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The mushroom coral fauna (Scleractinia: Fungiidae) of Brunei Darussalam (South China Sea) and its relation to the Coral Triangle

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Abstract. Brunei Darussalam is situated on the northwest coast of Borneo, just outside the westernmost boundary of the area presently recognised as the centre of maximum marine biodiversity, the so-called Coral Triangle. This diversity is particularly quantified with regard to numbers of reef coral species. Most coral reefs of Brunei are offshore, submerged patch reefs, which makes them hard to discern from the water surface. Few coral studies have been carried out here, although recently an extensive reef coral inventory has been published for Brunei. The present study builds on this inventory by presenting a focus on the mushroom coral fauna of Brunei, based on a survey of the family Fungiidae at 17 sites varying in distance offshore. The purpose of this study is to compare the mushroom coral fauna of Brunei with other faunas in the region, which have been surveyed in a similar manner. A total of 33 species has been recorded, which is similar to various locations in the Coral Triangle and other areas around northern Borneo.

Key words. Reef corals, species richness, submerged reefs, Borneo

INTRODUCTION

Brunei Darussalam has numerous submerged patch reefs, which together are less than 100 km^2 in extent and situated on the continental shelf in the South China Sea at the northwest coast of Borneo (DeVantier & Turak, 2009; Lane, 2011). Despite their proximity to the Coral Triangle (Hoeksema, 2007; Veron et al., 2009), little was known about these reefs until a few years ago, except for one study that was carried out several decades earlier (Chua et al., 1987). This lack of information in the past was not extraordinary when compared to many other reef areas in the South China Sea (Huang et al., 2014). However, reef surveys have been carried out lately to assess the reef environments and reef coral diversity of Brunei (DeVantier & Turak, 2009; Turak & DeVantier, 2011), and also to monitor threats to its coral fauna, such as coral bleaching and coral predator outbreaks (Lane, 2011, 2012).

In order to compare Brunei's reef coral assemblages with other coral faunas in Southeast Asia, in particular northern Borneo and the Coral Triangle, the mushroom coral family Fungiidae was selected as a proxy. Fungiid scleractinians have been included in previous studies for Brunei waters (Turak & DeVantier, 2011; Lane & Lim, 2013) but they never been surveyed comprehensively at this location. This family of over 50 species (Hoeksema, 1989, 2014; Gittenberger et al., 2011; Benzoni et al., 2012) has also been targeted in contemporaneous reef coral studies in nearby Sabah, eastern Malaysia (Waheed & Hoeksema, 2013, 2014; Waheed et al., subm), and in areas like Singapore (Hoeksema, 2009; Hoeksema & Koh, 2009) and Berau, East Kalimantan (Hoeksema et al., 2004).

This comparison will show how closely Brunei may be related to other areas in Southeast Asia and the Coral Triangle with regard to its mushroom coral fauna, which is of interest because the Coral Triangle receives much attention with regard to coral reef management (Clifton, 2009; Mills et al., 2010; Carpenter et al., 2011; White et al., 2014). The species richness of Brunei is also of biogeographical importance because this country is situated near the westernmost boundary of the Coral Triangle, which has shifted over recent years (Green & Mous, 2004, 2008; Hoeksema, 2007; Veron et al., 2009, 2011).

MATERIAL AND METHODS

Data sampling. Presence/absence of mushroom coral species (Scleractinia: Fungiidae) was recorded on water proof paper during SCUBA diving at 17 localities in April 2011 (Fig. 1, Table 1). The roving diving technique was employed from a maximum of approximately 30 m depth upward, which gives better results regarding species richness than other survey methods (Schmitt et al., 2002; Hoeksema & Koh, 2009). Most reefs were submerged, some with their shallowest point at 12 m depth. Species identifications were carried out according to Hoeksema (1989) with an updated classification by Gittenberger et al. (2011) and Benzoni et al. (2012). Photographs were taken as reference for identification. A selection of pictures was made and is presented in plates

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Table 1. Localities visited during mushroom coral field survey off Brunei in 2011.

Site no.	Date	Location	Coordinates
1	19 April	Abana Rock, southwest	05°06'24"N 115°04'10"E
2	19 April	Pelong Rocks, southwest	05°04'44"N 115°03'05"E
3	19 April	Pelong Rocks, south-southwest	05°04'41"N 115°03'06"E
4	20 April	Colombo Reef, Champion Shoal	05°12'28"N 114°43'35"E
5	20 April	Otterspool Rock	05°04'12"N 114°39'03"E
6	21 April	Littledale Shoal, south	05°06'10"N 114°45'51"E
7	21 April	Littledale Shoal, north	05°06'27"N 114°45'36"E
8	23 April	Abana rock, north	05°06'28"N 115°04'13"E
9	23 April	Two Fathom	05°05'45"N 114°58'12"E
10	25 April	Nankivell Rock	05°05'24"N 114°32'44"E
11	25 April	Hornet Reef (Brunei Patches)	05°01'13"N 114°43'54"E
12	27 April	Littledale Shoal, east	05°06'06"N 114°45'59"E
13	27 April	Littledale Shoal, north	05°06'27"N 114°45'36"E
14	28 April	Chearnley Shoal	04°52'05"N 114°19'10"E
15	28 April	Porter Patch	04°53'32"N 114°24'08"E
16	29 April	Pelong Rocks, northeast	05°04'56"N 115°03'13"E
17	29 April	Pelong Rocks, north	05°04'59"N 115°03'12"E

(Figs. 3–6) for species comparison. Four other sites were visited but excluded from the analysis because they were either shipwrecks or a 13 m deep sandy shoal with only a thin cover of solitary zoantharians of the genus *Sphenopus* (Reimer et al., 2012).

Analysis. In order to verify whether sampling was sufficient for obtaining a representative indication of the mushroom coral fauna for the whole area, species richness estimators were calculated using EstimateS 8.20 (Colwell, 2009). These estimators are illustrated as species accumulation curves in which the sample order has been randomised and the values have been averaged. The calculated mean values and standard deviations of the species richness at the sample numbers show an averaged rate at which additional species were found in the course of consecutive dives with an asymptote that indicates the expected total species richness (Magurran, 2004). The species richness estimators used for incidence data (presence/absence) are Chao 2 and ICE (Colwell, 2009). Presence/absence data for two *Cycloseris* species that previously belonged to the Siderastreidae (Benzoni et al., 2007, 2012), were recorded for Brunei but not for each separate site. These taxa were therefore excluded from the species richness analysis. Regarding the total of 17 survey sites, species were considered rare (when found at 1–3 sites), uncommon (at 4–6 sites), moderately common (at 7–11 sites), common (at 12–14 sites), and very common (at 15–17 sites). The present results are compared with those of previous studies dealing with the mushroom coral fauna of Brunei (Chou et al., 1987; Turak & DeVantier, 2011) and with those in other areas where the same method was used. Some specimens sampled by Turak & DeVantier (2011) have been deposited at the Fisheries Department Marine Biodiversity Centre, Brunei Darussalam. This collection was examined for partial verification of earlier species records that were not obtained by the present survey.

