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Mesophotic mushroom coral records at Brunei Darussalam support westward extension of the Coral Triangle to the South China Sea waters of Northwest Borneo

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Abstract. This communication reports the discovery of two additional fungiid coral species, *Cycloseris hexagonalis* and *Lithophyllon spinifer*, from a relatively deep shelf reef in Brunei waters. These new records plus two earlier excluded ones, *Cycloseris explanulata* and *C. wellsi*, raise the known number of mushroom coral species at this Northwest Borneo location to 37 which is comparable to the number (n=35) reported for reefs of the nearby Tungku Abdul Rahman Park/Kota Kinabalu area, outside but close to the currently recognized northwest boundary of the zone of maximum marine biodiversity, the Coral Triangle (CT). The fungiid species richness at Brunei is compared with those of other sites in this eastern part of the South China Sea (SCS), and the adjacent westernmost CT ecoregion. A relatively high or comparable mushroom coral richness at all these sites, a richness which is higher than several central CT reef ecoregions, supports the argument for a westward shift of the CT boundary to the SCS waters of Northwest Borneo.

Key words. Scleractinia, Fungiidae, Spratly, coral reefs, species richness

INTRODUCTION

The Fungiidae (mushroom corals) are an Indo-Pacific family of Scleractinia which, in recent decades, has been intensively researched taxonomically and biogeographically (Hoeksema, 1989, 1993a, b, 2009, 2013, 2014, 2015; Hoeksema & Dai, 1991). They are also well studied phylogenetically (Wells, 1966; Cairns, 1984; Hoeksema, 1989; Gittenberger et al., 2011; Benzoni et al., 2012) and are thus an ideal group for studying patterns of diversity both within the Coral Triangle (CT) and for assessing boundary limits of the CT zone, as in this paper.

A recent inventory of mushroom corals for continental shelf waters of Brunei, Northwest Borneo, a South China Sea marine domain close to but generally considered to be outside the maximum marine biodiversity Coral Triangle (CT) zone (Fig. 1), recorded 33 taxa (Hoeksema & Lane, 2014). This fungiid richness is comparable to that for nearby locations off northwestern Sabah (Waheed & Hoeksema, 2014 (n=35); Waheed et al., 2015a (n=32)), but is notably less rich than for Sabahan regions within the CT (Waheed & Hoeksema, 2013 (n=44); Waheed et al., 2015b (n=39)) and for earlier reports for some other, more central, CT ecoregions (Hoeksema, 1992, 2007; Hoeksema & Putra, 2000 (max n=40)).

This communication reports the discovery of two additional fungiid species records from an upper mesophotic reef top (32 m depth) in Brunei waters. Mesophotic reef coral faunas (> 30 m deep) are characterised by species tolerating low light intensities (Kahng et al., 2010; Bongaerts et al., 2013; Ohara et al., 2013). Among mushroom coral species, clear differences in depth ranges can be distinguished with, for example, some species, such as *Pleuractis moluccensis* and most species of *Cycloseris*, showing an occurrence on reef slope bases at depths exceeding 30 m (Hoeksema, 2012a, b). Furthermore, in terms of richness, the present paper also notes two additional, previously excluded fungiid records, and considers the implications of this increased count in the context of biodiversity richness for the South China Sea (see Huang et al., 2015, 2016; Veron et al., 2015), and in terms of delineation of the westernmost CT boundary.

MATERIAL AND METHODS

Following a comprehensive mushroom coral diversity survey of fringing and submerged bank reefs on the Brunei shelf in April 2011 (Hoeksema & Lane, 2014), an additional 12 SCUBA dives, using regular air, were made in 2014 by the first author on several shelf-based reefs that were not visited in 2011 – for example Silk Rock, Brunei Patches, Mampak Patches – plus an isolated coral pinnacle, Louisa Reef, at the southwest edge of the Spratly group. Louisa Reef (N06°19.9' E113°14.5') is a low-tide reef approximately 1.5 × 0.5 km, arising from very deep water (> 2000 m) and separated from the Brunei continental shelf by the Palawan Trough

