New Scleractinian corals (Cnidaria: Anthozoa) from Sabah, North Borneo. Description of one new genus and eight new species, with notes on their taxonomy and ecology

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Key words: taxonomy; ecology; new species; biodiversity; coral reefs; Indo-Pacific; centre of diversity.
Eight new species and one new genus of Scleractinian corals from Darvel Bay, North-western Borneo are described and illustrated. *Enigmopora darveliensis, Acropora ridzwani, Lithophyllon ranjiti, Pectinia crassa, Mycedium spina, Plerogyra multilobata, Plerogyra diabolotus,* and *Plerogyra cauliformis.*
The evolutionary and distributional significance of the species is discussed. Borneo's unique equatorial location and stable geological history are held responsible for its high diversity of corals with a number of unique species. The morphology of *Enigmopora darveliensis* is discussed and compared to other supposedly primitive extant corals. The endemic status of most of the *Plerogyra* species, with their unusually large polyps, is due to their narrow ecological niche; lower, extremely protected slopes with high contents of humic substances. Most of the species have fragile structures. The role of Borneo as a centre of diversity is discussed in relation to species variability and distribution.

Introduction

Borneo has had a longer more stable equatorial presence than all other continental areas. Other landmasses have moved more recently to tropical surroundings, or been subject to more dramatic uplifts by plate tectonics. The geological history of Borneo has been described thoroughly (Hall, 1998, Metcalfe, 1998, Moss & Wilson, 1998). In late Jurassic times, minor landmasses of Gowandan origin drifted in on the southeastern side of Borneo. In the late Cretaceous, smaller stumps of Eurasian origin drifted into the area, among these the Segama block, which forms the southern borders of Darvel Bay (Metcalfe, 1996). There have been equatorial coastlines in the Borneo area for at least 165 Ma.

Geological time-scale changes in current patterns and fluctuations in sea levels have been described, and their consequences for coral diversity is much debated (Veron, 1995). Since the formation of the semi-enclosed Sulawesi Sea Basin in the Middle Miocene (Hall, 1998) this area has most likely upheld the highest stable sea temperature compared to all other tropical waters. The steep topography of the Sulawesi Sea basin (Umbgrove, 1947) has enabled corals to follow sea-level changes without much horizontal displacement. The Bornean coastlines can be expected to have maintained the most stable warm sea temperature regime of any seas around the world. The area has maintained its status as a centre of biological diversity since the earliest models of Stehli & Wells (1971) and later elaborated by Veron (1995). New evidence on species level confirms the high diversity status of the region (Veron, 2000). The coral fauna of the area is poorly investigated; the coral fauna of the southern part of the Sulawesi Sea has been described by Moll (1983) and Moll & Borel Best (1984). The family *Fungiidae* was described thoroughly by Hoeksema (1989). The status for the Philippine coral fauna has been summarised by Veron & Hodgson (1989). In 1940 the coral fauna of the calm Tomini Bay on the eastern coast of Sulawesi has been described as a distinct calm water centre of diversity (Umbgrove, 1940) and later elaborated by Wallace (1997, 1999a). An equivalent protected area on the eastern coast of Borneo is the Darvel Bay area. A list of the more common corals of the Bohey Dulong area is given by Wood & Tan (1987).

The main ecological difference between the Darvel and Tomini Bays is the degree of continental influence. Brown turbid waters with high humic content, low pH values and even more sheltered conditions prevail in Darvel Bay. The photosynthetic activity in the water column causes the organic matter to flocculate out as loose "cornflake-sized clumps" (Chave & Suess, 1970). The consequences of similar but smaller freshwater outlets on reefs have been described by Kawhata et al. (2000). An extremely fluffy, muddy and silty bottom is found from around 10-m depth in the inner part of the bay. Temperatures range from 29.5 to 32 degrees in the outer part of the bay. The wind is never extreme as the area is outside the typhoon belt and the climate is wet all year round with the heaviest rain falling from November to March.

Material and Methods

Corals were collected in 1998 and 1999 during two month long expeditions to the Darvel Bay and the Semporna area. A smaller collection comes from the West coast of Sabah from localities outside Kota Kinabalu and along the Northwest coast. Corals were also collected from the Barambagan Island and Maraud Bay on the Northcoast of Borneo. The specimens were collected using scuba equipment, photographed close-up and labelled in situ, or immediately after ascent, with data on depth, polyp shape and colour pattern. The collections during the first expedition covered Darvel Bay only and emphasis was given to collection of all hermatypic corals. Around 800 specimens were collected. During the second expedition, around 900 specimens were acquired. Collections were concentrated primarily on the *Acropora* species and the family *Euphyllidae* (Veron, 2000). Collections were also made on other reefs around Sabah in order to better understand the regional species distribution and variability. A description of the localities in Darvel Bay and a preliminary list of the collected species have been published by Ditlev et al. (1999) and De Silva et al. (1999). Most of the material described below is deposited in the coral reference collection in Kota Kinabalu at the Borneo Marine Research Institute, Universiti Malaysia Sabah, BMRI. Material of some of the new species is deposited in the National Museum of Natural History, Leiden, The Netherlands, RMNH; these are mentioned in the descriptions.

Description of the new genera and species

The term peritheca refers to the surface structures of the coenosteum. With the Family Euphyllidae all measurements are based on the complete type series.

Family Acroporidae Verrill, 1902

Enigmopora gen. nov.

Description.— The genus is similar to *Acropora* (Oken, 1815) but has solid septa reaching the columella. Mature parts of the coral have a septal arrangement similar to the genus *Porites*, with dorsal and ventral directives, four lateral pairs and a free ventral pair (Bernard, 1903). The genus is considered a primitive predecessor to *Acropora* and possibly has a common ancestorship with other Portuales plan-derived corals in the group "complex corals" of Romano & Palumbi (1996). Similarities between some key members of this group are mentioned in the remarks below.

Etymology.— The name refers to the puzzling variability in septal structures found between young and mature parts of the colony.

Enigmopora darveliensis spec. nov.
(figs 1-4)

Material.— Holotype, RMNH 31170, Sabah, Darvel Bay, Pulau Sakar, 8.ix.1998, H. Ditlev.

Description.— Arborescent to caespitose corals with straight to evenly curved branches. Branches long and evenly tapering. Mature branches around 15 mm across. The branch distance is irregular, with angles from 30 to 90 degrees. The growth form is indeterminate with many developing incipient axial corallites.

Axial corallites are 3-4 mm in outer diameter. The inner diameter is around 1 mm. The radial corallites are in two sizes. The larger corallites are lipped and around 1 mm across. The smaller corallites are around half the size and without lips. The larger radial corallites are situated in irregular longitudinal rows. Lips barely touching near the tips. Lips short and rounded to dimidiate with sharp straight edge. The lips gradually disappear downward the stems due to gradual growth in coenosteal thickness. The corallites on the lower part are flush or slightly insert.

Septa on the lower part of the branches set in Poritid pattern (Bernard, 1903) with closed pairs. The dorsal directive septum reaches the centre of the corallite and the lateral pairs reach 3/4 R. The ventral pair is slightly smaller. The lower leg of the lateral pairs and the 2 directive septa are best developed and slightly exsert and plate shaped. The edge of the septa is curved, highest slightly closer to the wall than the centre and steeply plunging close to the centre. The columella is slightly thickened and fused with the dorsal directive. The wall is slightly raised in a solid ring with around 12 small dents. The wall is separated from the peritheca with a distinct furrow.

The septa are gradually less developed upwards through an opening of the lateral pairs so 12 free septa may be seen in a few corallites. Reductions in the dorsal directive septum leave a free columellar thickening, which in a few places stand as a central stylus.

The following reductions may gradually be seen. The lateral pairs remain unfused. One or both members of the ventral pair are reduced so 11 or 10 independent septa can be seen. One of the members of the lateral pairs is more or less reduced leaving 8 or even 6 septal elements. The septa are all more uniform in size although the dorsal directives remain the largest. Near the tip the plate shaped septa are reduced to irreg-

Fig. 1, *Enigmopora darveliensis* (RMNH 31170); 0.6 ×.

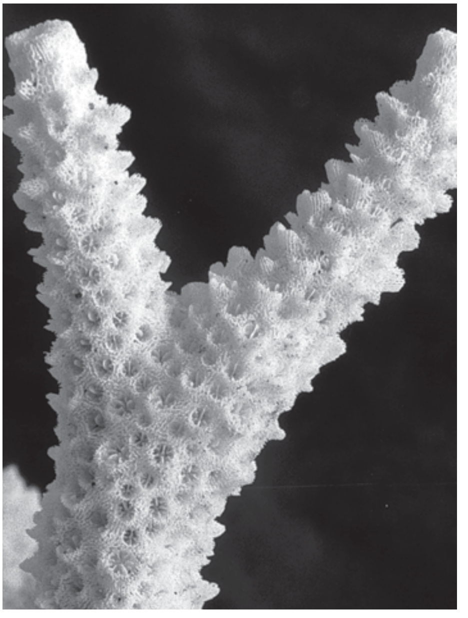

Fig. 2, *Enigmopora darveliensis* (RMNH 31170); 2.5 ×.

ular horizontal rods. The walls are formed as solid tubes. The septa do not continue unto the lip.

