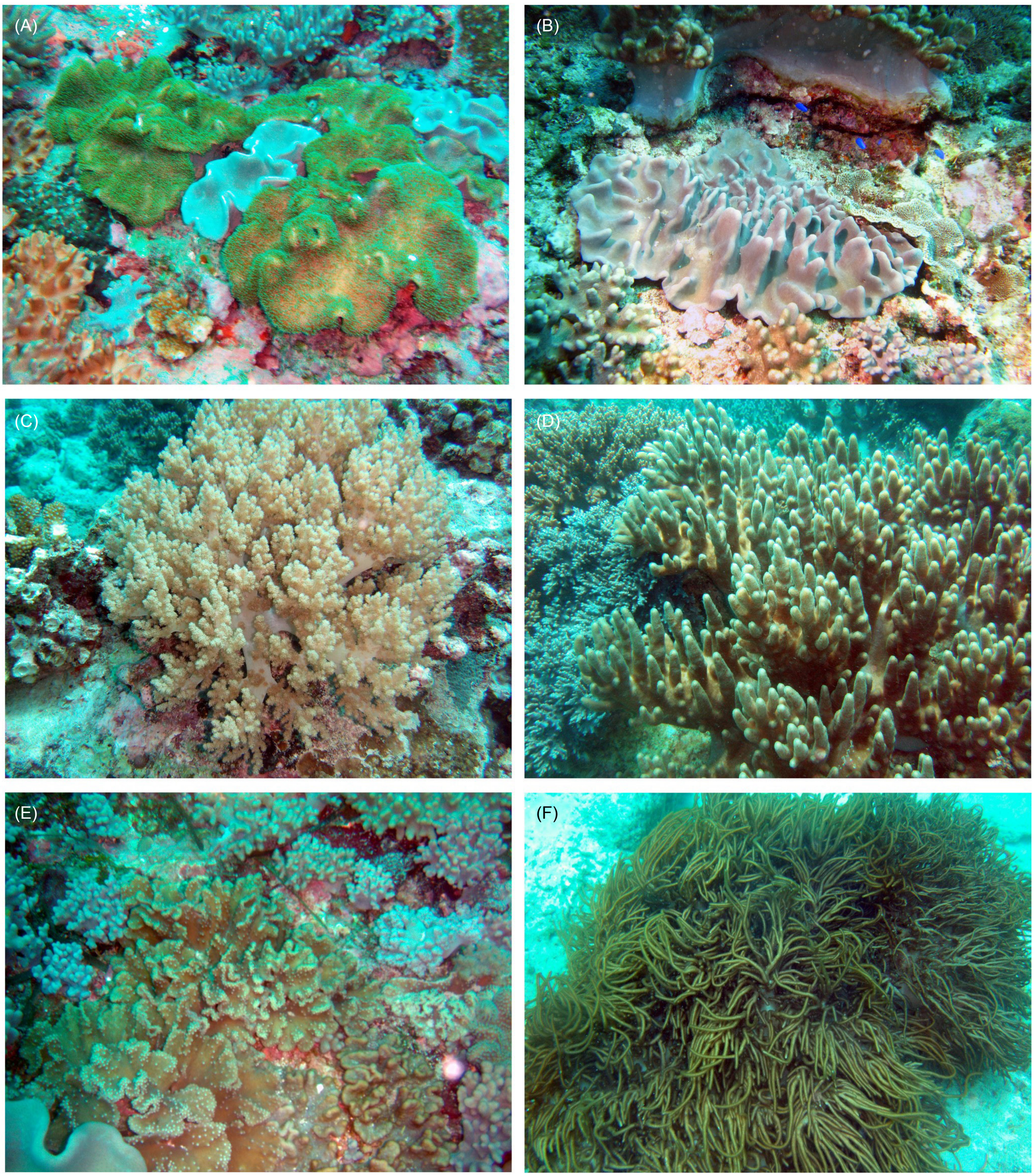

Fig. 6. Underwater photographs of Dongsha Atoll octocorals: (A) *Sarcophyton ehrenbergi*, (B) *Lobophytum hsiehi*, (C) *Litophyton* sp., (D) *Sinularia ceramensis*, (E) *S. brassica*, (F) *S. flexibilis*.

matched existing reference material of that species; we were unable to obtain sequence data from any specimens of *L. hsiehi*.