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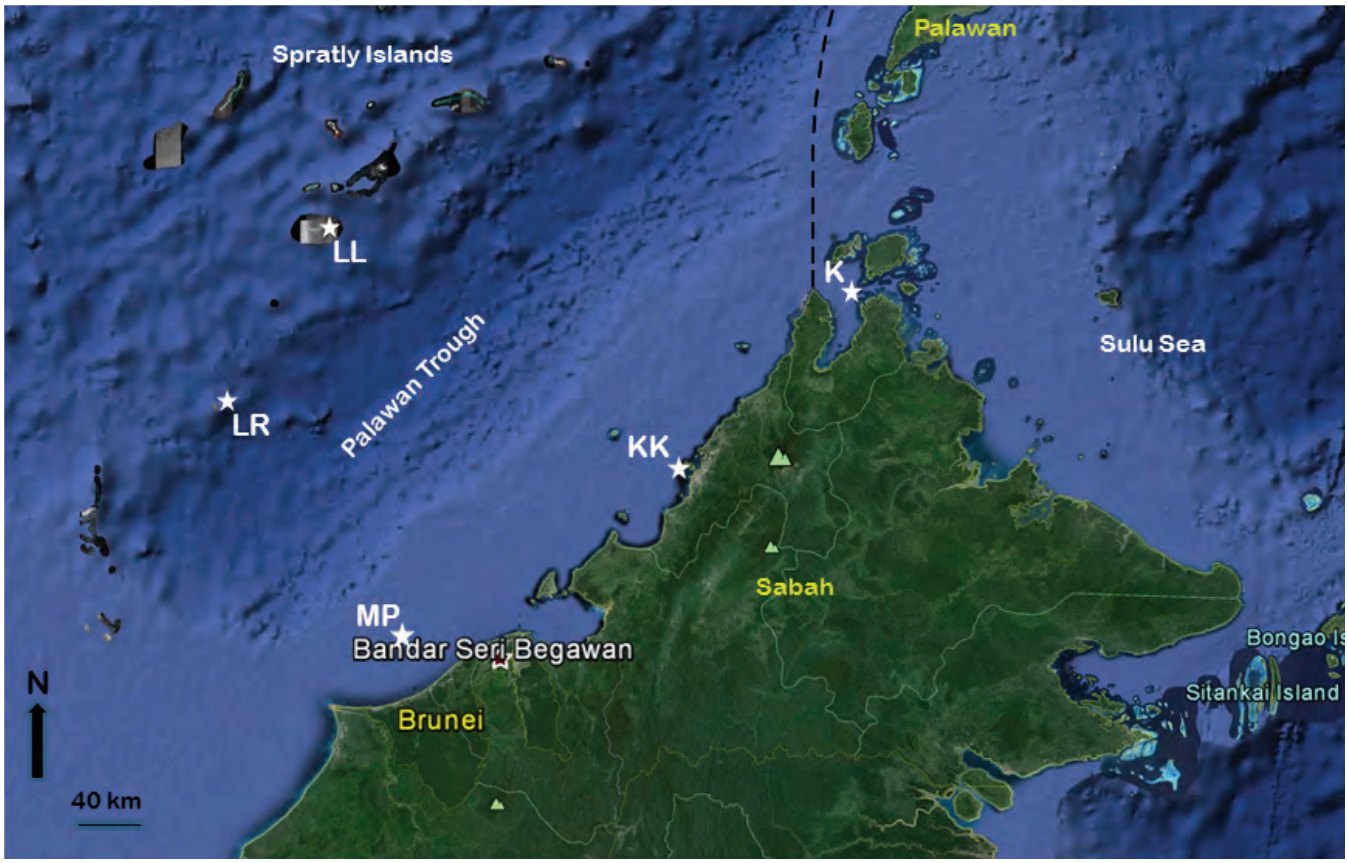

Fig. 1. Map of N.W. Borneo region. White stars designate Fungiidae survey locations. MP = Mampak Patches and LR = Louisa Reef (this study); LL = Layang Layang atoll, KK = islands of the Tungku Abdul Rahman Park near Kota Kinabalu, K = Kudat area (from the literature). Dashed black line represents current western limit of the Coral Triangle (map modified from Google Earth image).