The peritheca has a coarse fenestrate, pseudocostate structure set in a pattern along the growth axis and in one or two concentric rings around larger corallites. The pseudocostae are as broad as the space between them, are irregularly forking, and end blindly in an intricate elongated meshwork. The pseudocostae are interconnected by synapticulae leaving long slits and oval to round holes. The pseudocostae on the lower stems have large coarse simple dents, some of which are a little elongated. The lips are only present on the upper half of the branches and disappear downwards as they are gradually covered by growth in coenosteal thickness.

A thin, smooth epitheca is found on the lowermost part of the live part of the coral. The tips of the perithecal spines may be seen sticking through the epitheca. Furthermore the epitheca has a scale-shaped structure formed by microscopically fine concentric furrows set in equal distance around the perithecal spines. At other places, the epitheca is smooth with fine irregular striations along the edge. Some live polyps are maintained sticking through in areas otherwise covered with epitheca. Some of the tumour-like thickenings around the infesting barnacles may be covered partially by epitheca.

The coenosteum seen in cross section 7 cm below the tip shows an axial corallite developed with 12 deep fossae between solid fused septa. The structures are skewed and the central part is thickened by columellar outgrowths. Near the edge concentric synapticulae forms tabulate layers, which are slightly but clearly thicker than the radiating walls and septal structures.

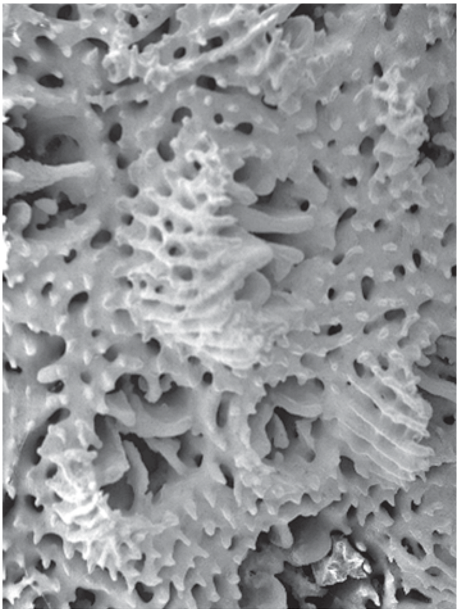

Fig. 3, *Enigmopora darveliensis* (RMNH 31170); upper part with developed lips; 16 ×.

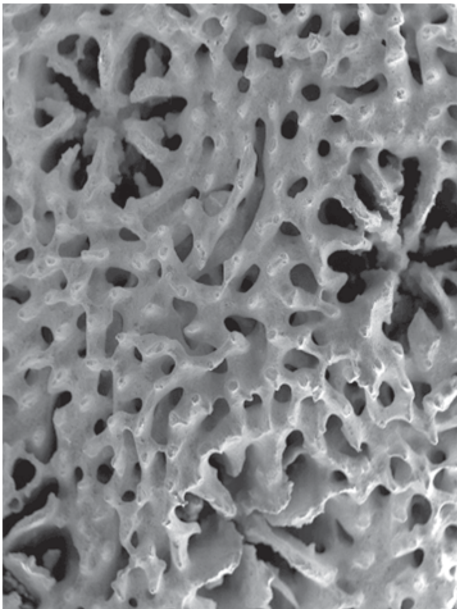

Fig. 4, *Enigmopora darveliensis* (RMNH 31170); lower part with flush corallites; 23 ×.

The specimen was found at two meters depth. The colour of the live specimen was brown. The locality is turbid with moderate currents.

Etymology.— The species is named after the type locality.

Remarks on close relatives.— The species is closest to the *Acropora aspera* group (Wallace & Wolstenholme, 1998) with coarse striate peritheca, costae on the lips; dentation on the peritheca, plate shaped septa and well developed directives. The variable calice size and lip development is also a noteworthy similarity.

According to Wallace (pers. comm.) a species with similar plate-shaped septa, *Acropora squamata* Latypov, 1992, has been described from the Cambodian part of the Gulf of Thailand. This however has digitate branches, regular hexameral septal structures and more axial corallites on each branch and there is no mention of poritid septal structures in the description.

The group has its main ecological distribution on emergent continental reef flats. The ecology and geographical distribution of the species *A. aspera* and *A. pulchra* are discussed by Ditlev (1978). *Enigmopora darveliensis* is in this context considered a primitive less reduced predecessor surviving in the centre of diversity on reef-flats. The 12 fusing septa in the deeper coenosteal part of the axials are similar to what is seen in *Acropora aspera*. The fusings are more irregular in *Acropora gomezi* and only eight septa show fusion. Four unfused structures are present and the columellar mass is much reduced. In other *Acropora* species only eight septal structures can be found here, two of which are free and the central thickening is lacking (*Acropora secale*). A full investigation of these traits might reveal characters of systematic importance.

It is striking that a primitive acroporid like *Enigmopora* has well-developed larger axial corallites, eo ipso. Comparisons between the upper and lower part of the specimen reveal a gradual reduction in skeletal development towards the tip. There is no close relationship to the very *Montipora* like *Acropora tongianensis*.

The cladistic analysis of Wallace (1999) argues generally on gradual development of more complex structures, this may hold for development of regular branching structures. For the development of corallite structures the evolution may primarily be through reductions (as demonstrated in the present new species) leading to evolution tree reversals. It is in this connection noteworthy that the septal structures are omitted in her cladistic analysis.

The development of large incipient axial corallites and smaller flush radials is clearly a poorly controlled and irregular morphological process working over short distances in *E. darveli*. This might be interpreted as a primitive trait. A process leading to formation of determinate branching pattern and uniform radial corallites will demand a process working over large distances and be more specific in its regulating powers.

The septal arrangement is similar to *Poritiidae* and ontogenetically early stages of *Siderastrea* and bears great resemblance to *Madracis*.

Acropora ridzwani spec. nov.
(figs 5-7)

Material.— Holotype, BMRI 2693, Sabah, Darvel Bay, Tabawan NE, 23.viii.1999, H. Ditlev, BMRI collection Kota Kinabalu.

Description.— Medium sized, fragile, small stalked, flat tables without vertical branchlets. Tables usually around 2 m across. The branching pattern is indeterminate and hand shaped spreading without distinct main axes. The branches are round in cross section, long and evenly tapering. The axial corallites are around 2.2 mm across. The thickness of the wall less than 0.4 mm. Outwardly inclined radial corallites are set in an angle around 45 degrees and situated in rows along the sides of the branches. The radial corallites are short, slightly concave curving and tubular. This gives the branches a distinct coarse serrated outline seen from above.

A few convexly arched pocket-shaped radial corallites are set on the side of smaller incipients. A few smaller short, tube shaped radials situated in an irregular row along the upper side. The lower side has very few and scattered flush corallites. The corallite walls have very open and elongated reticular fenestrate structure. The coenosteum is reticulate, very porous and irregularly lengthwise furrowed with simple spines, which may fuse.

The colour is uniformly dull greyish brown. The species is rather common on shoals and exposed lower slopes on the East coast of Northern Borneo from 15 to 30 m depth.

Etymology.— The species is named in honour of the leader of Borneo Marine Research Institute, Dr Ridzwan Abdul Rahman.

Remarks on close relatives.— The species is found in deeper waters often together with *Acropora plumosa*, which has a resembling gross morphology, but has the corallites sitting in a uniformly radiating pattern around the branches, and the main branches form clearly defined larger radiating main axes.

Fig. 5, *Acropora ridzwani* (BMRI 2693); 0.66 ×.