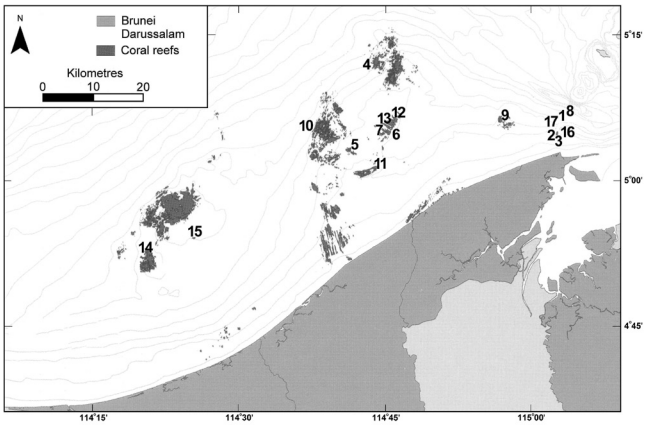

Fig. 1. Map of the coastal area of Brunei indicating survey sites listed in Table 1. Adapted from Brunei Shell Petroleum Company Snd. Bhd. and Environmental Resources Management Hong Kong.

RESULTS

Thirty-two mushroom coral species were recorded at the 17 sites sampled in the field (Table 2). An additional one, *Zoopilus echinatus*, was found during the earlier survey by Turak & DeVantier (2011), which could be confirmed during the present study, giving a total of 33 Fungiidae species for Brunei. The number of species per site varied from 11 to 26 species (Table 2). The species accumulation curves (Fig. 2) showed that the expected number of 33 species (ICE, Chao 2) for Fungiidae is close to the observed number of 32 species, and that with additional sampling, one more species is to be expected. This additional one is represented by *Zoopilus echinatus* (Table 2; Fig. 7). The 33 species are listed below, while earlier records that could not be confirmed are also mentioned.

Table 2. Records (presence/absence) of mushroom coral species encountered off Brunei at 17 localities in 2011 (nomenclature after Gittenberger et al., 2011). *Cycloseris explanulata* and *C. wellsi*, although present at Brunei (Fig. 4A, B), were not included in the records, because they were not yet considered Fungiidae at the time of the survey (Benzoni et al., 2012).

Site number Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Records
Ctenactis albitentaculata	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	0	13
Ctenactis crassa	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	17
Ctenactis echinata	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	17
Cycloseris costulata	1	1	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1	14
Cycloseris cyclolites	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	3
Cycloseris fragilis	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0	1	1	7
Cycloseris mokai	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	0	6
Cycloseris sinensis	1	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0	6
Cycloseris somervillei	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	3
Cycloseris tenuis	0	0	0	1	1	1	1	0	1	0	1	1	1	0	1	0	0	9
Cycloseris vaughani	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Danafungia horrida	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	17
Danafungia scruposa	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	17
Fungia fungites	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	17
Halomitra pileus	1	1	1	1	0	0	1	1	0	1	0	1	1	1	1	0	0	11
Heliofungia actiniformis	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	13
Herpolitha limax	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	16
Lithophyllon concinna	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	17
Lithophyllon repanda	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	17
Lithophyllon scabra	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	3
Lithophyllon undulatum	1	1	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1	14
Lobactis scutaria	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	14
Pleuractis granulosa	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	16
Pleuractis gravis	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	15
Pleuractis moluccensis	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	14
Pleuractis paumotensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	17
Pleuractis taiwanensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Podabacia crustacea	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	14
Podabacia motuporensis	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	5
Polyphyllia talpina	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	16
Sandalolitha dentata	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1	14
Sandalolitha robusta	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	15
Zoopilus echinatus[1]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1[1]
Total species number	**24**	**21**	**25**	**16**	**11**	**20**	**23**	**24**	**24**	**24**	**26**	**23**	**23**	**23**	**25**	**24**	**23**	**33**

[1]Record of *Zoopilus echinatus* is based on a museum specimen (Fig. 7)

SPECIES ACCOUNT

Ctenactis albitentaculata Hoeksema, 1989
(Fig. 6A)

Ctenactis albitentaculata – Turak & DeVantier, 2011: 140.

This free-living species is common at Brunei: recorded at 13 out of 17 sites (Table 2). Occasionally, clusters of 3–6 specimens were observed, all with tentacles extended.

Ctenactis crassa (Dana, 1846)
(Fig. 6B)

Ctenactis crassa – Turak & DeVantier, 2011: 140.

This free-living species is very common at Brunei: recorded at all 17 sites (Table 2).

Ctenactis echinata (Pallas, 1766)
(Fig. 6C)

Fungia echinata – Chou et al., 1987: 47.
Ctenactis echinata – Turak & DeVantier, 2011: 141.

This free-living species is very common at Brunei: recorded at all 17 sites (Table 2).

Cycloseris costulata (Ortmann, 1889)
(Fig. 3I)

Cycloseris costulata – Turak & DeVantier, 2011: 126.
Cycloseris erosa – Turak & DeVantier, 2011: 127.
Cycloseris vaughani – Turak & DeVantier, 2011: 130.

This free-living species is common at Brunei: recorded at 14 out of 17 sites (Table 2). It was not observed in fragmenting shape. Although the illustrated specimen has a violet margin (Fig. 3I), the usual colour of this species is even brown (Gittenberger & Hoeksema, 2006). It has also been recorded as *C. erosa* (Döderlein, 1901) (see Turak & DeVantier, 2011), which actually is a synonym for *C. tenuis* (see Hoeksema, 1989). The colouration of a specimen illustrated and identified as *C. vaughani* by Turak & DeVantier (2011) is typical for *C. costulata* (compare Hoeksema, 1989; Hoeksema & Van Ofwegen, 2004; Gittenberger & Hoeksema, 2006). The costae of another specimen illustrated and identified as *C. vaughani* by Turak & DeVantier (2011) resembles those of *C. boschmai* Hoeksema, 2014, which has not been found during the present study, although it has been recorded at the reefs of Kota Kinabalu, located 150 km away in a NE direction (Waheed & Hoeksema, 2014). In comparison to *C. boschmai* and *C. vaughani*, C. *costulata* has less pronounced lower order costae.

***Cycloseris cyclolites* (Lamarck, 1816)**
(Fig. 3D–F)

Cycloseris cyclolites – Turak & DeVantier, 2011: 126.

This free-living species is rare at Brunei: recorded at 3 out of 17 sites (Table 2). It was observed in complete (Fig. 3D) and in fragmenting shape (Fig. 3E, F), the so-called *Diaseris* form (see Hoeksema, 1989: Figs. 83, 84).

***Cycloseris explanulata* (Van der Horst, 1922)**
(Fig. 4A)

Psammocora explanulata – Turak & DeVantier, 2011: 105. This encrusting species is uncommon at Brunei (Turak & DeVantier, 2011). At the time of this survey it was considered to belong to the Siderastreidae, but based on morphological and molecular evidence (Benzoni et al., 2007), it was moved to the Fungiidae (Benzoni et al., 2012). Although this species was noted in the field, sites for this taxon were not recorded in the presence/absence survey.