Other taxa

All other taxa were identified to the genus level based on a congruence of morphological characters and molecular barcodes. Species-level identifications were not possible, however, for the alcyoniid genera *Klyxum* and some *Cladiella* and for the majority of Nephtheidae genera as a result of the need for taxonomic revisions coupled with a lack of reference sequences with confirmed species IDs. Previous work has demonstrated that neither the *mtMutS* nor *COI* barcodes resolve species boundaries adequately in *Klyxum* and *Cladiella* (Benayahu et al. 2012). Although the *28S rDNA* barcode provides better resolution for species in those genera (Benayahu et al. 2012), we encountered some incongruence between morphological and molecular identifications (data not shown) that limited our ability to assign species names with confidence to some specimens.

Both molecular and morphological data support the conclusion that the Nephtheidae genera *Capnella*, *Lemnalia*, *Litophyton* (Fig. 6C), *Paralemnalia*, and *Stereonephthya* are each represented by just a single species at Dongsha. No or only minimal (< 0.2%) variation in *mtMutS* + *igr1* + *COI* haplotypes were observed among specimens within any of those genera. Although all colonies of *Dendronephthya* also shared an identical mitochondrial haplotype, morphological differences suggested that 3-4 species may be present at Dongsha. Previous molecular work has shown that mitochondrial barcode markers may not exhibit sufficient variation to distinguish morphospecies of that genus (Park et al. 2012).

DISCUSSION

Diversity and biogeography of Dongsha Atoll octocorals

The octocoral fauna of the Taiwanese reef systems, including southern Taiwan and the Penghu Archipelago, has been studied extensively (*e.g.* Benayahu and Perkol-Finkel 2004; Benayahu et al. 2004; Benayahu and McFadden 2011; Benayahu and Ofwegen 2011; Ofwegen and Benayahu 2012; Benayahu et al. 2012). Dongsha Atoll shares a number of common species with both of these other reef systems (Table 1). This resemblance is in particular indicated by the shared occurrence of species whose type locality is southern Taiwan (*Sarcophyton nanwanensis*) and the Penghu Archipelago (*Aldersladum jengi*, *Lobophytum hsiehi*, *Sinularia penghuensis*, *S. soongi*, and *S. wanannensis*). Octocoral diversity is higher at Dongsha Atoll than at Penghu, however, comprising 15 genera in seven families compared to 11 genera in just three families, respectively. Notably, the family Xeniidae is absent at Penghu while at Dongsha xeniids are present although rather rare.

The alcyoniid genera *Cladiella*, *Lobophytum*, *Sarcophyton* and *Sinularia* are the most species-rich and numerically dominant octocorals in all three Taiwanese reef systems, although the species richness of alcyoniids at Dongsha is about twice that of the more northerly reef system of Penghu. Dongsha has 7, 5 and 27 species of *Lobophytum*, *Sarcophyton* and *Sinularia*, respectively, compared to 4, 3 and 16 species of those same genera at Penghu (Benayahu et al. 2012). Three species of *Sinularia* encountered most frequently at Penghu (*S. molesta*, *S. ornata*, *S. peculiaris*) have not been reported from Dongsha, whereas several of the most common species found at Dongsha are not present at Penghu (*S. ceramensis*: Fig. 6D, *S. brassica*: Fig. 6E, *S. flexibilis*: Fig. 6F, *S. tumulosa*: Fig. 7A) or are rare there (*S. acuta*: Fig. 7B, *S. maxima*; Fig. 7C, *S. lochmodes*: Fig. 3A, *S. slieringsi*). Species such as *S. penghuensis*: Fig. 3D and *S. wanannensis*: Fig. 7D are, however, common at both locations, as are *Cladiella australis*: Fig. 7E, *Lobophytum crassum*: Fig. 5C, *L. hsiehi*: Fig. 6B, and *Sarcophyton trocheliophorum*: Fig. 5D. The reefs of southern Taiwan (Kenting National Park) are reported to have a species richness similar to that of Dongsha and to share many of these same common taxa (Benayahu et al. 2004). However, because studies there were conducted prior to the use of molecular barcoding markers to facilitate species identifications, further studies and re-examination of material from Kenting using such an integrative approach might yield different estimates of both species richness and identity of the taxa present.