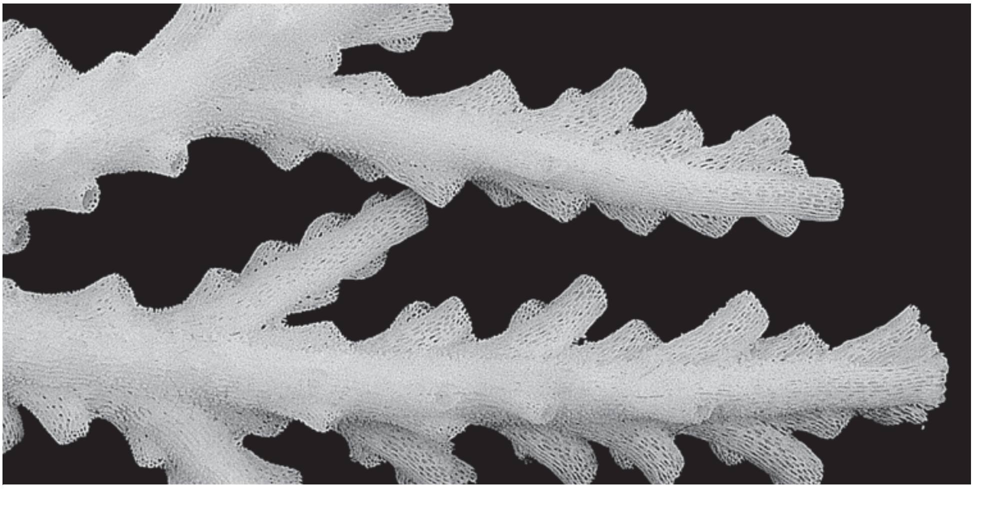

Fig. 6, *Acropora ridzwani* (BMRI 2693); branch tips; 2.5 ×.

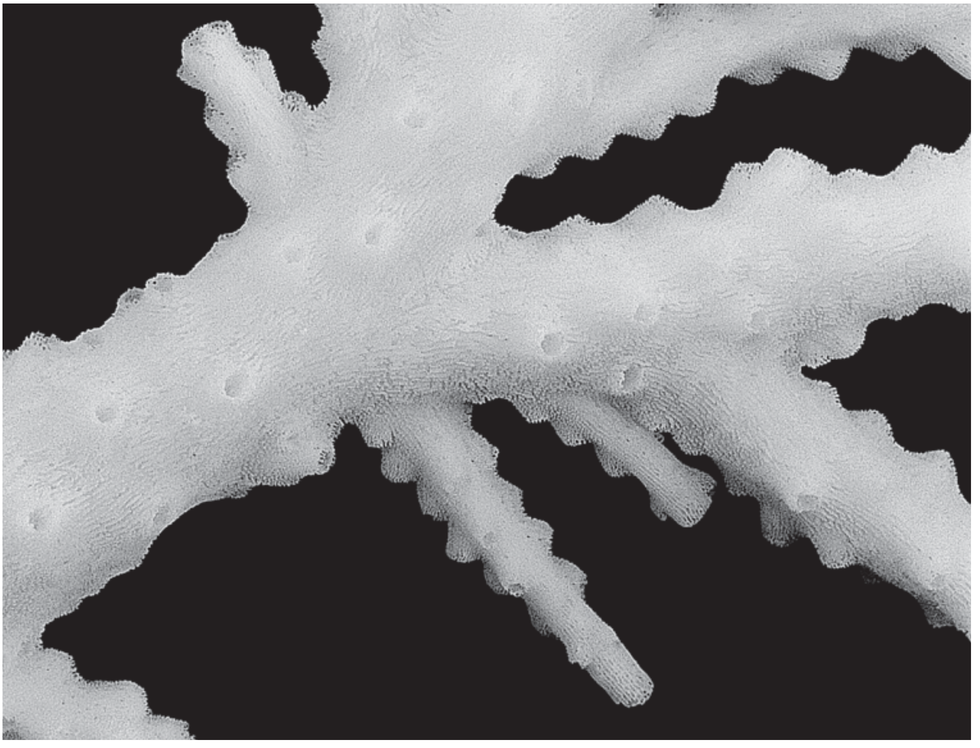

Fig. 7, *Acropora ridzwani* (BMRI 2693); lower branch; 2.5 ×.

Family Fungiidae
Lithophyllon ranjithi spec. nov.
(figs 8-12, 29-30)

Lithophyllon lobata; Veron, 2000: 307, figs 5-6. **Syn. nov.**

Material.— Holotype, RMNH 31171, 421, Sabah, Darvel Bay, Bagahak, 15.ix.1998, 15 m. The following specimens are paratypes: RMNH 31172, 508, Sabah, Darvel Bay, Bakapit, 18.ix.1998, 15 m; RMNH 31173, 420, Sabah, Darvel Bay, Bagahak, 15.ix.1998; BMRI 137, Sabah, Darvel Bay, Pulau Sakar NE, 8.ix.1998, 12 m; BMRI 97, Sabah, Darvel Bay, Sakar NE, 8.ix.1998, 15 m; BMRI 186, Sabah, Darvel Bay, Sakar NE, 8.ix.1998, 18 m; BMRI 244, Sabah, Darvel Bay, Pulau Sakar SW, 9.ix.1998, 25 m; BMRI 327, Sabah, Darvel Bay, Pulau Baik, 13.ix.1998, 20 m; BMRI 261A, Sabah, Darvel Bay, Pulau Sakar SW, 9.ix.1998; BMRI 563, Sabah, Darvel Bay, Pulau Liang S, 20.ix.1998, 15 m.

Description.— Fixed thick solid horizontal plates with more or less free edges; the latter are slightly undulating and lobed. Coral polystomatous and up to 50 cm across. Smaller corals have a distinct primary stomodaeum. A central hump is more or less developed.

The septa are inequal cyclically and of two kinds. Primary septa are 2-5 times as broad as the secondaries. The space between septa is as thin as the secondary septa.

Fig. 8, *Lithophyllon ranjithi* (RMNH 31171); 0.5 ×.

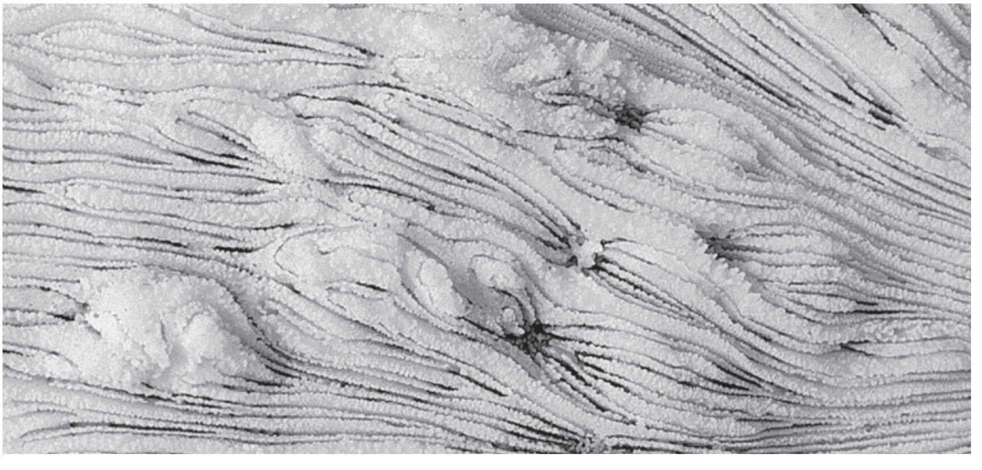

Fig. 9, *Lithophyllon ranjithi* (RMNH 31171); edge zone; 2.5 ×.

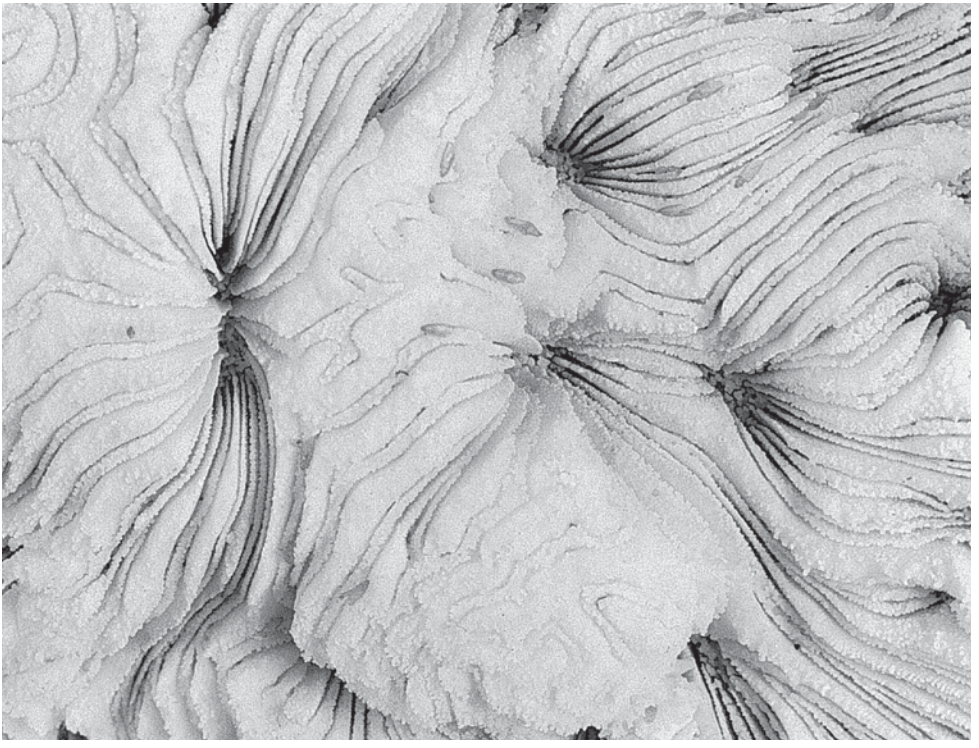

Fig. 10, *Lithophyllon ranjithi* (RMNH 31171); central part; 2.5 ×.