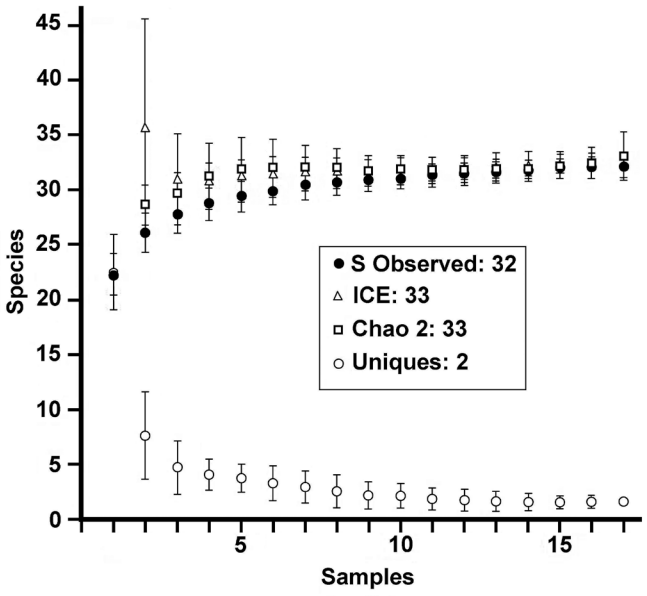

Fig. 2. Species richness estimators (Colwell, 2009) for Fungiidae recorded at 17 sites off Brunei. The curves indicate that the occurrence of one additional species is possible when the maximum number of observed species (S Obs = 32) is compared to the maximum expected numbers (ICE, Chao 2 = 33). Only two species (Uniques) are each represented by a single individual.

***Cycloseris fragilis* (Alcock, 1893)**
(Fig. 3A, B)

Cycloseris patelliformis – Turak & DeVantier, 2011: 128.
Diaseris distorta (partim) – Turak & DeVantier, 2011: 130.
Not *Diaseris fragilis* – Turak & DeVantier, 2011: 131 (= *C. sinensis*).

This free-living species is moderately common at Brunei: recorded at 7 out of 17 sites (Table 2). It was observed in complete and in fragmenting shape. It has also been recorded as *C. patelliformis* (Boschma, 1923) (see Turak & DeVantier, 2011), which actually is a synonym of *C. fragilis* (see Hoeksema, 1989). Live specimens photographed in Indonesia and identified as *D. distorta* by Turak & DeVantier (2011) show thin septa, which are typical for *C. fragilis* and not for *C. distorta* (compare Hoeksema, 1989). *Diaseris* is considered a synonym of *Cycloseris* (Hoeksema, 1989; Hoeksema & Waheed, 2011, 2012).

***Cycloseris mokai* (Hoeksema, 1989)**
(Fig. 4C)

Lithophyllon mokai – Turak & DeVantier, 2011: 145.

This encrusting species is uncommon at Brunei: recorded at 6 out of 17 sites (Table 2).

***Cycloseris sinensis* Milne Edwards & Haime, 1851**
(Fig. 3C)

Cycloseris sinensis – Turak & DeVantier, 2011: 145.
Diaseris distorta (partim) – Turak & DeVantier, 2011: 130.

This free-living species is common at Brunei: recorded at 6 out of 17 sites (Table 2). It was observed in complete and in fragmenting shape, the so-called *Diaseris* form (see Hoeksema, 1989: Figs. 48–54). A fragmented specimen identified as *Diaseris distorta* and shown in a black and white photograph by Turak & DeVantier (2011) is actually a specimen of *C. sinensis*.

***Cycloseris somervillei* (Gardiner, 1909)**
(Fig. 3G, H)

Not *Cycloseris somervillei* – Turak & DeVantier, 2011: 131 (= *Lobactis scutaria*).

This free-living species is rare at Brunei: recorded at 3 out of 17 sites (Table 2). The prominent lower order costae (Fig. 3H) are characteristic for this oval and relatively large *Cycloseris* species.

Table 3. Mushroom coral records from Indo-Pacific areas as comparison to the present results from Brunei (33 species), with a distinction between records from inside and outside the Coral Triangle.

Area	Number of Species	Reference
Coral Triangle		
Kudat, Sabah	39	Waheed et al., subm
Semporna	44	Waheed & Hoeksema, 2013
East Kalimantan	40	Hoeksema et al., 2004
Cebu, Philippines	37	Hoeksema, 2007
North Sulawesi	33	Hoeksema, 2007
South Sulawesi	38	Hoeksema, 2007, 2012b, c
Wakatobi, SE Sulawesi	31	Hoeksema, 2003
Togian Bay	28	Wallace et al., 2000
Bali	36	Hoeksema & Putra, 2000
Komodo	39	Hoeksema, 2007
Ambon	36	Hoeksema, 2007
West Halmahera	36	Hoeksema, 2010
Raja Ampat, West Papua	40	Hoeksema, 2008
Madang, Bismarck Sea	40	Hoeksema, 1992, 1993, 2007
Outside Coral Triangle		
Kota Kinabalu, Sabah	35	Waheed & Hoeksema, 2014
Seychelles	20	Hoeksema, 1994
Red Sea	19	Hoeksema, 1989
Arabian Gulf	1	Hoeksema, 1989; Riegl et al., 2012
Phuket, Andaman Sea	23	Hoeksema, 2007
West Sumatra	21	Hoeksema, 2007
Koh Tao, Thailand	20	Hoeksema et al., 2012
Singapore	19	Hoeksema & Koh, 2009
Jakarta, NW Java	29	Hoeksema, 2007
Central Java Sea	26	Hoeksema, 2007
Taiwan	26	Hoeksema & Dai, 1991; Hoeksema, 2007
Palau	30	Hoeksema, 2007
Vanuatu	35	Hoeksema, 2012a
Gambier Islands	6	Hoeksema & Benzoni, 2012

Cycloseris tenuis (Dana, 1846)
(Fig. 3J)

Not *Cycloseris tenuis* – Turak & DeVantier, 2011: 129 (= *Pleuractis granulosa*, *Cycloseris* spp.).

This free-living species is moderately common at Brunei: recorded at 9 out of 17 sites (Table 2). The lower order costae are large and roughly ornamented. The species has a typical greyish-brown colour with dark brown around its mouth and white lips (Gittenberger & Hoeksema, 2006). The specimens from Indonesia illustrated by Turak & DeVantier (2011) are wrongly identified.

Cycloseris vaughani (Boschma, 1923)
(Fig. 3K)

Not *Cycloseris vaughani* – Turak & DeVantier, 2011: 129 (=*Cycloseris costulata*).

This free-living species is rare at Brunei: recorded only at Colombo Reef, Champion Shoal (Table 2). The lower order costae are larger and sharper than in its congeners. The species has a patchy greyish-brown colour, usually with a radiating pattern (Fig. 2K; Hoeksema, 1989; Hoeksema & Van Ofwegen, 2004). The specimens illustrated by Turak & DeVantier (2011) are wrongly identified.

Cycloseris wellsi (Veron & Pichon, 1980)
(Fig. 4B)

Coscinarea wellsi – Turak & DeVantier, 2011: 110.