Character-based DNA barcodes as a tool for octocoral identification

The identification of shallow-water Indo-Pacific octocorals to the species level is extremely challenging, particularly within speciose genera such as *Sinularia* (*e.g.* Benayahu et al. 2012; McFadden et al. 2014). Morphospecies are distinguished primarily on the basis of differences in colony growth form and the distribution and shape of sclerites within the tissues (*e.g.* Fabricius and Alderslade 2001; McFadden et al. 2009). A high level of taxonomic expertise is required to evaluate the latter, and the degree to which such morphological characters may vary intraspecifically

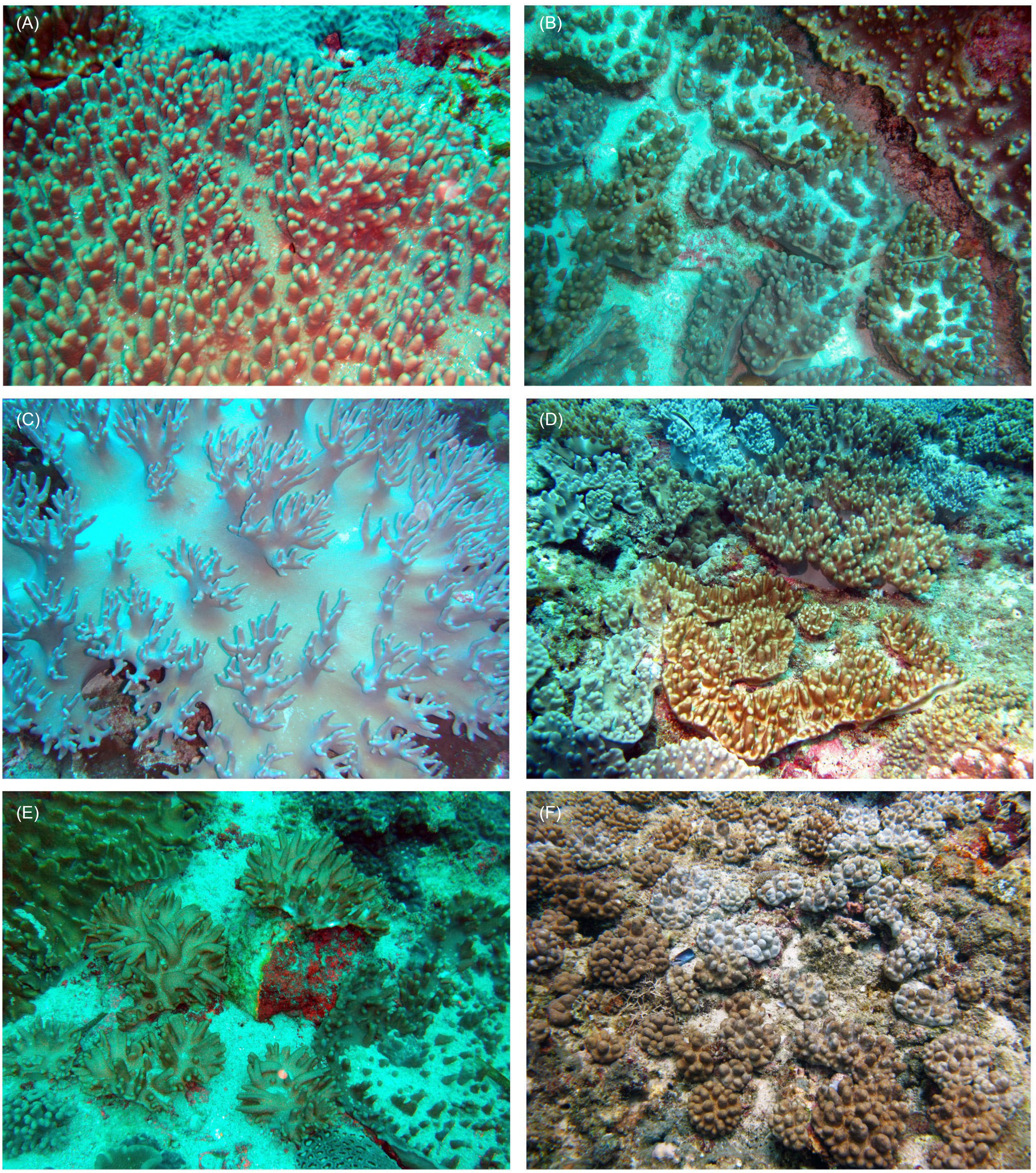

Fig. 7. Underwater photographs of Dongsha Atoll octocorals: (A) *Sinularia tumulosa*, (B) *S. acuta*, (C) *S. maxima*, (D) *S. wanannensis*, (E) *Cladiella australis* and (F) *Cladiella* sp.

has been assessed for only a few *Sinularia* species (*e.g. S. brassica*: Benayahu et al. 1998; *S. leptoclados*: Verseveldt 1980; Ofwegen et al. 2013; *S. polydactyla*: Verseveldt 1980; Ofwegen et al. 2016). Moreover, most of the earlier studies were based on limited numbers of specimens, did not examine the entire range of intraspecific variation in morphological characters, and lack supporting molecular data. Although the use of molecular barcode markers facilitates the identification of taxa without the need for extensive taxonomic expertise, the single-gene markers currently available are inadequate to discriminate closely-related species within most genera (McFadden et al. 2006 2009 2011 2014). For instance, in a previous survey of octocorals in Palau, application of genetic distance thresholds using the *mtMutS* DNA barcode discriminated 80% of *Sinularia* morphospecies, while the overall concordance between identifications based independently on morphology vs. barcode sequences was 77.6% (McFadden et al. 2014). When the molecular barcode was combined with assessment of colony growth form; however, 96% of specimens were identified to the species level. In the present study we used a similar combined approach, reconciling morphological characters with barcode sequences in order to discriminate taxa and assign appropriate binomials.