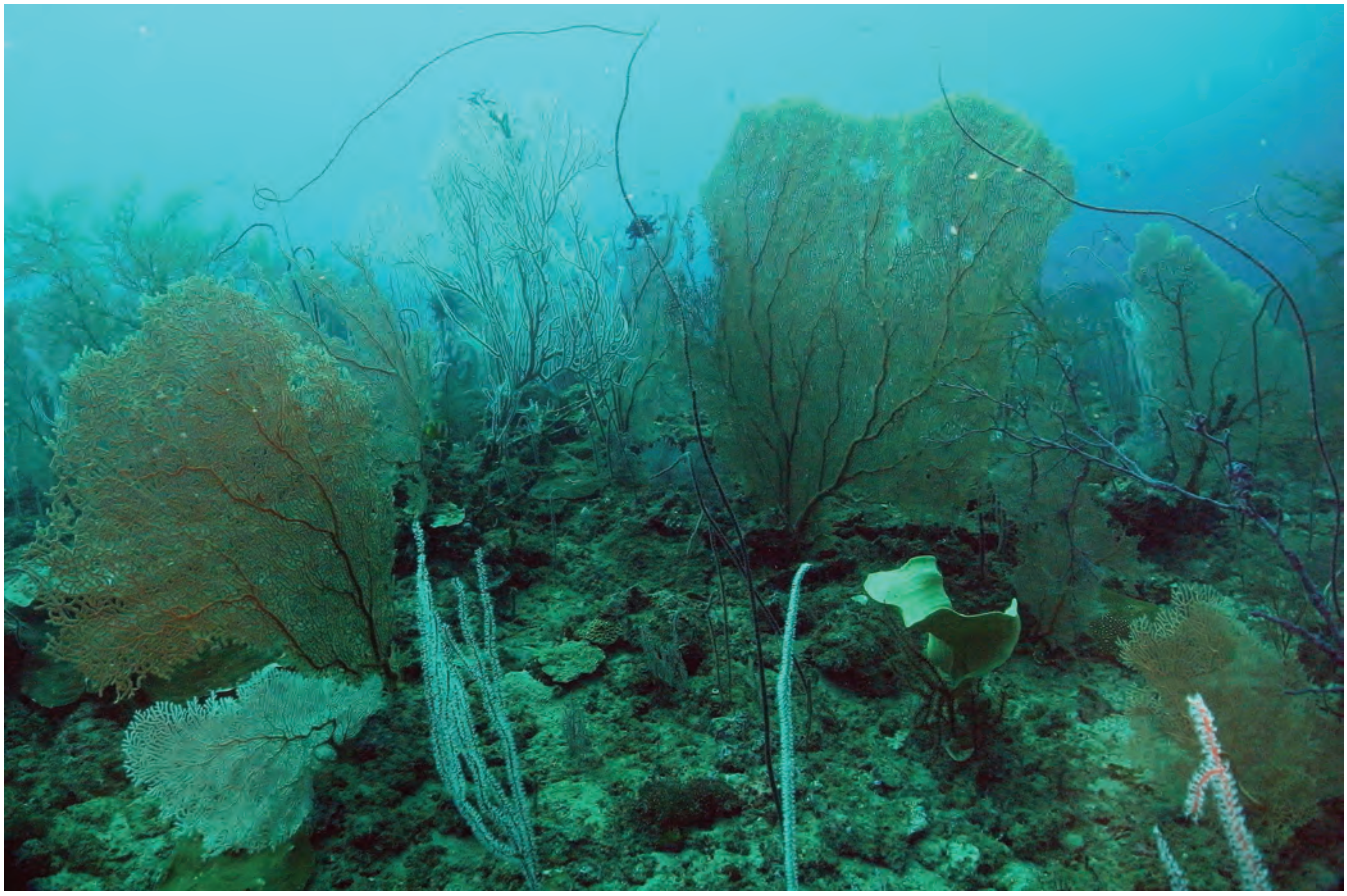

Fig. 2. View of the benthic community at the top of Mampak Patches, Brunei Darussalam (32 m deep).

Table 1. The distribution of Fungiidae in the South China Sea (SCS) and in regions of the SCS bordering, or close to, the western Coral Triangle boundary. SCS = South China Sea; Brunei = Brunei Darussalam; KK = Kota Kinabalu, Sabah, Malaysia; Layang – Layang (Malaysia); Spratly = Spratly Islands (sovereignty contested); W. Palawan (Philippines); Kudat, N. Sabah, Malaysia. Citations, a: Huang et al., 2015; b: Hoeksema & Lane, 2014; c: Waheed & Hoeksema, 2014; d: Waheed et al., 2015(a); e: Waheed et al., 2015(b); f: Hoeksema, 1989; g: Pilcher et al., 1999; §: this study.

