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SCLERACTINIA OF EASTERN AUSTRALIA

PART II

Families Faviidae
Trachyphylliidae

by

J. E. N. Veron

Michel Pichon

and

Maya Wijsman-Best

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I

Introduction

The Faviidae is one of the most important families of hermatypic corals. It is the biggest in terms of number of genera, and ranks next to the Acroporidae in number of species and overall abundance in most reef biotopes throughout the Indo-Pacific.

Owing to their abundance, the Faviidae have always made up a large part of all taxonomically important reef coral collections, including those of the earliest taxonomists, e.g. Forskål, who in 1775 published an account of twenty-three species of corals from the Red Sea, eight of which are Faviidae. The subsequent taxonomic history of the group has been long and complex, because of abundance and diversity and also because of the wide variations in skeletal structure shown by many species. The result has been a succession of exceedingly complex and obscure synonymies and an enormous number of nominal species. The division of the scleractinian genus *Madrepora* was begun by Lamarck, who recognised the following genera for corals now known to belong to the Faviidae: *Echinopores* and *Explanaires*; *Monticulaires*; *Astrées*; *Méandrinés*.

It is interesting to note that this first subdivision was primarily based on growth forms. *Echinopores* and *Explanaires* have a predominantly lamellar or foliaceous growth form, with well defined corallites. *Monticulaires* bear characteristic star-shaped cones. *Astrées* have distinct, more or less rounded corallites, and *Méandrinés* include all corals with centres arranged in valleys, in a brain-like formation.

The effect of this treatment was to separate into distinct units two very well defined genera, which have had little or no subsequent change. These are *Echinopores* and *Explanaires*, named *Echinopora* since Dana, and *Monticulaires*, named *Hydnophora* by Fischer de Waldheim (1807), apparently overlooked until Edwards & Haime's revision, and almost continually in use since then. This framework was followed by de Blainville (1830, 1834) and Dana (1846), the latter adding only two new genera to the Faviidae, *Caulastrea* and *Trachyphyllia* (under the name *Manicina*).

The next significant step towards refining the classification of the Faviidae was accomplished by Edwards & Haime, particularly in their 1857 monograph. Their breakdown of Lamarck's genera, *Astrées* and *Méandrinés*, led to a situation which was in many ways a precursor of the present one (Table 1). In some instances, however, they considered as different genera several groups of species which are now included in the same genus. This was the case, for instance, for *Aphrastraea*, *Prionastraea* and *Metastraea*, which have all been absorbed into the genus *Favites*. This treatment is undoubtedly a result of the fact that the subdivisions into genera made by Edwards & Haime were based on a small number of skeletal characteristics which are now known to be highly variable.

A significant achievement of the Edwards & Haime classification was the subdivision of their Subfamily *Astraeidae* into a group of genera reproducing by gemmation (Agèle 'Astracées') and a group of genera reproducing by fissiparity (Agèle 'Faviacées' and 'Lithophylliacées'). They thereby introduced the budding conditions, extratentacular *versus* intratentacular, as a taxonomic criterion. This distinction was maintained by Duncan in his revision of 1884. In both publications however, the meandroid species, although specifically recognised 'fissipares' by Edwards & Haime, were isolated from the *Astraeidae* with distinct corallites. Most subsequent authors took the budding conditions into account, but attributed to this character a somewhat variable importance. Matthai (1914, 1928) and Crossland (1952) did not suggest any nomenclatural status to their groups of species. Furthermore, it is

noteworthy that they still maintained the distinction between meandroid and non-meandroid species. Conversely, Vaughan (1918) raised each group to the rank of Family (named Orbicellidae and Faviidae), a move followed by Yabe, Sugiyama & Eguchi (1936).