When intraspecific and interspecific genetic distance values are both low and overlap extensively, as they often do in *Sinularia* and other octocoral genera (McFadden et al. 2011 2014), methods of species discrimination that rely on arbitrary threshold values may fail when even a small amount of intraspecific variation or sequencing error is present. Character-based barcodes, however, are more robust to such noise, as species-diagnostic nucleotide characters (pure characteristic attributes, PuCAs) can be distinguished from characters that vary intraspecifically, and only the former can be used to identify species (DeSalle et al. 2005; Rach et al. 2008; Zou et al. 2011; Bergmann et al. 2013; Paknia et al. 2015). For example, *Sinularia ceramensis* from Dongsha Atoll exhibited intraspecific variation at 8 of 735 nucleotide positions in the *mtMutS* barcode sequence, leading to intraspecific genetic distances that ranged from 0-0.7% and overlapped with some interspecific genetic distances. All individuals of *S. ceramensis*, however, shared diagnostic PuCAs at two nucleotide positions in *mtMutS* (T at position 204 and C at position 294) (Fig. 2), allowing them to be discriminated unequivocally from all other species regardless of the noise contributed by intraspecific variation. Unlike threshold-based methods; however, application of character-based barcodes requires that a sufficient number of individuals of a species be sequenced in order to distinguish species-diagnostic PuCAs from nucleotides that vary intraspecifically.

Although application of a character-based rather than a genetic distance-based barcode allowed better discrimination of species of *Sinularia* that differed from one another by only 1-2 diagnostic nucleotides (genetic distances < 0.3%), we nonetheless encountered distinct morphospecies that shared identical *mtMutS* sequences and therefore could not be distinguished using either a character- or distance-based approach. Among the species belonging to the confusing 5C (“leptoclados”) sub-clade of *Sinularia*, *S. acuta*, *S. abrupta*, *S. penghuensis*, and *S. slieringsi* shared identical *mtMutS* haplotypes, and *S. wanannensis* differed from them at only a single nucleotide position (Fig. 2). Further investigation of those morphospecies using multilocus next-generation RADseq methods supports the genetic distinctions among them, however, and also suggests that a nuclear gene barcode marker such as *28S rDNA*—perhaps in combination with *mtMutS*—may better discriminate closely-related *Sinularia* species (unpub. data).