Primary septa have 35 irregular columnar dentations per cm on the primaries on the outer part of the coral. On the central part of the coral the primaries are furcating, or raised in lobes, near to the stomodea and secondarily broadly thickened. Primary septa may be discontinuous and raised in lobes shortly before their termination. The septal edges are granulated with dentation broader than long, or the dentation may be situated along the sides in two distinct rows. The dentation is absent in the thickest septa and their surface is covered in evenly sized irregular fusing granular knobs.

Close to the edge the secondary septa are smaller and sometimes furcating in three; the mid part of which is often upgraded to first order and forming a distinct lobe or a longer first order septa. Secondary centres may eventually be formed at the outer discontinuous end of some of such upgraded septa. These upgrades are often secondarily furcating with a short terminated branch on the inner side of a centre to form a thickened boss that make the developing centre outwardly inclined. This principle of morphological propagation allows for an irregular growth in thickness. Lines of fusing septa due to lack of surface space for continuous septal growth in one plane are sometimes present (similar patterns can be seen in *Fungia fungites).* The fissures are short and not raised in ridges. The synapticulae are hardly visible, broad and with small fossae close to the edge. Older parts have secondary thickenings filling in the fossae.

Centres on the central swollen part are 0.5-1 cm long and 3 mm broad. The columella consists of a dense group of distinct granulated and irregularly fusing trabeculae.

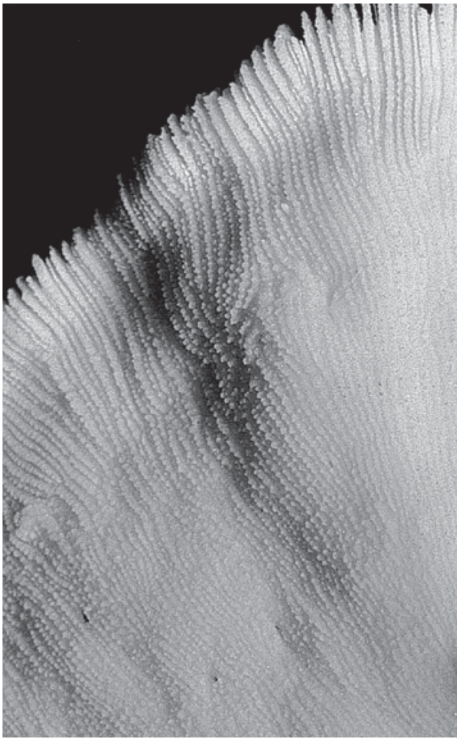

Fig. 11, *Lithophyllon ranjithi* (RMNH 31171); costae; 2.5 ×.

Fig. 12, *Lithophyllon ranjithi* (RMNH 31172); 2.5 ×.

Secondary centres are scattered over the corallum, decreasing in size towards the edge. The centres are more or less outwardly inclined.

The wall is solid with small scattered depressions visible on the aboral side. The depressions are mostly set between the irregular radiating secondary thickened bands. The costae are set in two to four cycles with short, broad, granulated dentation. The costae are broad and best developed near the edge, the lower side with a few scattered solid knobs occasionally developing into rootlets.

The colour of the live coral is brown with more yellowish blotches on some large centres and in irregular patterns. The stomodaeum is darker brown but never of a differing colour. The species is found commonly below a depth of 10 m in the inner part of Darvel Bay on steep hard substratum and more than 25 specimens have been observed, all fixed.

The type specimen is 24 times 30 cm large solid plate, which is 8 mm thick near the rounded edge. The central part is gradually thickened to around 20 mm and has a central thickened hump around 5 cm across and 2 cm high. The hump is carrying around 10 centres. The specimen is fixed by an eight times 10 cm large solid base and by a few low rootlets near the edge.

Etymology.— The species is named after Dr M.W. Ranjith N. De Silva.

Remarks on close relatives.— The three presently known species can be identified with the following key:

1. Septa thinner than the space between them and with thin pointed dentation. Columella formed by twisted trabeculae. Large lobed colonies, centres not swollen. Synapticulae readily visible. The stomodaeum differently coloured than the rest of the live coral .... ***L. undulatum***
- Septa thicker than the space between them and with granulated surface. Synapticulae hidden. Columella papillary or absent.
2. Small encrusting colonies with close set centres .... ***L. mokai***
- Large, thick, foliaceous colonies with irregular scattered centres .... ***L. ranjithi***

Family Pectinidae Vaughan & Wells, 1943

Pectinia crassa spec. nov.
(figs 13-15)

Pectinia ayleni; Veron, 2000: 352. **Syn. nov**.

Material.— Holotype, BMRI 3157, Sabah, Darvel Bay, Pulau Tabawan NE, 27.viii.1999, H. Ditlev; paratypes, BMRI 860, Sabah, Semporna, Pulau Mantabuan, 6 m, 19.ix.1998, H. Ditlev.

Description.— The fixed large colonies are built as loose multilayered masses of small foliaceous plates. The edge of the plates is drawn out as tongue shaped structures with ragged edges. The septa are developed in two to three irregular cycles. Close to the edges one to three of the primary septocostae build vertical radiating plates, forming new tongues along the edge. The septa are raised into one to three mm exsert round tipped plates along the edge of the coral. The edge of the solid septa has granulated to frosted tipped fine dentation. The centres are scattered and outwardly inclined with skewed septa. The centres are slightly sunken in. The lower side of the folia may carry a few small incipient strongly inclined centres.

The type specimen is 22 cm across and a part of a colony one m across and 50 cm high. Most specimens observed in nature are between one and two meters across and found along the reef edge. The colour is greyish yellow and browns. The species is found on moderately exposed upper slopes with high coverage between other *Pectinidae, Porites spp,* and *Acropora* staghorn.

Etymology.— The species is named after the coarse crassiform granulated septal edges.

Remarks on close relatives.— The species is readily identified by the small uniformly multilayered lobes and the swollen septal edges.

Mycedium spina spec. nov.
(figs 16-18)

Material.— Holotype, BMRI 2533, Sabah, Darvel Bay, Bagahak, 10.viii.1999, H. Ditlev.

Description.— Thin foliaceous coral with the edge drawn out in flat, broad rami with angular points. The primary septocostae forms the growth axis. Rami growing out in more criss-crossing horizontal layers from the central thin, foliaceous part. The centres are scattered over the central part, non-inclined, 3-4 mm across and defined by raised teeth on the primary septa. Five to nine primary septa reach the loose trabecu-

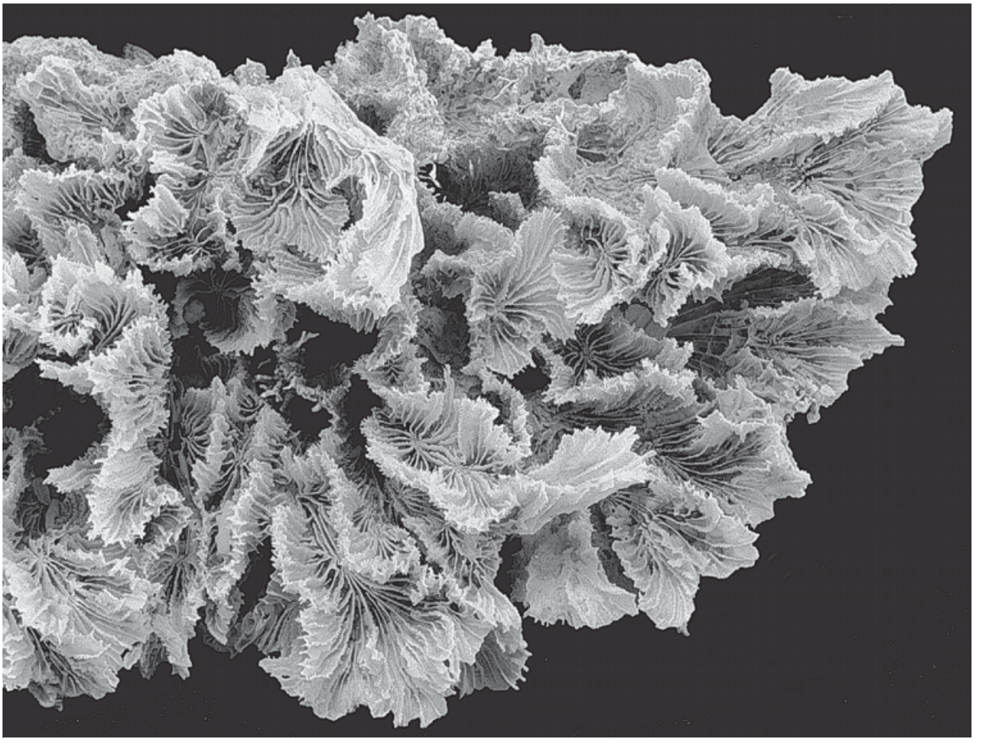

Fig. 13, *Pectinia crassa* (BMRI 3157); 0.75 ×.