	Species	SCS (a, b, c, d, §)	Brunei (b, §)	KK (c)	Layang–Layang (d, g)	Spratly (a, f)	W. Palawan (a)	Kudat (e)
1	*Ctenactis albitentaculata*	1	1	1	1	0	1	1
2	*Ctenactis crassa*	1	1	1	1	1	1	1
3	*Ctenactis echinata*	1	1	1	1	1	1	1
4	*Cycloseris boschmai*	1	0	1	1	0	0	1
5	*Cycloseris costulata*	1	1	1	1	1	1	1
6	*Cycloseris curvata*	0	0	0	0	0	0	1
7	*Cycloseris cyclolites*	1	1	1	1	1	1	1
8	*Cycloseris distorta*	0	0	0	0	0	0	1
9	*Cycloseris explanulata*	1	1	0	1	1	1	0
10	*Cycloseris fragilis*	1	1	1	0	1	1	1
11	*Cycloseris hexagonalis*	1	1	0	0	1	1	0
12	*Cycloseris mokai*	1	1	1	1	1	1	1
13	*Cycloseris sinensis*	1	1	1	1	1	1	1
14	*Cycloseris somervillei*	1	1	1	0	1	1	1
15	*Cycloseris tenuis*	1	1	1	1	1	1	1
16	*Cycloseris vaughani*	1	1	0	0	1	1	1
17	*Cycloseris wellsi*	1	1	0	0	1	1	0
18	*Danafungia horrida*	1	1	1	1	1	1	1
19	*Danafungia scruposa*	1	1	1	1	1	1	1
20	*Fungia fungites*	1	1	1	1	1	1	1
21	*Halomitra pileus*	1	1	1	1	1	1	1
22	*Heliofungia actiniformis*	1	1	1	1	1	1	1
23	*Heliofungia fralinae*	1	0	0	0	0	1	1
24	*Herpolitha limax*	1	1	1	1	1	1	1
25	*Lithophyllon concinna*	1	1	1	1	1	1	1
26	*Lithophyllon ranjithi*	1	0	0	1	0	0	1
27	*Lithophyllon repanda*	1	1	1	1	1	1	1
28	*Lithophyllon scabra*	1	1	1	1	0	1	1
29	*Lithophyllon spinifer*	1	1	1	0	0	1	1
30	*Lithophyllon undulatum*	1	1	1	1	1	1	1
31	*Lobactis scutaria*	1	1	1	1	1	1	1
32	*Pleuractis granulosa*	1	1	1	1	1	1	1
33	*Pleuractis gravis*	1	1	1	1	1	1	1
34	*Pleuractis moluccensis*	1	1	1	1	1	1	1
35	*Pleuractis paumotensis*	1	1	1	1	1	1	1
36	*Pleuractis taiwanensis*	1	1	1	0	0	1	1
37	*Podabacia crustacea*	1	1	1	0	1	1	1
38	*Podabacia motuporensis*	1	1	1	1	0	1	1
39	*Podabacia sinai*	1	0	1	1	0	0	0
40	*Polyphyllia talpina*	1	1	1	1	1	1	1
41	*Sandalolitha boucheti*	1	0	0	1	0	0	1
42	*Sandalolitha dentata*	1	1	1	1	1	1	1
43	*Sandalolitha robusta*	1	1	1	1	1	1	1
44	*Zoopilus echinatus*	1	1	1	0	1	1	0
	TOTALS	42	37	35	32	32	38	39

(Fig.1). At Louisa Reef, the maximum diving depth was 40 m. At the cluster of Mampak reef patches visited (Fig. 1) the reef-top depth ranged from 32 to 38 m and at one of these reef locations, namely North Patch: N05°02.305' E114°26.449' – 33.5 km offshore, two additional species of the family Fungiidae were recorded at a depth of 32 m. The reef community at this mesophotic site showed a predominance of fan corals and whip corals and a low density of scleractinians (Fig. 2). In situ photographs were taken using a Sea & Sea DX–2G housed camera system and YS–110α strobe. Images of bleached and dried specimens were taken using a Canon EOS M mirrorless, digital camera and 50 mm macro lens. Details of the new records are provided in the Species Account and fungiid distributions in this region are now updated and consolidated (Table 1) based on current data.

Abbreviations.

LKCNHM: Lee Kong Chian Natural History Museum (formerly the Raffles Museum)

RMNH Coel: Naturalis Biodiversity Centre (Coelenterate collection), formerly Rijksmuseum van Natuurlijke Historie, Leiden

UBDRC: Universiti Brunei Darussalam Dept. of Biology Reference Collection

SPECIES ACCOUNT

Cycloseris hexagonalis (Milne Edwards & Haime, 1848)

(Figs. 3A–D)

Fungia hexagonalis Milne Edwards & Haime, 1848: p. 89, pl. 6 Figs. 2–2f

Cycloseris hexagonalis – Milne Edwards & Haime, 1851: p. 113; Veron, 2000 (partim.): p. 239, Fig. 4; Gittenberger et al., 2011: Table 7; Hoeksema, 2012a: Fig. 6; Hoeksema, 2014: 75.

Fungia (*Cycloseris*) *hexagonalis* – Hoeksema, 1989: p. 59–64, Figs. 123–135, 613; Hoeksema, 1993a: 5; Hoeksema & van Ofwegen, 2004: [4 Figs.]