Regardless of whether a character- or threshold-based approach is used to discriminate taxa, the use of molecular barcodes to assign binomials relies on the establishment of a database that links sequence data to validated reference specimens (Puillandre et al. 2011 2012). A limitation to the establishment of such a database for octocorals is that sequences of type colonies along with their appropriate taxonomic descriptions (*i.e.* including SEM images of their entire suite of sclerites) are usually only available for recently described species. For most taxa, any reference sequences that are currently available derive from freshly collected (non-type) material, as old museum specimens often fail to yield DNA of a quality suitable for sequencing. Even if the newly collected reference material was identified by a skilled taxonomist, it has not always been compared directly to the respective type material and may not have been obtained from the type locality. Such practices introduce sources of error into the sequence database, and may result in molecular barcodes being assigned to reference specimens that have been mis-identified. These taxonomic errors are propagated further when the barcode sequence is then used to assign the incorrect binomial to additional material. Unfortunately, such errors can be difficult to detect and correct, especially when type material is not available for comparison, because it has either been lost or destroyed or its depository is not known. For most octocoral taxa, taxonomic revisions accompanied by barcoding of type material or other validated exemplars (including neotypes) will be necessary before it will be possible to use molecular barcodes alone to assign bionomials with a high degree of confidence.

Phylogenetic relationships among genera of the family Alcyoniidae

Molecular barcodes and morphological analyses both discriminated > 5 species in each of the alcyoniid genera *Cladiella*, *Lobophytum*, and *Sarcophyton* at Dongsha Atoll. The problems of species identification in these genera are similar to those in *Sinularia*, with the additional complication of a lack of congruence between morphologically defined genera and molecular clades (McFadden et al. 2006; Benayahu et al. 2012). McFadden et al. (2006) first recognized that *Sarcophyton* and *Lobophytum* comprise three morphologically and phylogenetically distinct clades, one of which includes nominal species of both genera (the ‘mixed’ clade). Suggestions that this third, ‘mixed’ clade should be considered a separate genus have been further complicated by the subsequent recognition that some nominal species of both genera fall outside of those three main clades (Benayahu et al. 2012), including *S. crassocaule*, *S. tumulosum* and *L. rigidum* (Fig. 4). Reconciliation of the genus-level taxonomy with the observed phylogenetic relationships among species will require either recognizing each distinct clade (*i.e.* clades M, C, S and L in Fig. 4) as a separate genus or, alternatively, synonymizing *Lobophytum* with *Sarcophyton* in order to recognize a single genus that encompasses a range of distinct morphologies.

The current taxonomic division between *Cladiella* and *Klyxum* also does not reflect the phylogenetic relationships among species assigned to those genera (Benayahu et al. 2012). Molecular evidence suggests that *C. australis* (Fig. 7E), the species of *Cladiella* most commonly encountered at Dongsha, actually belongs to the genus *Klyxum*. Indeed, both *C. australis* and *C. kashmani* (an Indian Ocean species) bear some morphological resemblance to *Klyxum* spp. as their colonies are rather flaccid in contrast to most typical *Cladiella* spp. (personal observations). In addition, both *C. australis* and *C. kashmani* feature elongated sclerites that differ from the usual dumbbells found in *Cladiella* (Benayahu and Schleyer 1996: figs. 4, 8-11). At both of the mitochondrial barcode loci we sequenced (*mtMutS* and *igr1+COI*), *C. australis* and the unidentified species of *Klyxum* collected at Dongsha shared identical haplotypes, which differed from other *Cladiella* species by 1.5%. At the nuclear *28S rDNA* locus, *C. australis* and *Klyxum* sp. differed from one another by 1.5% compared to a 7% average distance of both species from other *Cladiella*. Reassignment of *C. australis* (and *C. kashmani*) to *Klyxum* will necessitate revising the diagnosis of that genus to accommodate their different sclerite morphologies.