Fig. 14, *Pectinia crassa* (BMRI 860); upper side; 2.5 ×.

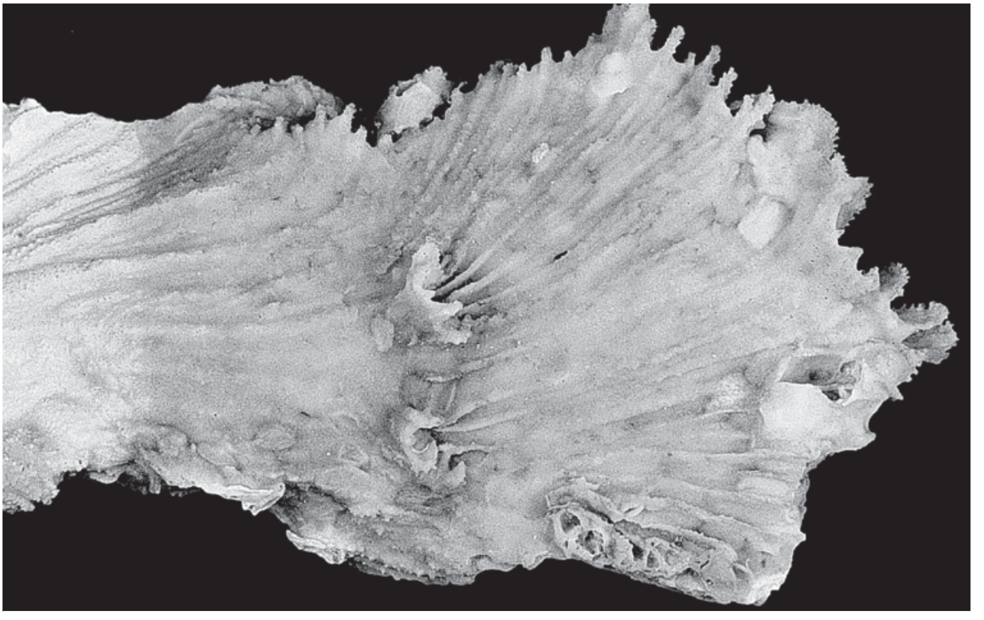

Fig. 15, *Pectinia crassa* (BMRI 860); lower side; 2.5 ×.

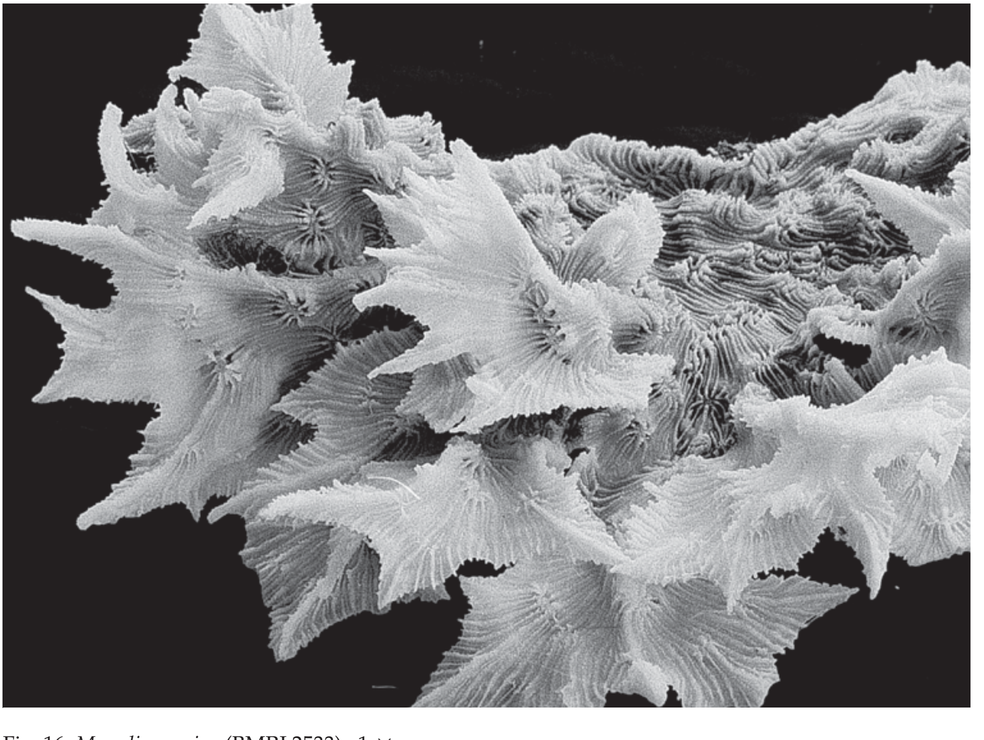

Fig. 16, *Mycedium spina* (BMRI 2533); 1 ×.

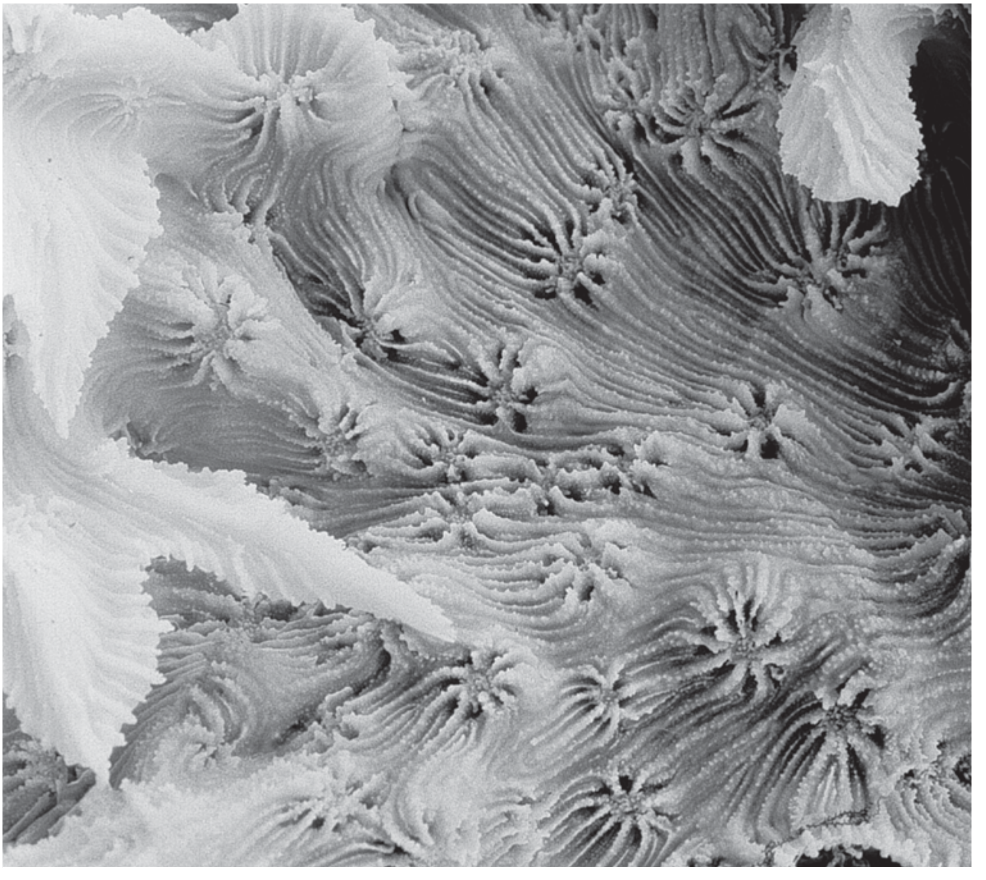

Fig. 17, *Mycedium spina* (BMRI 2533); 2.5 ×.

lar columella. Few smaller secondary septocostae are present. The costae are generally smooth with few small, scattered short dents. The edge of the folia is sharp. The underside has a few striations. The coenosteum is not vesicular. The species is readily identified from the structure of the edges.