An intermediate standpoint was adopted by Vaughan & Wells (1943) who gave these two groups of species (Edwards & Haime's 'gemmantens' and 'fissipares') the status of subfamilies, named Montastreinae and Faviinae respectively. This treatment has been widely accepted in recent years, in particular by Wells (1956), Nemenzo (1959), Eguchi (1968), Pillai (1972), Wijsman-Best (1972), Pillai & Scheer (1974) and Scheer & Pillai (1974). However, Chevalier (1971) adopted a different position, and did not recognise any subfamily within the Faviidae, for the following reason: 'On observe fréquemment dans plusieurs genres de Faviinae (en particulier chez *Favia*) l'apparition d'un bourgeonnement extratentaculaire à côté de la gemmation intratentaculaire qui demeure la règle'. Our own studies also indicate that, in many

Table 1. The main stages of development of Faviidae and Trachyphylliidae classification.

Lamarck 1801, 1816	de Blainville 1830, 1834	Dana 1846	Edward & Haime 1857	Duncan 1884	Matthai 1914, 1928	Wells 1956	Present Study	
	—	<i>Manicina</i>	<i>Trachyphyllia</i>	<i>Trachyphyllia</i> <i>Moseleya</i>	<i>Trachyphyllia</i> —	<i>Trachyphyllia</i> <i>Moseleya</i>	<i>Trachyphyllia</i>	Family Trachyphylliidae
<i>Echinopora</i> <i>Explanaria</i>	<i>Echinastrea</i>	<i>Echinopora</i>	<i>Echinopora</i>	<i>Echinopora</i>	<i>Echinopora</i>	<i>Echinopora</i>	<i>Echinopora</i>	
			<i>Leptastrea</i>	<i>Leptastrea</i>	<i>Leptastrea</i>	<i>Leptastrea</i>	<i>Leptastrea</i>	
			<i>Cyphastrea</i>	<i>Cyphastrea</i>	<i>Cyphastrea</i> <i>Diploastrea</i>	<i>Cyphastrea</i> <i>Diploastrea</i>	<i>Cyphastrea</i> <i>Diploastrea</i>	
			<i>Heliastrea</i>	<i>Heliastrea</i>				
<i>Astraea</i>	<i>Astraea</i>	<i>Astraea</i>	<i>Plesiastrea</i> <i>Favia</i> <i>Prionastrea</i>	<i>Plesiastrea</i> <i>Favia</i>	<i>Favia</i>	<i>Plesiastrea</i> <i>Favia</i>	<i>Plesiastrea</i> <i>Favia</i>	Family Faviidae
			<i>Aphrastraea</i> <i>Goniastrea</i>	<i>Aphrastraea</i> <i>Goniastrea</i>	<i>Goniastrea</i>	<i>Favites</i> <i>Goniastrea</i>	<i>Favites</i> <i>Goniastrea</i>	
<i>Monticularia</i>	<i>Monticularia</i>	<i>Monticularia</i>	<i>Hydnophora</i>	<i>Hydnophora</i>	<i>Hydnophora</i>	<i>Hydnophora</i>	<i>Hydnophora</i>	
<i>Meandrina</i>	<i>Meandrina</i>	<i>Meandrina</i>	<i>Coeloria</i> <i>Leptoria</i>	<i>Coeloria</i> <i>Leptoria</i>	<i>Coeloria</i> <i>Platygyra</i>	<i>Platygyra</i> <i>Leptoria</i>	<i>Platygyra</i> <i>Leptoria</i>	
—	—	<i>Caulastrea</i>	<i>Oulophyllia</i> <i>Caulastrea</i>	— <i>Caulastrea</i>	<i>Oulophyllia</i> <i>Caulastrea</i>	<i>Oulophyllia</i> <i>Caulastrea</i>	<i>Oulophyllia</i> <i>Caulastrea</i>	
			<i>Dasphyllia</i>					

Table 2. Recent evolution of the suprageneric classification (Faviidae and Trachyphylliidae).

genera	Vaughan & Wells 1943	Wells 1956	Chevalier 1971, and present study
<i>Diploastrea</i>	Fam. <i>Agathiphylliidae</i>		
<i>Echinopora</i> <i>Leptastrea</i> <i>Cyphastrea</i> <i>Montastrea</i>	Subfamily <i>Montastreinae</i>	Subfamily <i>Montastreinae</i>	
<i>Plesiastrea</i> <i>Favia</i> <i>Favites</i> <i>Goniastrea</i> <i>Hydnophora</i> <i>Platygyra</i> <i>Leptoria</i> <i>Oulophyllia</i> <i>Caulastrea</i>	Subfamily <i>Faviinae</i>	Subfamily <i>Faviinae</i>	Family <i>Faviidae</i>
<i>Moseleya</i> <i>Trachyphyllia</i>		Subfamily <i>Trachyphyllinae</i>	Family <i>Trachyphylliidae</i>