In addition to the observed incongruence between morphologically defined genera and molecular clades in *Sarcophyton*, *Lobophytum*, *Cladiella*, and *Klyxum*, species in these genera also exemplify the previously discussed challenges of using molecular barcodes to assign binomials when reference sequences are not derived from type material. For example, specimens identified in this study as *Sarcophyton crassocaule* (based on morphology) are not a close genetic match to reference material collected at a different geographic location and identified as that same species by a different taxonomic expert (Fig. 4). No sequence data are currently available for type material of *S. crassocaule*, and the high degree of intraspecific morphological variation exhibited by this species has been noted previously, indicating some confusion regarding its morphology-based diagnosis (Verseveldt 1982). Further in-depth study is necessary to reconcile the morphological and genetic variation in this species, as well as its apparently close relationship to *L. rigidum* (Fig. 3F). The only morphological description of *L. rigidum* is presented in the original description of its type colony (Benayahu 1995), and there are no data on intraspecific variability in that species. Similarly, specimens identified in other studies as *Lobophytum crassum* exhibit considerable sequence variation, and some haplotypes match reference sequences attributed to different morphospecies (Fig. 4). Interestingly, this species features a bewildering array of colony and sclerite variation (*e.g.* Verseveldt 1983: 25-32), which might also explain the noted sequence variation. Without further examination and sequencing of type material it is not clear if all of these genetically different forms are indeed *L. crassum*, or if the observed genetic polymorphisms are indicative of cryptic species. The same is true for *Cladiella pachyclados* (see Benayahu et al. 2012). Until sequences can be obtained from type specimens, or from newer material collected from type localities that is a close morphological match to the original types (*e.g.* Ofwegen et al. 2016), the use of molecular barcodes to assign Latin binomials in these genera will continue to be fraught with uncertainty.

CONCLUSIONS

Dongsha Atoll features a highly diverse octocoral fauna. Octocorals are the dominant benthic organisms at the surveyed sites, and members of the family Alcyoniidae—mainly the genera *Lobophytum*, *Sarcophyton* and *Sinularia*—may constitute 60-70% live coverage on some of the reefs (personal observations). Our photographic records also reveal the competitive abilities of certain octocorals to dominate reef areas and successfully overgrow some stony corals (Figs. 7F; 8A-C) or to hamper their growth when they closely interact (Fig. 8D). Undoubtedly, the exact nature of such competitive interactions should be further studied along with the adaptive features of Dongsha octocorals in order to understand their success there.

Integrative approaches that combine morphological, molecular, and other lines of evidence to distinguish among species have greatly facilitated our ability to assess the species-level diversity of octocorals and to compare community compositions among diverse locations (McFadden et al. 2014). As shown in the current