This encrusting species is rare at Brunei (Turak & DeVantier, 2011). Previously it was considered to belong to the Siderastreidae but based on morphological and molecular evidence (Benzoni et al., 2007) this species was moved to the Fungiidae (Benzoni et al., 2012). Although this species was noted in the field, sites for this taxon were not recorded in the presence/absence survey.

Danafungia horrida (Dana, 1846)
(Fig. 4I)

Fungia horrida – Turak & DeVantier, 2011: 135.
Fungia klunzingeri – Turak & DeVantier, 2011: 135.

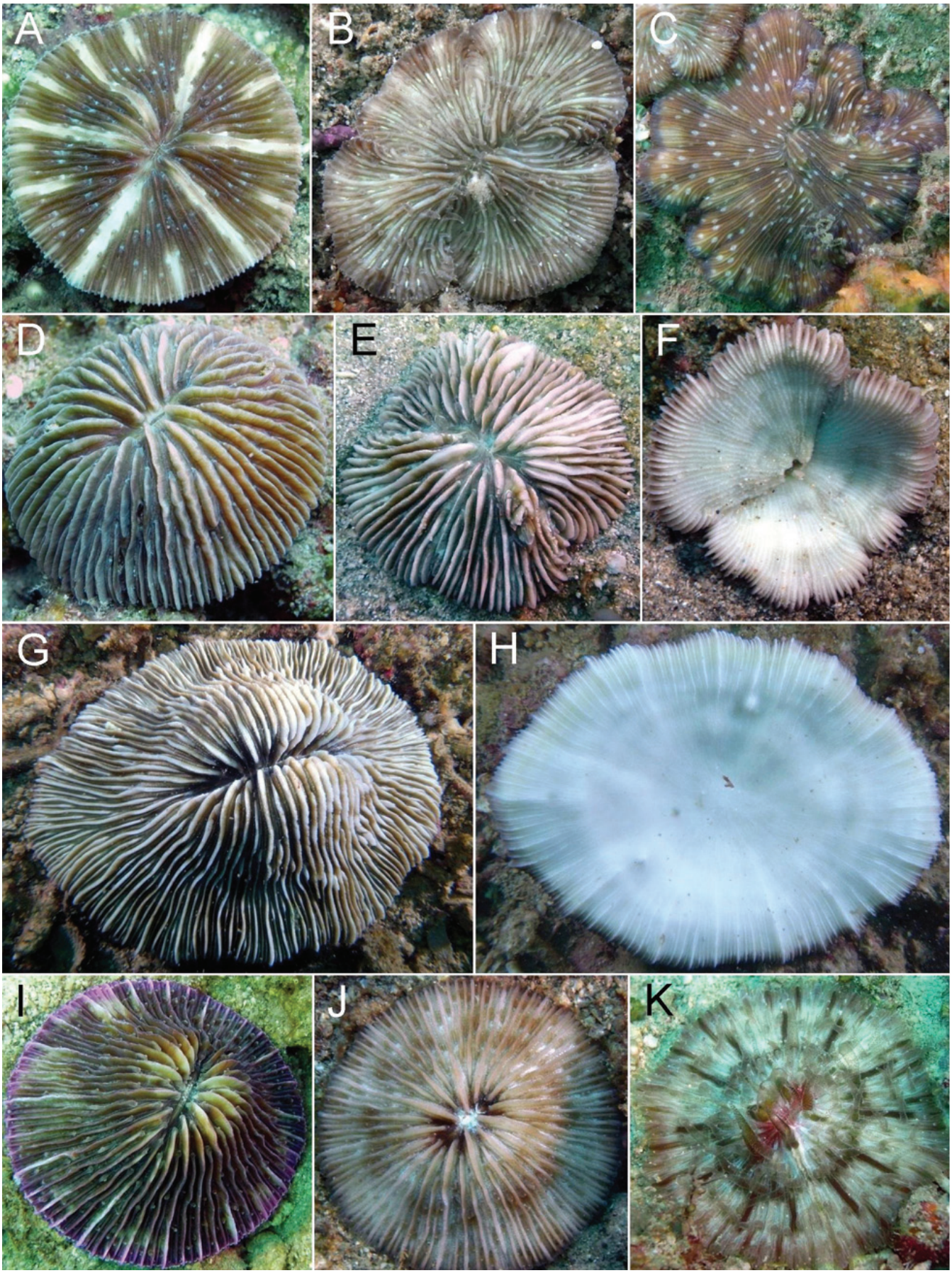

Fig. 3. A, B, *Cycloseris fragilis*, complete coral at Hornet Reef (Brunei Patches), fragmenting coral at Abana Rock, north; C, *Cycloseris sinensis*, fragmenting coral at Abana Rock, north; D–F, *Cycloseris cyclolites* at Hornet Reef (Brunei Patches), complete coral, fragmenting coral upper and lower side; G, H, *Cycloseris somervillei* at Chearnley Shoal, upper and lower side of a coral; I, *Cycloseris costulata* at Pelong Rocks, northeast; J, *Cycloseris tenuis* at Hornet Reef (Brunei Patches); K, *Cycloseris vaughani* at Colombo Reef (Champion Shoal).