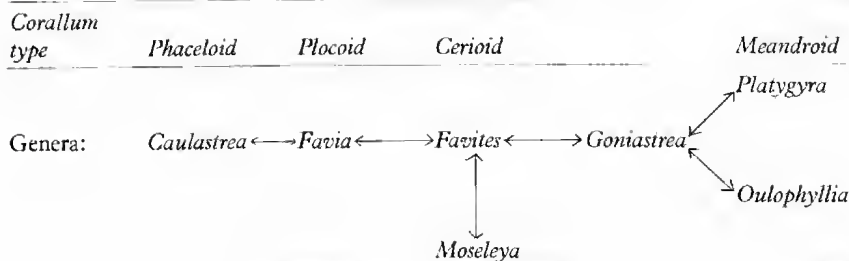
genera and species, both modes of budding are present, one of them usually being dominant. This supports Chevalier's conclusion that there are no grounds for establishing two separate subfamilies, Faviinae and Montastreinae (Table 2). Typical examples of this situation are *Favia laxa* (Klunzinger), *Favites pentagona* (Esper) and *Montastrea valenciennesi* (Edwards & Haime), all formerly belonging to the subfamily Faviinae, although displaying to some extent extratentacular budding conditions. (The extratentacular budding is dominant in the latter species, which is accordingly placed in the genus *Montastrea* in this paper.)

Verrill (1901) established a Subfamily Trachyphylliinae for two recent Indo-Pacific genera *Trachyphyllia* and species incorrectly referred to *Callogyra*. Although Verrill's criteria for establishing a new Subfamily were largely inappropriate, the isolation of these two genera turns out to be justified. Yabe, Sugiyama & Eguchi (1936) incorporated *Caulastrea* and the fossil genus *Antillophyllia* (= *Trachyphyllia*) in Verrill's Trachyphylliinae, which was also raised to the rank of Family. The characteristics of trachyphylliid corals were correctly but incompletely defined by Wells (1956) who, however, included *Moseleya* in his Trachyphylliinae. Both *Caulastrea* and *Moseleya* are now considered as members of the Family Faviidae. After these amendments, the remaining trachyphylliid corals display marked differences in septal structure and ornamentation from all other Faviidae. They are therefore considered as a distinct Family, following Chevalier's (1975) treatment.

Within the Faviidae, a number of genera are without well defined limits owing to their variability, the range of which extends from one genus to another. Generic distinctions become difficult, particularly in the group *Favia/Favites/Goniastrea*. The separation between the former two is mainly based on the corallum morphology, plocoid for *Favia* and cerioid for *Favites*. However, a number of species of *Favites* (e.g. *Favites rotundata* and *Favites complanata*) often display plococerioid conditions. This was the reason put forward by Matthai (1914) for accepting only one genus, *Favia*, for the species commonly referred either to *Favia* or *Favites*. Matthai's understanding of *Favia* was even larger than this, for it also included (regardless of the dominant extratentacular budding) *Favia solidior* and *Favia versipora*, which are presently referred to the genera *Montastrea* and *Plesiastrea* respectively. Such examples serve to illustrate the necessity of relying upon several skeletal features to define the lower taxa.

In the same way, the distinction between *Favites* and *Goniastrea* may also be unclear. Basically, *Favites* has no internal septal lobes arranged in a separate fan-system, whereas in *Goniastrea* there are multitrabecular paliform lobes organised in one, or even several, divergent fan systems, distinct from the fan system of the septum itself. Within some species this distinction is not clear; thus *Goniastrea palauensis* was described as a *Favia* by Yabe, Sugiyama & Eguchi (1936), then tentatively placed in *Goniastrea* by Chevalier (1971), and placed in *Favites* by Wijsman-Best (1972). It may also be noted that within the same species, the structure of the internal septal lobes may vary from simple tall monotrabecular spines to true pali.