Fungia hexagonalis – Hoeksema, 2008: Fig. 8.

Material examined. Five specimens, collected by DJWL 8 November 2014 at 32 m depth, South China Sea, Mampak Patches, North Patch: N05°02.305' E114°26.449'. Habitat: reef top, silty sand and rock amongst gorgonian fan corals and whip corals. Monostomatous and free-living. Skeletal diameters (maximum) range from (1) 58 mm; (2) 62 mm; (5) 64 mm; (3) 65 mm; (4) 66 mm. Specimens are lodged with following Catalogue Numbers and Institutions: 1 & 5: RMNH Coel.42102 @ RMNH; 2: UBDM.6.201411.1 @ UBDRC; 3 & 4: ZRC.CNI.1008 & ZRC.CNI.1009 @ LKCNHM. All specimens are full-grown with the corallum outline irregularly circular or slightly oval, but with marked upwardly-directed undulations giving an irregularly concave shape to the thin corallum (Figs. 3A–D). In one specimen (RMNH Coel.42102b) the under faces of two of the four corallum folds are completely fused (Fig. 3D). Septa tightly packed with lower order ones thick, exsert and solid. Thin, higher order septal fenestrations, if present, not visible due to dense packing of septa. Septal margins of lower series ornamented with fine conical or blunt dentations that grade into the dense granulations of the septal sides and are, in consequence, difficult to count. The marginal ornamentation of the fine septae shows coalescing expansions centrally. Small, pointed costal spines near the corallum margin generally number less than 50 per cm.

Lithophyllon spinifer (Claereboudt & Hoeksema, 1987)

(Figs. 3E, F)

Fungia (*Verrilofungia*) *spinifer* Claereboudt & Hoeksema, 1987: Figs. 190–201; Hoeksema, 1989: 79–83, Figs. 186–202; Hoeksema, 1993a: 6, 17, Fig. 14. Hoeksema & van Ofwegen, 2004: [9 Figs.]

Cycloseris colini Veron, 2000: 247, Figs. 4, 5; Veron, 2002: 99–101, Figs. 185–188.

Fungia spinifer – Hoeksema, 2008: Fig. 9.

Lithophyllon spinifer – Gittenberger et al., 2011: Table 7; Hoeksema, 2012c: Fig.8; Hoeksema & Waheed, 2012a: Table 1.

Material examined. one specimen, (RMNH Coel.42103) collected by DJWL 8 November 2014 at 32 m depth, South China Sea, Mampak patches, North Patch: N05°02.305' E114°26.449'. Habitat: reef top, silty sand and rock amongst gorgonian fan corals and whip corals. Monostomatous and free-living. Corallum almost circular, concave, with a raised septal mound around the central fossa. Maximum diameter 97mm.

Louisa Reef. During the brief offshore SCUBA diving visit to Louisa Reef at the southwest edge of the Spratly islands (3rd – 4th September 2014), the following additional location records for fungiids were made. All of these species also occur on Brunei's continental shelf reefs (Hoeksema & Lane, 2014). Confirmation of identifications was by the 2nd author, based on specimens and/or in situ photographs. Where specimens were collected, these are deposited in the UBD Reference Collection under the following catalogue numbers: *Ctenactis albitentaculata* (image only); *C. crassa* (UBDM.6.201409.1); *Cycloseris tenuis* (UBDM.6.201409.2); *Danafungia horrida* (UBDM.6.201409.3); *D. scruposa* (UBDM.6.201409.4); *Herpolitha limax* (image only); *Lobactis scutaria* (UBDM.6.201409.5); *Pleuractis gravis* (UBDM.6.201409.6).

DISCUSSION

The number of species of Fungiidae documented and reported for a mushroom coral survey in 2011 on Brunei reefs totaled 33 (Hoeksema & Lane, 2014). Two additional species, *Cycloseris explanulata* (Van der Horst, 1922) and *C. wellsi* (Veron & Pichon, 1980), were noted by Hoeksema & Lane (2014) but were not on the checklist and not counted as at the time of the 2011 survey they were considered members of the family Siderastreidae (Benzoni et al., 2007). Despite the subsequent reassignment of these two species to the Fungiidae (Benzoni et al., 2012) and their inclusion in Brunei's inventory (Huang et al., 2015), for consistency of comparison with other contemporary fungiid surveys in the region these two species were not included in Hoeksema & Lane (2014). Nevertheless they are now included in the present analysis. Two additional taxa, *Cycloseris hexagonalis*