The colour of the live coral is brown. Another and smaller bleached young specimen has been found and photographed in situ on a sheltered lagoon slope around 10 m depth at Bohey Dulong some miles further south. The specimen is deposited in BMRI.

The type specimen is 22 cm broad and was found in a crevice at a depth of 6 m on a moderately sloping protected continental slope with turbid water.

Etymology.— Named after its pointed outgrowths.

Remarks on close relatives.— All other species in the genus have smooth or lobed edges.

Family Euphyllidae Veron, 2000

Plerogyra multilobata spec. nov.
(figs 18-19, 23-24)

Material.— Holotype, BMRI 2514, P. Sakar N, 7.viii.1999, 8 m. The rest of the specimens are paratypes: BMRI 2512, P. Sakar N, 7.viii.1999, 12 m; BMRI 2728, P. Sakar NE, 13.viii.1999, 8 m; BMRI 2730, P. Baik, Inner Side, 16.viii.1999, 17 m; BMRI 2731, P. Sakar, N, 7.viii.1999, 6 m; BMRI 2759, Howard Shoal, 10.viii.1999, 10 m; BMRI 3312, P. Baik, Outer Side, 12.viii.1999, 9 m; BMRI 3313, Woodall Reef, 6.viii.1999, 15 m; BMRI 3314, Howard Shoal, 10.viii.1999, 7 m. All these specimens are collected by H. Ditlev and are deposited in BMRI. A small paratypes, RMNH 31174, P. Sakar NE, 7.ix.1998, 6 m, H. Ditlev.

Description.— Colonies are phacelomeandroid with branching, curved and bent series. The peritheca may be slightly swollen. The walls are sharp and may be weakly undulating. Valley width is around 16 mm (11-26) and depth around 10 mm (4-17).

Septa are of regular shape and irregular sizes with smooth sides and edges. Cycles of septa are irregular, but when recognisable 2-3 cycles are present. Fourth cycle is only rarely developed. Septa bend towards indistinct centres; they may be clearly raised above the wall on some colonies, up to 15 mm. There are around 8 (4-12) septa per 2 cm. Costae are sometimes present. When appearing they are very irregular, but corresponding to septa. Costae can be either fine or rough.

The polyps are elliptical with a more or less expanded oral disc. The edge of the polyp drawn out in usually swollen shaft shaped vesicles with a distinct row of 3-7

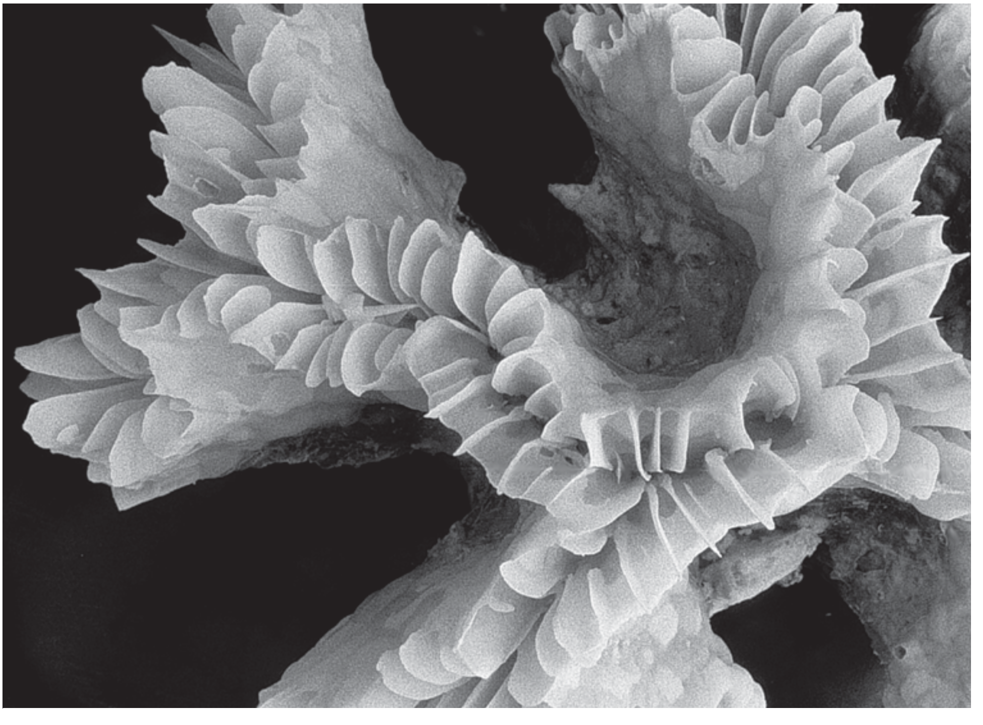

Fig. 18, *Plerogyra multilobata* (BMRI 2514); 1 ×.

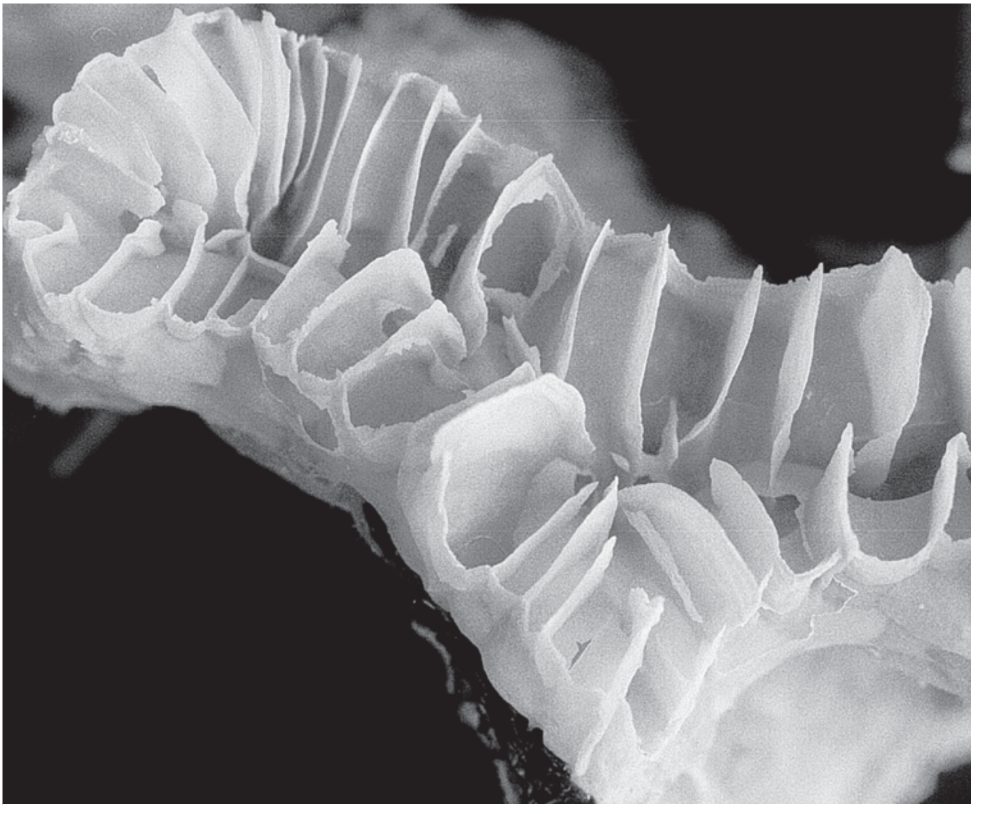

Fig. 19, *Plerogyra multilobata* (BMRI 2514); 2.5 ×.

bulbs along the upper edge. The bulbs may be long and slender with tentacle like gradually whitened tips or have swollen and rounded, evenly coloured tips, depending on the degree of expansion. Proximal to these structures other swollen bulbs may have similar tentacle like structures set in two irregular rows separated by the expanding oral disc, or set in a seemingly concentric pattern on their top. The polyps are paleish brown, greenish or bluish, with whitish knobs. The fingerprint like surface structure is sometimes clearly visible and is more coarse and irregular reticulate than those seen in *P. sinuosa*. The species is common on very turbid lower slopes in Darvel Bay and may be interpreted as a local turbid water specialist closely related to the following species.

Etymology.— The name refers to the multi-lobed vesicles.

Remarks on close relatives.— The distinction of the species is discussed under the next species.