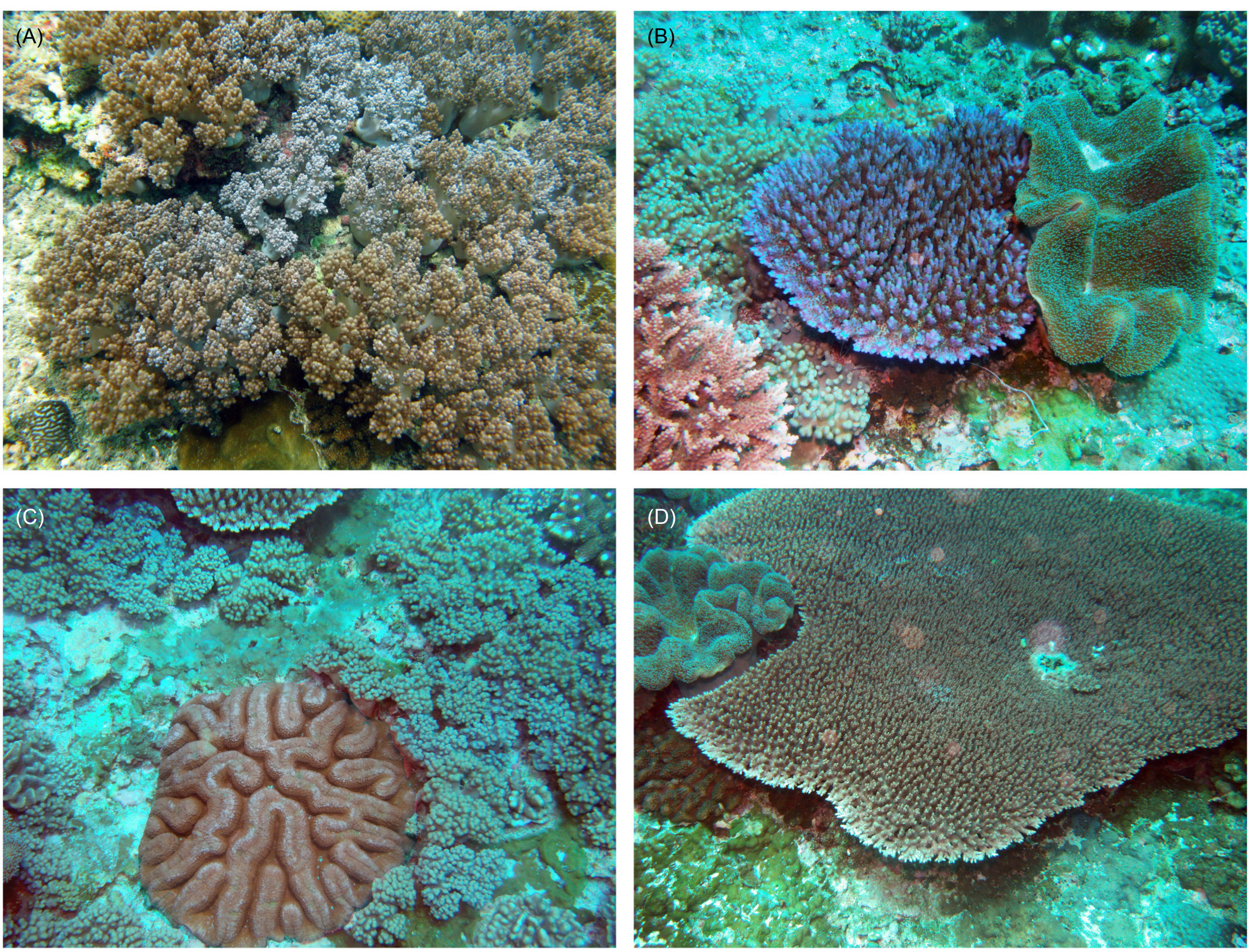

Fig. 8. Underwater photographs of Dongsha Atoll octocorals: (A) *Litophyton* sp. colonies densely occupy reef space, (B) colony of *Sarcophyton ehrenbergi* overgrowing *Acropora* sp., (C) colonies of *Sinularia penghuensis* surrounding colony of the stony coral *Symphyllia agaricia* and (D) colony of *S. ehrenbergi* inhibiting growth of *Acropora* sp.

study and elsewhere (McFadden et al. 2011), the use of character-based barcodes rather than genetic distance thresholds to distinguish taxa can overcome some – but not all – of the limitations imposed by the low levels of sequence variation that characterize the octocoral mitochondrial genome in general, and the most commonly used barcoding loci in particular. Although integrated approaches facilitate the recognition of cryptic species and have led to the correction of long-standing taxonomic errors (*e.g.* Ofwegen et al. 2013 2016), assignment of binomials to octocorals still remains a considerable challenge. Until reference sequences are available for a majority of museum types or taxonomically validated exemplars (*e.g.* recently collected material from type localities that has been compared directly to types, if they are available), the use of molecular barcodes to assign binomials will remain impossible in many genera, such as most of the Nephtheidae obtained at Dongsha. In those genera in which many barcodes are associated with reference specimens whose identity has not been validated by direct comparison to type material (*i.e.* most Alcyoniidae), the assignment of binomials remains susceptible to the inadvertent propagation of taxonomic errors. Although molecular barcoding is already a valuable approach to discriminating taxa and quantifying biodiversity in octocorals, most genera will require taxonomic revisions that include molecular characterization of species before it will be possible to use barcodes to assign Latin binomials with any certainty.

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