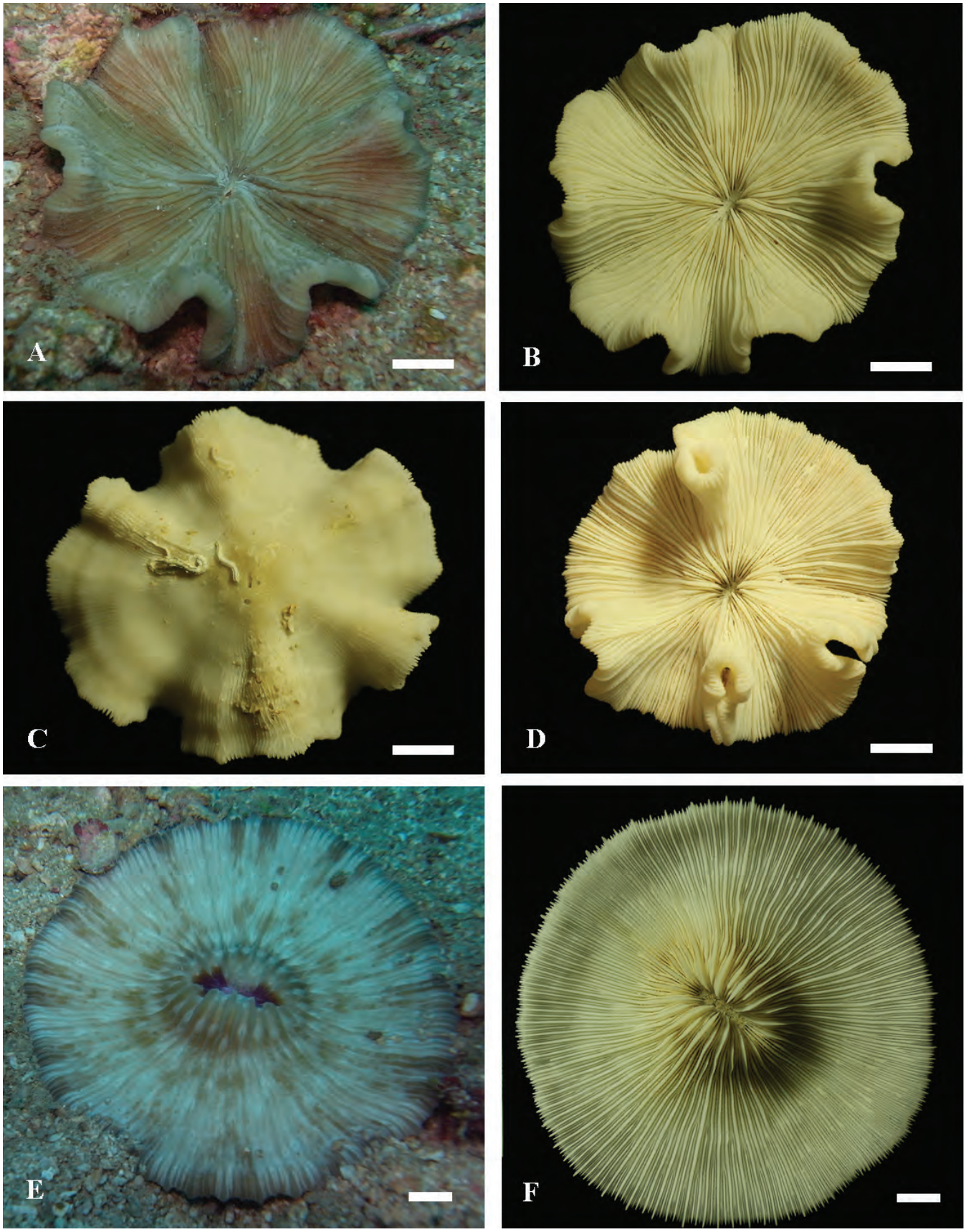

Fig. 3. A–D, *Cycloseris hexagonalis* [RMNH Coel.42102]; A, RMNH Coel.42102b photographed in situ, oral view; B, bleached skeleton, same specimen, oral view; C, underside of the same specimen, biofouled with serpulid polychaetes. D, RMNH Coel. 42102a. Corallum undulations are extreme and for two of them (upper and lower in the image) the undersurfaces of the corallum folds are fused. E, F, *Lithophyllon spinifer* [RMNH Coel.42103]. E, photographed in situ, oral view; F, bleached, oral view. Scale bars = 1cm.

and *Lithophyllon spinifer*, discovered in 2014 on a relatively deep (32 m), previously unvisited, reef top and reported here, brings the known richness of fungiids on the Brunei continental shelf to 37 (Table 1). This total is now actually higher than the confirmed number (n=35) reported for reefs at Kota Kinabalu (Waheed & Hoeksema, 2014), a location approximately 140 km northeast of Brunei (Fig. 1) and closer to the Sulu Sea/Palawan Coral Triangle (CT) ecoregion. However, for the Kota Kinabalu study, as for the earlier Brunei study (Hoeksema & Lane, 2014), the same two additional *Cycloseris* species (Benzoni et al., 2012) were not recognised as fungiids and not included at that time.