Plerogyra diabolotus spec. nov.
(figs. 20, 25-26)

Material.— Holotype, BMRI 3311, Mata Pahi, 14.ix.1999, 8 m. Paratypes: BMRI 3216, Mata Pahi East, 14.ix.1999, 8 m; BMRI 3306, Bagahak East Point, 26.viii.1999, 8 m; BMRI 3307, Mabul, Coral Garden, 10.ix.1999, 8 m; BMRI 3308, Mabul N, 10.ix.1999, 12 m; BMRI 3309, P. Baik, Inner Side, 25.viii.1999, 15 m; BMRI 2554, Howard Shoal, 14.viii.1999, 14 m. All these specimens are collected by H. Ditlev in Sabah and deposited in BMRI. A small paratype, RMNH 31175, Sabah, Darvel Bay, P. Sakar NE corner, 25.ix.1998, 12 m, H. Ditlev.

Description.— Phacelomeandroid fixed colonies with forking free series. The colonies are rarely more than 40 cm across. The peritheca is slightly swollen. Series are straight to curved. Wall thin, sharp and very ragged in height, partially following the raggedly exsert septa. Valleys are around 20 (14-33) mm across and around 15 (6-24) mm deep.

Septa are thin, well separated and set in up to four very irregular cycles. Septa have smooth sides and edges. The septal edge highest near the wall or flattened on the top. The septa are separated by ample vesicular endothecal dissepiments. The innermost part of the septum sometimes bent towards indistinct centres at the valley floor. Septa are up to 10 mm exsert. There are about 7 (5-10) septa every 2 cm. The peritheca is deeply cut and with slightly swollen vesicular blisters. Costae corresponding to the primary septa are sometimes present.

The polyp often has a broad expanded oral disc. The edge of the polyp is bent in undulating flounces. The bulbs are situated along the edge of the oral disc. Their shape is very variable, from short cone-shaped structures to more or less irregular swollen bulbs with short, more or less distinct, small white tips, depending on the degree of bulb expansion. When the oral disc is not expanded the polyp seems to be completely covered by the irregularly swollen lobes topped by more or less inflated irregularly pointed outgrowths. When the bulbs are not fully expanded, their tips are gradually more whitish.

The expanded tentacles are situated just proximal to the vesicles. The tentacles are short, evenly tapering, and pointed. Their surface has small grainy whitish dots. Translucent pale whitish green, brown, grey or bluish colours are all common. The oral disc may be radially white striped. The species is primarily found on more exposed localities than *P. multilobata*. The species is presumably widespread in Indonesian and Philippine waters.

Etymology.— The name refers to the ear-like lobed oral disc lined with pointed outgrowths resembling a devil's ear.

Remarks on close relatives.— The skeletons of the two new species *P. diabolotus* and *P. multilobata* cannot be distinguished from each other although *multilobata* is, on average, somewhat smaller in all structures. However, in both species the polyps are quite distinct. The specimens described as *P. lobata* by Veron & Pichon, 1979, are presumably a mixture of *P. diabolotus* and *P. lobata*. The type specimen of the latter species is illustrated by Matthai (1928) and similar to my specimens of *P. lobata*, from Borneo, which can be distinguished on the irregular slightly elongated, small swollen vesicles, broader valleys, and the lack of thin raised walls. The colonies of *P. lobata* are often more than 1 m across. Red Sea *Plerogyra* is close to *P. diabolotus* in skeletal details but the development of the polyp is less elaborate. *Plerogyra eurysepta* can be recognised on the more elongated vesicles, smaller colonies, and the 4 cm broad series.

Fig. 20, *Plerogyra diabolotus* (BMRI 3311); 1.25 ×.

Plerogyra cauliformis spec. nov.
(figs 21-22, 27-28)

Material.— Holotype, BMRI 2545, P. Baik, Outer Side, 4.viii.1999, 29 m. Paratypes: BMRI 2558, Bakapit, 9.viii.1999, 15 m; BMRI 2616, P. Baik South Point 16.viii.1999, 28 m; BMRI 2762, P. Sakar N, 13.viii.1999, 8 m; BMRI 2784, P. Baik, Outer Side, 12.viii.1999, 30 m; BMRI 3068, Adal 19.ix.1999, 35 m; BMRI 3069, P. Tabawan, Lagoon, 23.viii.1999, 22 m; BMRI 3070, Mabul, Coral Garden, 10.ix.1999, 12 m; BMRI 3072, Mabul, Coral Garden, 10.ix.1999, 10 m; BMRI 3138, Barambangan, Periok, 24.vi.1999, 6 m; BMRI 3151, Darvel Bay N, Bakapit Town, 19.viii.1999, 8 m; BMRI 3287, P. Tabawan S, 23.viii.1999, 23 m. All material is collected by H. Ditlev in Sabah and deposited in BMRI. Paratype, RMNH 31176, Darvel Bay N, Bagahak, 15.ix.1998, 12 m.

Description.— The colony usually phaceloid, but may be phacelomeandroid. The peritheca is much swollen, formed by bubbly and often flaky exothecal dissepiments. Phacelomeandroid colonies may have curved series. The phaceloid units vary in height from 2-20 cm over the swollen peritheca. The walls are undulating and rounded to sharp. Calice width around 18 (9-23) mm. Phaceloid corallites are somewhat elongated. The width of the corallites is around 21 (15-28) mm and length is between 17-36 mm. The calice depth is 13 (7-19) mm. Phaceleomeandroid series may be very long.

Fig. 21, *Plerogyra cauliformis* (BMRI 2545); 0.5 ×.

The number of septa every 2 cm is around 8 (5-14). Cycles of septa are irregular. Septa have smooth sides and edges. Septa are raised up to 10 mm above wall. Phaceloid colonies have straight septa towards the centre, while phacelo-meandroid colonies have the inner edge of the septa bent towards the indistinct centres in the valley floor. Costae, when present, correspond with the septa. Costae can be both fine and rough and may have teeth. Colonies from deeper water tend to have the phaceloid units raised higher than colonies from shallow water. Meandroid structures are best developed in the most exposed specimens.

The polyps are swollen and brown. The tentacles are slightly stalked and with an irregular warty surface with white rounded polygonal markings resembling small buds of cauliflower, which completely cover the polyp during the daytime. No expanded oral discs have been observed. The species have not been observed outside Sabah.

The holotype is a large mature colony, 27cm across with short phaceloid series united by ample deeply cut flaky peritheca.

Etymology.— The name of the species refers to the cauliflower-like appearance of the live polyp.

Remarks on close relatives.— The species is close to *P. simplex*, which is much

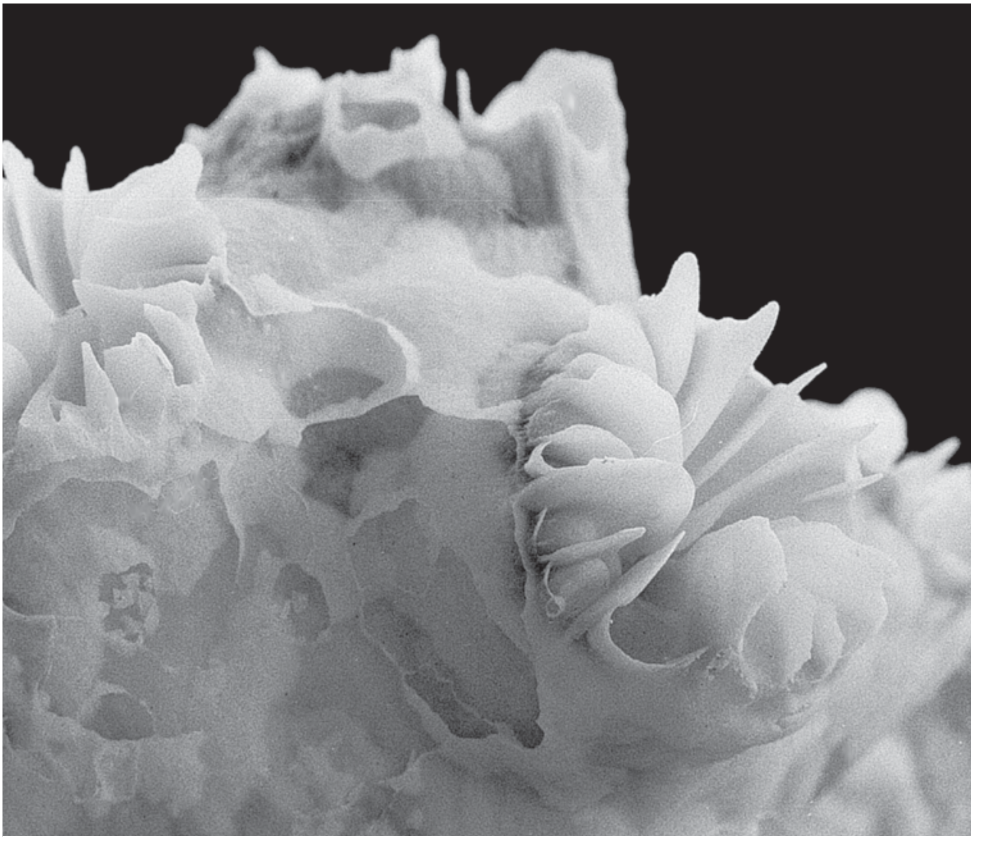

Fig. 22, *Plerogyra cauliformis* (BMRI 2545); 2.5 ×.

smaller in all structures. The phaceloid structures are much higher and the costae are much longer and more acute. The live coral is dark brown. The vesicles have a smooth surface and a uniform paleish yellow colour.