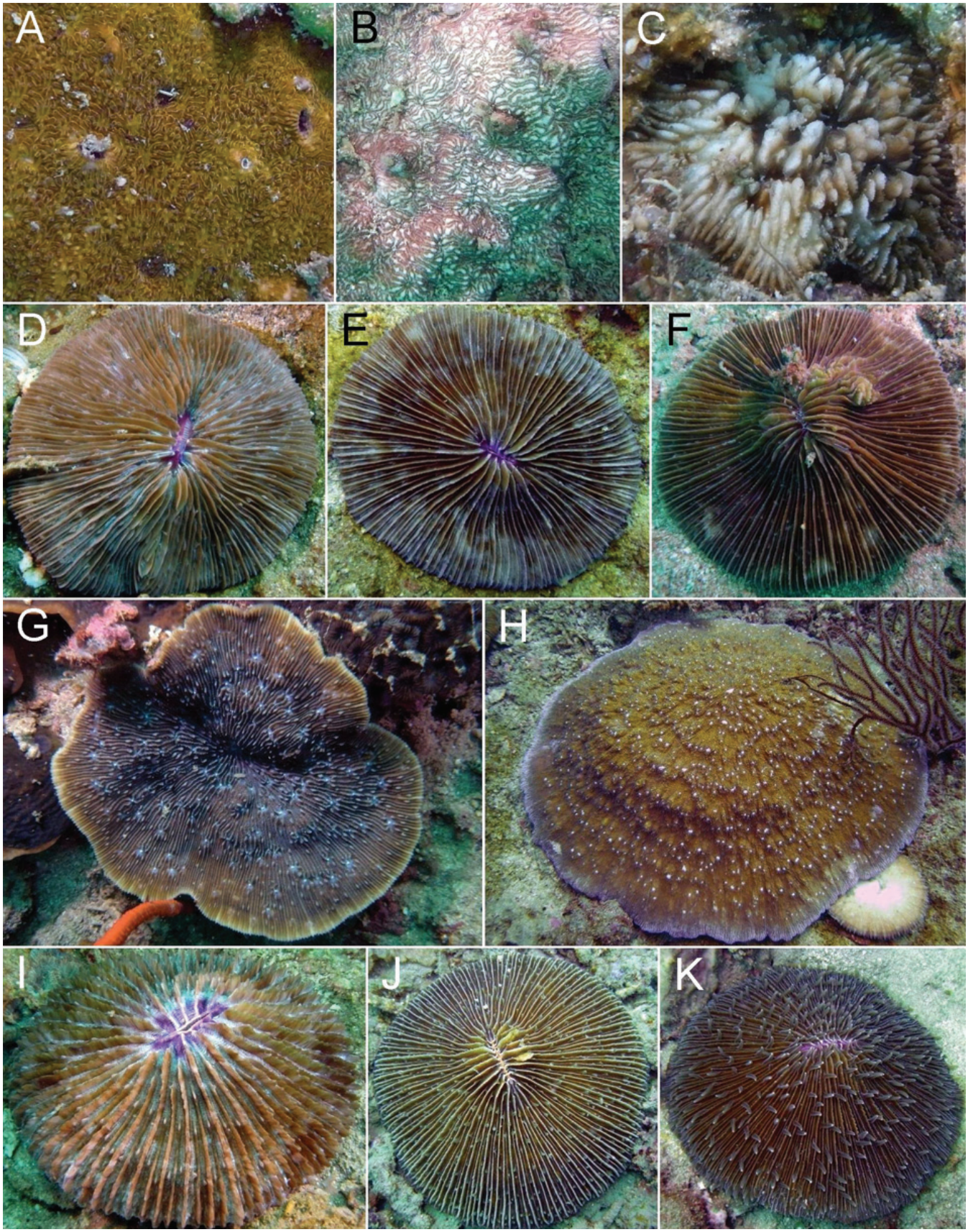

Fig. 4. A, *Cycloseris explanulata* at Porter Patch; B, *Cycloseris wellsi* at Abana Rock, north; C, *Cycloseris mokai* at Littledale Shoal, south; D, *Lithophyllon scabra* at Hornet Reef (Brunei Patches); E, *Lithophyllon concinna* at Abana Rock, south; F, *Lithophyllon repanda* at Abana Rock, north; G, *Lithophyllon undulatum* at Abana Rock, south; H, *Halomitra pileus* at Abana Rock, south; I, *Danafungia horrida* at Pelong Rocks, northeast; J, *Danafungia scruposa* at Pelong Rocks, southwest; K, *Fungia fungites* at Abana Rock, south.

This free-living species is very common at Brunei: recorded at all 17 sites (Table 2).

***Danafungia scruposa* (Klunzinger, 1879)**
(Fig. 4J)

Fungia corona – Turak & DeVantier, 2011: 132.
Fungia danai – Turak & DeVantier, 2011: 133.
Fungia scruposa – Turak & DeVantier, 2011: 138.

This free-living species is very common at Brunei: recorded at all 17 sites (Table 2).

***Fungia fungites* (Linnaeus, 1758)**
(Fig. 4K)

Fungia fungites – Chou et al., 1987: 47; Turak & DeVantier, 2011: 133.

This free-living species is very common at Brunei: recorded at all 17 sites (Table 2).

***Halomitra pileus* (Linnaeus, 1758)**
(Fig. 4H)

Halomitra pileus – Chou et al., 1987: 47; Turak & DeVantier, 2011: 144.

This free-living species is common at Brunei: recorded at 11 out of 17 sites (Table 2). High numbers of very large specimens (diameter > 50 cm) were observed at various localities.

***Heliofungia actiniformis* (Quoy & Gaimard, 1833)**
(Fig. 5A)

Heliofungia actiniformis – Chou et al., 1987: 47; Turak & DeVantier, 2011: 131.

This free-living species is common at Brunei: recorded at 13 out of 17 sites (Table 2).

***Herpolitha limax* (Esper, 1797)**
(Fig. 6D)

Herpolitha limax – Chou et al., 1987: 47; Turak & DeVantier, 2011: 141.
Herpolitha weberi – Turak & DeVantier, 2011: 142.

This free-living species is very common at Brunei: recorded at 16 out of 17 sites (Table 2). *H. weberi* is a junior synonym of *H. limax* (see Hoeksema, 1989).

***Lithophyllon concinna* (Verrill, 1864)**
(Fig. 4E)

Fungia concinna – Turak & DeVantier, 2011: 132.

This free-living species is very common at Brunei: recorded at all 17 sites (Table 2).

***Lithophyllon repanda* (Dana, 1846)**
(Fig. 4F)

Fungia repanda – Turak & DeVantier, 2011: 137.

This free-living species is very common at Brunei: recorded at all 17 sites (Table 2).

***Lithophyllon scabra* (Döderlein, 1901)**
(Fig. 4D)

Fungia scabra – Turak & DeVantier, 2011: 137.

This free-living species is rare at Brunei: recorded at 3 out of 17 sites (Table 2).

***Lithophyllon undulatum* Rehberg, 1892**
(Fig. 4G)

Lithophyllon undulatum –Turak & DeVantier, 2011: 146.

This free-living species is common at Brunei: recorded at 14 out of 17 sites (Table 2).

***Lobactis scutaria* (Lamarck, 1801)**
(Fig. 5H)

Cycloseris somervillei – Turak & DeVantier, 2011: 129.
Fungia scutaria – Turak & DeVantier, 2011: 138.

This free-living species is common at Brunei: recorded at 14 out of 17 sites (Table 2).

***Pleuractis granulosa* (Klunzinger, 1879)**
(Fig. 5C)

Fungia granulosa – Turak & DeVantier, 2011: 134.

This free-living species is very common at Brunei: recorded at 16 out of 17 sites (Table 2).

***Pleuractis gravis* (Nemenzo, 1955)**
(Fig. 5D)

Fungia gravis – Turak & DeVantier, 2011: 134.

This free-living species is very common at Brunei: recorded at 15 out of 17 sites (Table 2).

***Pleuractis moluccensis* (Van der Horst, 1919)**
(Fig. 5E)

Fungia moluccensis – Turak & DeVantier, 2011: 136.

This free-living species is common at Brunei: recorded at 14 out of 17 sites (Table 2).

***Pleuractis paumotensis* (Stutchbury, 1833)**
(Fig. 5F)

Fungia paumotensis – Turak & DeVantier, 2011: 136.