Both of the newly recorded Brunei taxa reported here are known from a few localities in the central part of the Indo-West Pacific (Hoeksema, 1989). *Cycloseris hexagonalis*, originally known in the South China Sea only at Tizard Bank (northern Spratly) and W. and S.W. Luzon (Hoeksema, 1989), is now known to extend to Brunei off N.W. Borneo (Table 1). *C. hexagonalis* corals may occur in aggregations on sandy substrates, as at the present Brunei locality, and as encountered also in Semporna, NE Borneo (Hoeksema, unpublished observation). The distribution of *Lithophyllon spinifer*, originally known in the South China Sea only for Macclesfield Bank, north of the Spratly islands (Hoeksema, 1989), is currently known to extend to Kota Kinabalu (Hoeksema & Waheed, 2012; Waheed & Hoeksema, 2014), W. Palawan (Huang et al., 2015) and now Brunei (Table 1). *L. spinifer* is most common on sandy bottoms of deep reef bases (Hoeksema, 2012a) but it is also known from soft substrates in sheltered bays (Hoeksema, 2008; Waheed & Hoeksema, 2013; Gittenberger et al., 2015)

Adjacent to the western CT boundary that extends northwards from the northern tip of Sabah (Green & Mous, 2008) (see Fig. 1), the inventory of Fungiidae for the oceanic Spratly islands' extensive and diverse reef forms might be expected to be high but this is not the case. The counts for Layang–Layang (Pilcher et al., 1999; Waheed et al., 2015a), an isolated Spratly atoll off western Sabah (Fig. 1), and for the Spratly archipelago as a whole (partly shown in Fig.1) (Huang et al., 2015) are relatively depauperate, with only 32 fungiid species each. The reduced richness encountered at Layang–Layang is likely due to limited habitat (reef area ca. 4 km^2; steep or near-vertical outer walls) and a recent outbreak of the corallivorous sea star, *Acanthaster planci* (Waheed et al., 2015a), whereas for the entire Spratly area – a 30,000 km^2 archipelagic ecoregion, reef area 1150 km^2 (Spalding et al., 2001) – the low tally probably relates to the relative remoteness and inaccessibility of most of this internationally contested region and, in consequence, the limited number of biodiversity studies there by reef scientists. The prospects for comprehensively filling this data gap for Fungiidae, and reef corals generally, in this oceanic ecoregion do not look promising as, during the last 10–15 years, coral cover at Spratly is reported to have declined overall from more than 60% to around 20% due to extensive reclamation and other development activities (Hughes et al., 2013).

The Kudat/West Palawan area in the western part of the Palawan/North Borneo CT ecoregion (Green & Mous, 2008) bordering the western CT boundary (Fig. 1) is, at 39 mushroom coral species (Table 1) (Huang et al., 2015; Waheed et al., 2015b), richer in fungiids (by 1–6 species) than any of the neighbouring or nearby areas/ecoregions in the South China Sea. Nevertheless the discovery of a high richness of mushroom corals on Brunei's shelf reefs (37 species), concurs with the earlier delineation of a mushroom coral triangle that included the non-Sunda Shelf, northeast area of the South China Sea (Hoeksema, 2013) and adds to the argument (based on all reef-forming Scleractinia) for extension of the western CT boundary further into the South China Sea to include not only the West Palawan reefs inshore of the Palawan Passage (the deep Palawan Trough) (Green & Mous, 2008) but also the reefs off the northwest coast of Borneo, including Brunei Darussalam. The CT zone is in fact recognised as being only weakly delineated from surrounding ecoregions with regard to reef corals, (Veron et al., 2009; Veron et al., 2015) and a recent global assessment of the distribution of zooxanthellate Scleractina (Veron et al., 2015), indicates that the islands and reefs of the Sunda Shelf (southern South China Sea) are now considered to qualify for inclusion in the CT zone. Although the analysis of Veron et al. (2015) includes both confirmed and strongly predicted taxa in their distribution maps, their findings and the findings in this paper do suggest that shelf regions in the South China Sea have attained a high diversity of fungiids, and zooxanthellate scleractinians as a whole, since the onset of the Holocene marine transgression and submergence of the shelf following the last glacial maximum (Voris, 2000).