Remarks on the occurrence of other corals

Most species occurring in Darvel Bay have large polyps. Members of the coral families *Pectiniidae* and *Mussidae* are common. The most striking aspect is the lack of *Pocillopora*. A single specimen of *P. damicornis* was found during the whole expedition; it was situated on a rope hanging from an old wreck! Shallow water *Acropora* tables are extremely rare in the bay. Near the spring-layer, the *Acropora elegans* and *loripes* groups (Wallace 1998, 1999b) show surprisingly high densities and an unrivalled diversity. The species are all sharing a flattened morphology and most polyps are situated along the sides of the branches. Compared to the descriptions of these species the specimens from the bay are all larger, better calcified, and have a higher tendency towards a morphology with radial corallites situated along the sides of the branches. The genus *Montipora* is poorly represented, whereas the *Euphyllidae* are extremely diverse and very common, especially on lower slopes. *Leptoseris* is well represented along the lower slope, primarily by pseudoramose forms. The reefs in the inner part generally have coral densities rarely exceeding 50% and irregular steep slopes.

The outer shoals in the bay house low reefs with large monosepecific and compound stands with at least four species of partially ramose *Galaxea* and four species of *Pachyseris*. The Fungiids found here reach enormous dimensions in dense populations. These reefs have yet to be described in detail. A preliminary list covering approximately 70% of the collected species around Sabah is published by Ditlev et al., 1999.

Branching and otherwise loose growthforms are a general feature of the corals of Darvel Bay. Compared to more current exposed localities the number of commensals like tube- worms, crustaceans and territorial fish are very low. Seen in a gradient from Borneo over Sulawesi to New Guinea there is a general tendency in intra and inter-species variability towards smaller polyps.

Discussion and conclusions

The coral species described in this paper, with presumably limited distribution, adds a new element in the high diversity centre debate. There is a fair number of surviving strictly equatorial primitive species with limited distribution. The species are confined to sheltered localities with high organic content and can be considered species especially well adapted to such localities. They generally have larger polyps compared to closely related species from more open localities with clearer water. The intraspecific variability shows similar tendencies, this is in agreement with the resource partitioning theories proposed by Porter (1976). The species *Enigmopora darveli, Acropora ridzwani, Mycedium spina, Plerogyra mulitlobata* and *Plerogyra cauliformis* are presumably relicts and/or local specialists with little potential of surviving in more open localities, and thus they have never spread to other localities in the region. The author has not found any of them in Northern Sulawesi, the archipelago around Baik Island, NW New Guinea and along the West coast of Thailand. The extensive collections in Leiden from Sulawesi and other parts of Indonesia do not contain similar material. The species described in this paper should be added to the list of 31 regional endemics reported by Veron (2000).

Seen in geological timescale, it is most likely that species may have spread from the Sulawesi Sea to the continents arriving from colder surroundings because of continental drift and the emergence of hard bottom due to volcanic activity. The general current pattern makes the area a crossroad for currents on the open eastern coast of a continental mass. The number of specialised species confined to a comparatively small area indicates a high stability. This confirms with Borneo's long career as a tropical island. Judged from the published maps on continental drift (Metcalfe 1996, Ridder-Neumann 1996 Wilson & Rosen, 1998) catastrophic events, changes in current patterns, sea-level changes due to continental drift and uplifts within the last 100 million years have had the smallest consequences for Borneo and the Sulawesi Sea, compared to other tropical seas. Darvel Bay must be considered a rearing tank and refuge for deep-water species. The low pH in the water and the sudden photosynthetic induced raise in pH of 0.5 units in connection with the spring layer (Ditlev et al., 1999) are extreme ecophysiological conditions to which the species are adapted. Comparable ecophysiological conditions presumably have prevailed over larger areas during the

Cretaceous, when high atmospheric CO_2 levels predominated, and when corals primarily were found in deeper waters (Scott, 1988). Catastrophic events are generally described as shorter periods with low oxygen tensions and increased sedimentation. The corals of Darvel Bay have the best ecological tolerances for surviving such hardship compared to coral species with their main distribution in less foul waters.

The physiographic conditions are not favourable for the preservation of fossils, due to acid and anoxic sulphur rich sediments found in the bay. The reason for reefs to be primarily preserved at higher latitudes (Ziegler et al., 1984) may also be due, beside the higher isolation to lower organic nutrient levels disfavouring the destructive processes performed by Sponges, Bivalves Polychaetes and Sipunculans on dead skeletal material. Less organic and sulfuretic sediment is another facilitating factor for fossil preservation. These factors skew the paleontological record in disfavour of continental- equatorial material. The hermatypic corals may very likely have survived periods of hardship here leaving few or no paleontological traces.

The distribution pattern for the species is still poorly known. Most endemism seems to be regional, judging from the *Acropora* distributions given by Wallace, 1998, and from personal experience. Most of the supposed *Acropora* endemics are found in a band from Borneo to Northern New Guinea. Muddy bays are not places to find dive centres and they are generally poorly investigated. Possible areas to find similar conditions would be near mangrove localities stretching from Borneo over the Central Philippines to Northern New Guinea, an area from where the coral fauna is still poorly investigated. Judged from distribution maps the deep water *Acropora* groups (*loripes*, *elegans* and *echinata*) have their centre of diversity in the Sulawesi Sea, especially the first two groups. They may have evolved here from a surviving deepwater predecessor on the Eastcoast of Borneo. Two small specimens from the area (BMRI 3113 & 3114) similar to *Acropora pichonoi* but with longer and free branchlets are noteworthy in this connection. Their taxonomical status is still unresolved.

The centre of diversity for the surf swept upper slope, table forming stout *Acropora* groups, i.e. the *rudis* and *humilis* groups, are clearly associated with the western Sumatra-Malacca ridge. The high wave energy regimes along the west Australian-Indonesian and Malacca Peninsular arch act as a strong barrier for the distribution of species with sheltered locality adaptations. The same is presumably true for the high wave energy regimes of the northern Great Barrier Reef and the Torres Strait.

The frequency of new species found during the present investigation is still around one per 10 dives, as also experienced by Wallace (1998) in nearby Indonesian waters. More species can thus be anticipated. The reality of a present day centre of coral diversity in the Zulu and Sulawesi Seas is supported by the eight new species here described. The most likely source for inoculation of tropical shallow water marine fauna to the Australian continent is the Sulawesi Sea.

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Fig. 23, *Plerogyra multilobata;* live polyp.

Fig. 24, *Plerogyra multilobata;* live polyp closeup.

Fig. 25, *Plerogyra diabolotus;* live polyp.

Fig. 26, *Plerogyra diabolotus;* live polyp closeup.

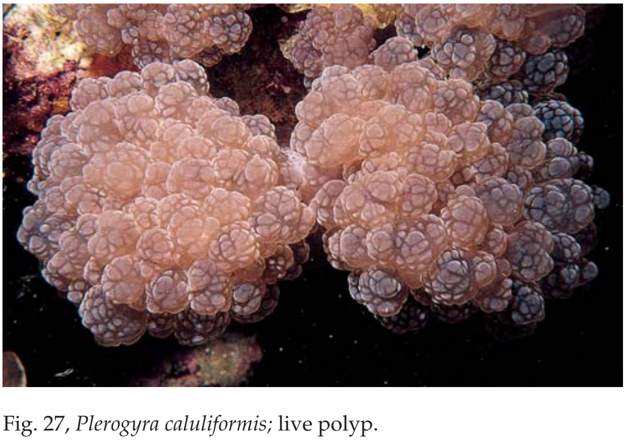

Fig. 27, *Plerogyra caluliformis;* live polyp.

Fig. 28, *Plerogyra caluliformis;* live polyp closeup.

Fig. 29, *Lithophyllon ranjithi;* holotype, live polyp.

Fig. 30, *Lithophyllon ranjithi;* live polyp with closer set centers.