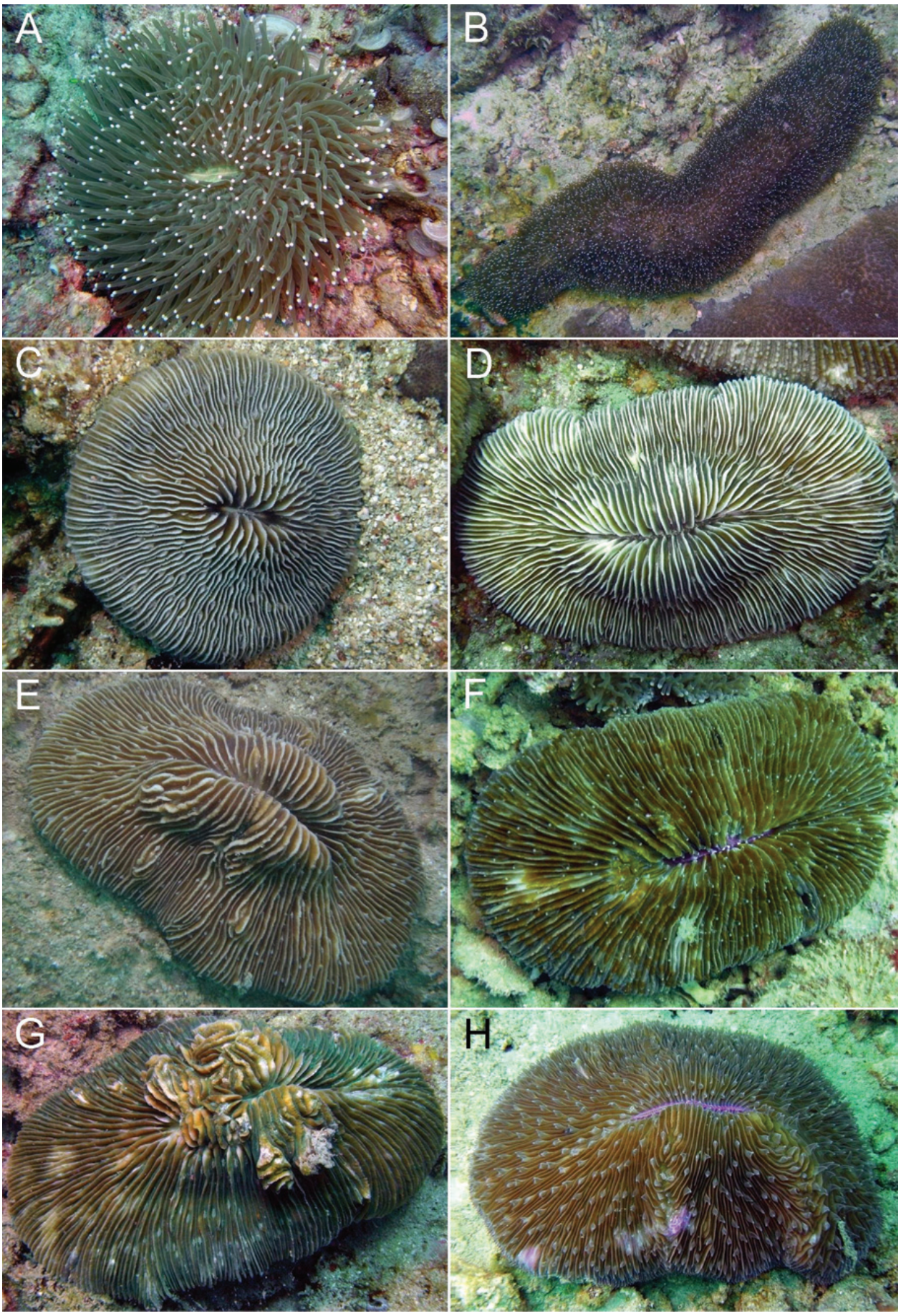

Fig. 5. A, *Heliofungia actiniformis* at Littledale Shoal, north; B, *Polyphyllia talpina* at Pelong Rocks, southwest; C, *Pleuractis granulosa* at Littledale Shoal, south; D, *Pleuractis gravis* at Littledale Shoal, south; E, *Pleuractis moluccensis* at Pelong Rocks, southwest; F, *Pleuractis paumotensis* at Abana Rock, south; G, *Pleuractis taiwanensis* at Pelong Rocks, north; H, *Lobactis scutaria* at Pelong Rocks, northeast.

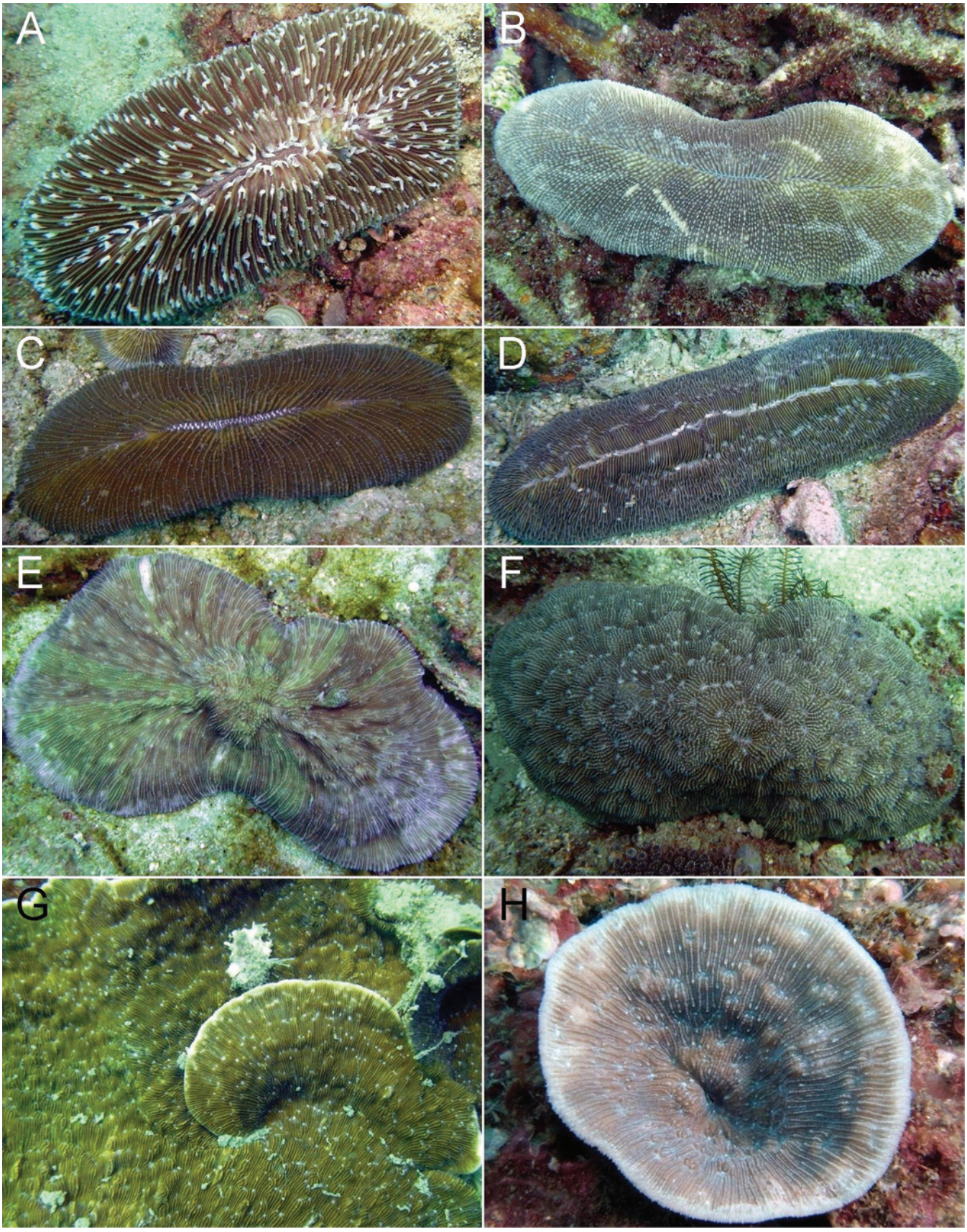

Fig. 6. A, *Ctenactis albitentaculata* at Littledale Shoal, north; B, *Ctenactis crassa* at Otterspool Rock; C, *Ctenactis echinata* at Abana Rock, south; D, *Herpolitha limax* at Littledale Shoal, south; E, *Sandalolitha dentata* at Porter Patch; F, *Sandalolitha robusta* at Littledale Shoal, south; G, *Podabacia crustacea* at Pelong Rocks, south-southwest; H, *Podabacia motuporensis* at Two Fathom Rock.