Some recent inventories on mushroom coral faunas indicate that species numbers east of the CT have likewise been underestimated. For example, fungiid richness values for Vanuatu (n=35; Hoeksema, 2012c) and eastern Australia (n=37; Hoeksema, 2015) are higher compared to earlier studies. Research in other areas, such as New Caledonia and southern Japan, give similar results (Hoeksema, in prep). Because of the global importance of the CT for nature conservation (Walton et al., 2014; Weeks et al., 2014; White et al., 2014) and the fact that delineation of CT limits is a work in progress, it is relevant to verify marine species diversity of surrounding areas, not only to fine-tune CT limits, but to highlight comparably rich surrounding areas that might otherwise receive less attention than they deserve.

The two new mushroom coral records at Brunei were obtained during surveys on submerged reefs at mesophotic depths. Both species predominantly occur on sandy substrates of reef bases (Hoeksema & Moka, 1989; Hoeksema, 2012a). *Lithophyllon spinifer* usually show a preference for greater depths (12 to 42 m) but it is not restricted to mesophotic reef zones (Claereboudt & Hoeksema, 1987; Claereboudt, 1988; Hoeksema, 1993a, 2008, 2012a; Waheed & Hoeksema, 2013, 2014; Gittenberger et al., 2015). *Cycloseris hexagonalis* is a rare species and little is known about its depth distribution except that the present authors have encountered this species

on sandy, lower reef slopes in Espiritu Santo (Vanutau), Semporna (Northeast Sabah and Lembeh Strait (North Sulawesi) (Hoeksema & Lane, unpublished observations). All *C. hexagonalis* at Brunei and the aforementioned localities were encountered complete and unfragmented, while at one Indonesian location (Banda) the same species has also been reported to occur as wedge-shaped, self-fragmenting individuals (Hoeksema, 1989). Several other *Cycloseris* species, both at Brunei and Sabah, have been observed in both conditions, complete or fragmented (Hoeksema & Waheed, 2011, 2012b; Hoeksema & Lane, 2014).

The present results suggest that deep diving (> 30 m) in other localities may likewise result in new local species records. Recently, a large assemblage of a new species for Japan (*Pachyseris foliosa*) was found at mesophotic depths off Okinawa (Ohara et al., 2013). Also in Okinawa, a presumed locally extinct coral species (*Seriatopora hystrix*) was rediscovered at > 35 m depth (Sinniger et al., 2013). In the Great Barrier Reef, submerged reefs are also recognised as an important underexplored coral habitat (Harris et al., 2013). Recent surveys of the deep staghorn coral fauna of the GBR revealed new records of three *Acropora* species for Australia (Muir et al., 2015). Additional studies on the mushroom coral fauna of the GBR at greater depths will probably result in new species records as well (Hoeksema, 2015). In the Caribbean, mesophotic reef zones also have specific coral communities with species that are not found in shallower depths (Bongaerts et al., 2013; Hoeksema et al., 2016). Species new to science are also being discovered at greater depths, such as *Euphyllia baliensis* from 27–37 m at Bali (Turak et al., 2012). Based on molecular analyses, an unknown mesophotic *Leptoseris* species was discovered at Hawaii (Luck et al., 2013). Recent marine surveys at New Caledonia at ca. 60 m depth have revealed undescribed mushroom coral species (Hoeksema & Benzoni, in prep.). All these new findings suggest that species richness records of fungiids and other scleractinians at localities within and outside the Coral Triangle may depend on the availability of mesophotic reef zones and their exploration. This may have consequences for the delineation of the Coral Triangle and the position of Brunei herein, because of the high abundance of submerged reefs off Northwest Borneo (DeVantier & Turak, 2009; Hoeksema & Lane, 2014) and the presence of atolls surrounded by deep water in the SCS (Zhao et al., 2013, 2016; Waheed et al., 2015a; Hsiao et al., 2016; this study). Such reefs are also the habitat of the recently described *Leptoseris kalayaanensis*, which, although not deep, has so far only been reported from reef walls and overhangs in the northern SCS (Licuanan & Aliño PM, 2009; Hoeksema et al., 2010; Waheed et al., 2015). Regardless of the position of the CT boundary, it is clear that knowledge of the reef coral fauna of the CT and of the northern SCS, particularly its atolls and seamounts, is far from complete and that, due to significant threats (e.g., Madin, 2015; Mora et al., 2016; Zhao et al., 2016), urgent protection measures are needed, both for known coral assemblages (Huang et al., 2016) and yet to be discovered coral taxa.

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