This free-living species is very common at Brunei: recorded at all 17 sites (Table 2). Several specimens were infested by acoel flatworms of the genus *Waminoa* (see Hoeksema & Farenzena, 2012)

***Pleuractis taiwanensis* Hoeksema & Dai, 1991**
(Fig. 5G)

Fungia taiwanensis – Turak & DeVantier, 2011: 139.

This free-living species is rare at Brunei: recorded only at north Pelong Rocks (Table 2).

***Podabacia crustacea* (Pallas, 1766)**
(Fig. 6G)

Podabacia crustacea – Turak & DeVantier, 2011: 146.

This attached species is common at Brunei: recorded at 14 out of 17 sites (Table 2).

***Podabacia motuporensis* Veron, 1990**
(Fig. 6H)

Podabacia motuporensis – Turak & DeVantier, 2011: 147.

This attached species is uncommon at Brunei: recorded at 5 out of 17 sites (Table 2).

***Polyphyllia talpina* (Lamarck, 1801)**
(Fig. 5B)

Polyphyllia talpina – Chou et al., 1987: 47; Turak & DeVantier, 2011: 142.

This free-living species is very common at Brunei: recorded at 16 out of 17 sites (Table 2).

***Sandalolitha dentata* Quelch, 1884**
(Fig. 6E)

Sandalolitha dentata – Turak & DeVantier, 2011: 143.

This free-living species is common at Brunei: recorded at 14 out of 17 sites (Table 2).

***Sandalolitha robusta* (Quelch, 1886)**
(Fig. 6F)

Sandalolitha robusta – Chou et al., 1987: 47; Turak & DeVantier, 2011: 143.

This free-living species is very common at Brunei: recorded at 15 out of 17 sites (Table 2).

***Zoopilus echinatus* Dana, 1846**
(Fig. 7A, B)

Zoopilus echinatus – Turak & DeVantier, 2011: 144.

This free-living species is rare at Brunei (Turak & DeVantier, 2011). It was not recorded during our survey (Table 2), but the photograph taken at Silk Rock (Turak & DeVantier, 2011) and a specimen fragment in the collection of the Brunei Fisheries Department (Fig. 7A, B) leave no doubt about the occurrence of this species at Brunei, which underlines the importance of museum specimens as reference material in biodiversity studies (Hoeksema et al., 2011).

UNCONFIRMED RECORDS

The following four species were not recorded during our survey (Table 2). Their presence at Brunei was reported by Turak & Devantier (2011), but without photographic evidence (photographs of live animals were taken outside

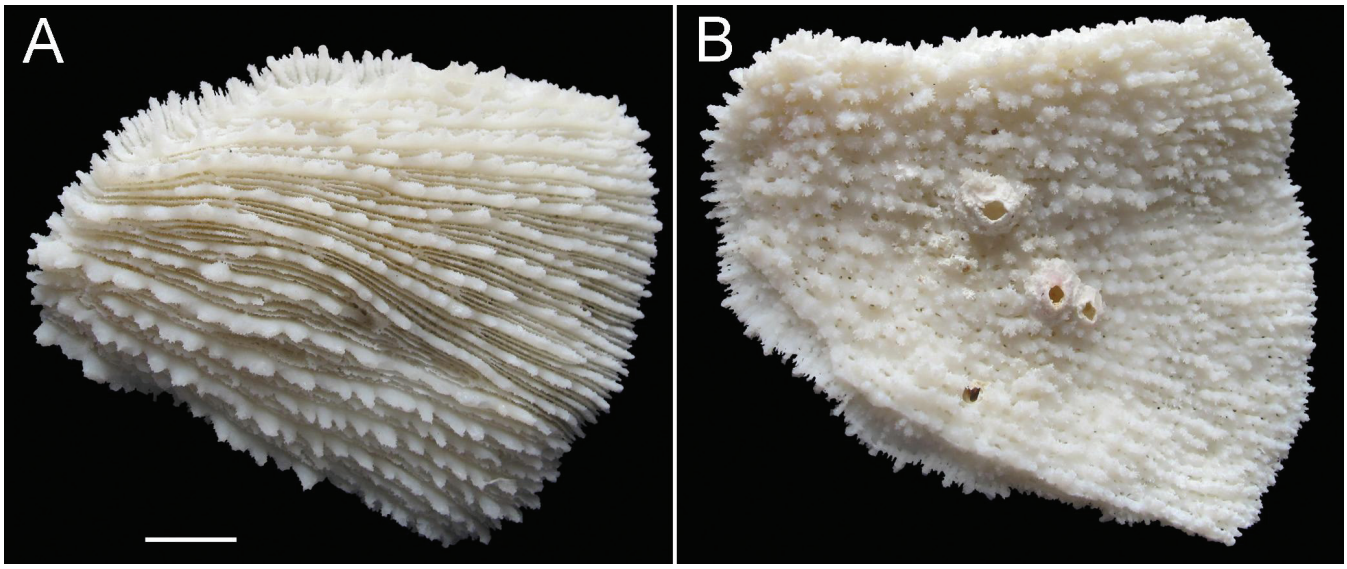

Fig. 7. *Zoopilus echinatus*. A fragment with regenerated margins from Silk Rock, 10 m depth, 21 October 2008, Coll. L. Devantier. A, upper surface; B, lower surface. Scale bar = 0.5 cm.

Brunei). Without access to collected material and photos, the occurrence of these species at Brunei cannot be confirmed in the present study.

Cycloseris distorta (Michelin, 1842)

Cycloseris distorta – Turak & DeVantier, 2011: 130.

A fragmented coral identified as *Diaseris distorta*, shown in a black and white photograph by Turak & DeVantier (2011), is actually a specimen of *C. sinensis*. Colour photographs of live specimens taken in Indonesia (Turak & DeVantier, 2011) actually represent *C. fragilis*, which can be recognised because of its very thin septa (see Hoeksema, 1989).

Cycloseris hexagonalis (Milne Edwards & Haime, 1848)

Cycloseris hexagonalis – Turak & DeVantier, 2011: 127.

One colour photograph of a live specimen published by Turak & DeVantier (2011) was taken in the Philippines; the origin of the other one is not mentioned. The identity and origin of a third coral (diameter 6 cm) showing the aboral side in a black and white photograph is unclear. This specimen shows prominent lower order costae, while *C. hexagonalis* of that size usually shows a nearly smooth aboral side with costae that are almost invariable in size (Hoeksema, 1989). Because Turak & DeVantier (2011) state that *C. hexagonalis* may resemble *C. tenuis*, which has very coarsely ornamented lower order costae, the occurrence of *C. hexagonalis* at Brunei remains uncertain.

Lithophyllon ranjithi Ditlev, 2003

Lithophyllon lobata – Turak & DeVantier, 2011: 145.

One colour photograph of a live specimen published by Turak & DeVantier (2011) was taken in Indonesia; the origin of other photographs is unclear. They present this species as *L. lobata*, a junior synonym of *L. undulatum* (see Hoeksema, 1989). The syntypes of *L. lobata* are large, thin, twirled foliaceous corals with thin septa and mouths scattered over the whole upper surface, whereas specimens of *L. ranjithi* are thick laminar corals in one plane with folded margins, thick septa, and mouths concentrated at the centre of the upper surface. *L. ranjithi* is known from East Sabah and East Kalimantan (Ditlev, 2003; Hoeksema et al., 2004; Waheed & Hoeksema, 2013), and it has also been observed in the Kudat region at north Sabah and at Layang-Layang atoll in the South China Sea (Waheed & Hoeksema, in prep.). It was not found at the reefs of Kota Kinabalu (Waheed & Hoeksema, 2014), which are only about 150 km away from Brunei in a NE direction.

Lithophyllon spinifer (Claereboudt & Hoeksema, 1987)

Fungia spinifer –Turak & DeVantier, 2011: 139.

Colour photographs of a live specimen published by Turak & DeVantier (2011) were taken in Indonesia. An additional black and white photograph (locality not indicated) only shows a quarter portion of the upper surface of a thin, coral, which could be a juvenile specimen of *L. spinifer* or belong to *Cycloseris fragilis*. Specimens of *L. spinifer* are shaped like a saucer, usually with a thick, bulging central area, a corallum margin turning upward, and strongly developed lower order costae (Claereboudt & Hoeksema, 1987; Hoeksema, 1989, 1993).

DISCUSSION

The present result of 33 confirmed mushroom coral species records (*Cycloseris explanulata* and *C. wellsi* excluded) is less than the 44 counted by Turak & DeVantier (2011). This difference is partly based on the inclusion of various synonyms by the latter. Moreover, several of the earlier species records could not be confirmed because they were not found during the present survey and because hardly any voucher specimens or photographic evidence from the earlier study were available for these species.

The number of 33 Fungiidae species found at Brunei is close to the total of 35 recorded at Kota Kinabalu, which is in close proximity to Brunei, but distinctly less than the 39 found in the Kudat area at the northernmost tip of Borneo, the 44 of Semporna at the eastern coast of Sabah, and the 40 species recorded at East Kalimantan (Table 3). Southeast Asian areas outside the Coral Triangle have records that range from 19 at Singapore to, 20 at Koh Tao in the Gulf of Thailand, 21 at West Sumatra, 23 at Phuket, Andaman Sea, 26 in the central Java Sea, 29 at NW Java, and 26 at Taiwan (Table 3). Vanuatu in the West Pacific has 35 species of recorded mushroom coral species, Palau 30, and the remote Gambier Islands only six. Furthermore, 20 species of Fungiidae were recorded in the Seychelles, western Indian Ocean, and 19 in the Red Sea (Table 3). Overall, there is a distinct decrease in mushroom coral species numbers from the central Indo-Pacific towards the periphery of the Indo-Pacific (Hoeksema, 1989).

Indo-West Pacific areas inside the Coral Triangle (other than those already mentioned) have recorded numbers like 40 at West Papua, 40 in northern Papua New Guinea, 39 at Komodo, 36 at Ambon, 33 at North Sulawesi, 37 at central Philippines, 38 at South Sulawesi, 36 at West Halmahera, and 36 at Bali (Table 3). On the other hand, some areas inside the Coral Triangle may also show low species numbers, which may be related to low habitat diversity: for example, 31 species in the Wakatobi Islands off SE Sulawesi and 28 species in the Togian Bay of central Sulawesi. Other areas in eastern Indonesia have species numbers ranging from 26 to 33, but these were only visited briefly (Hoeksema & Moka, 1989). Regardless, all these numbers indicate that the total number of 33 mushroom coral species found at Brunei is comparable to the species richness of various areas in the Coral Triangle.

Although there is variation in recorded species diversity among areas within the Coral Triangle, there are no clear species diversity gradients (Hoeksema, 2007, 2013; Veron et

al. 2009), such as the latitudinal gradient in the adjacent South China Sea (Huang et al., 2014). This CT variation shown by mushroom corals in particular and all reef corals together can be attributed to differences in habitat diversity and sampling effort (Best et al., 1989; Hoeksema & Moka, 1989; Wallace et al., 2000; Bellwood & Hughes, 2001; Hoeksema, 2007). On the other hand, there are clear diversity gradients from the Coral Triangle away towards the margins of the IWP (Hoeksema, 1989; Bellwood & Meyer, 2009a). Therefore, owing to its close proximity to the Coral Triangle, Brunei is not expected to have a much lower species richness than areas within the Coral Triangle (but see Huang et al., 2014).

The present northwestern boundary of the Coral Triangle would exclude Brunei. Its position is based on scleractinian species richness in ecoregions as defined by Veron et al. (2009, 2011). Earlier, this northwestern boundary was located more westward, situated along the continental shelf in the South China Sea and delimited by the large river outlets of Sarawak, to the southwest of Brunei (Green & Mous, 2004; Hoeksema, 2007; Spalding et al., 2007). The eastward shift of the northwestern boundary (Veron et al., 2009, 2011) implies that the boundary would start from the northernmost tip of Borneo. The ecoregion "Palawan/north Borneo" indicated by Spalding et al. (2007) has been replaced by the "Sulu Sea" ecoregion by Veron et al. (2009, 2011), which excludes the northwest coast of Borneo in the South China Sea. The present results based on the mushroom coral species richness of Brunei (n=33), but also those from Kota Kinabalu (n=35), comprising an even smaller research area (Waheed & Hoeksema, 2014), suggest that the position of the northwestern boundary of the Coral Triangle needs to be reconsidered.

Precise data on the species richness pattern in and around the Coral Triangle and the exact position of its boundaries may help to explain which processes in the past resulted in the present-day concentration of species here (Hoeksema, 2007, 2013; Barber, 2009; Bellwood & Meyer, 2009b; Briggs, 2009). In the present study the family Fungiidae is used as a proxy subset of scleractinian reef corals to compare the coral diversity of Brunei with coral faunas of adjacent areas. The results show that the use of such an exemplar taxon in short-term surveys using presence/absence data may serve well in comparisons of species numbers among small study areas. The results can be tested for accuracy by the application of species richness estimators and can serve as a substitute for data obtained during labour-intensive studies involving all reef coral species present, in which the maximum number of species remains uncertain.

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