Within this group of species, there is also some similarity between the meandroid *Goniastrea* species and *Oulophyllia*, and between *Oulophyllia* and *Platygyra*. These affinities broadly correspond with various stages of a continuous series in the corallum growth-form, as follows:



This does not necessarily imply a corresponding phylogenetic relationship between these genera, although it is likely that these would follow a similar pattern.

Of the remaining genera of the Faviidae, most are comparatively well defined (*Leptoria*, *Hydnophora*, *Diploastrea*, *Cyphastrea*, *Leptastrea* and *Echinopora*). By contrast, *Montastrea* and *Plesiastrea* have always been at the centre of a taxonomic debate. One of the many reasons for this is that *Montastrea* itself has a complex taxonomic history, which involves the generic names *Orbicella* Dana, *Heliastrea* Edwards & Haime, and *Favia* Oken, as well as many species names. Another reason is that Vaughan & Wells (1943) and Wells (1956) denied the existence of *Montastrea* in the Indo-Pacific, thereby maintaining the long existing confusion not only between these genera, but also among their species. It was not until 1971 that Chevalier clarified this problem by pointing out that *Plesiastrea* has true pali, composed of a multitra-becular, independent, diverging system, and that this, together with an apparent lack of direc-tive mesenteries in *Plesiastrea* polyps, is a sufficient basis on which to distinguish these genera.

The present understanding of these genera has led us to consider the former *Favia valenciennesi* (Edwards & Haime) (already removed from *Favia* and put into *Plesiastrea* on the basis of budding conditions by Rosen, 1968) as a probable *Montastrea*. Conversely, Wells' *Plesiastrea russelli* (1954) is presently included in the genus *Favites*.

The vast majority of species of the Faviidae have massive or thickly encrusting plocoid, cerioid or meandroid colonies. The only notable exceptions are, as already mentioned, in the genera *Echinopora* (lamellar to ramose branching), *Carulastrea* (phaceloid) and *Hydnophora* (branching). This tendency towards massive growth forms appears to be linked with the capacity of the Faviidae to occupy a maximum diversity of biotopes. Thus, *Favia pallida* and *Cyphastrea serailia* may frequently have a very great depth range and have been dredged from 88 and 91m respectively; and conversely, *Platygyra sinensis* and *Goniastrea aspera* may frequently be observed to withstand regular emersions of several hours daily. Likewise, most Faviidae have a wide geographic distribution, and the majority of the genera and species extend throughout the whole Indo-Pacific province. They are not, however, as widely distributed as some genera, such as *Porites* and *Pocillopora*, and are rare or absent from marginal belts such as Hawaii, Marquesas, the south African coast and the eastern Pacific region.

Out of the sixty-three species considered in this paper, about half extend from the Red Sea to the western Pacific, and some have been recorded as far as the Gambier Islands (S.E. Tuamotus). On the other hand, there is a group of species which seems to be restricted to the eastern Indian Ocean and western Pacific. Some of these, however, may be more widespread than indicated in this study because of their variability or because of taxonomic problems reflecting regional skeletal variation. However, it should be noted that latitudinally, the Faviidae are also widespread, with a number of species living in the warm Kuroshio current along the coast of Honshu (Japan), as far as 33° N lat. However, *Plesiastrea versipora* is exceptional in being a truly eurythermic species, spreading between 33° 47' N lat. (Tanabe-Wan, Japan) and 39° S lat. (Bass Strait, Australia), thereby encountering an annual mean surface temperature range between approximately 28°C (equatorial regions) and approximately 16°C (Bass Strait), with minimum temperatures of 12°C or less.

Another striking feature of the distribution of the Faviidae is the inversion in the relative abundance of some related species between the Red Sea — western Indian Ocean and the western Pacific. For instance, *Echinopora gemmacea*, *Montastrea annuligera* and *Cyphastrea micropithabna* are more abundant in the Red Sea and western Indian Ocean than are *Echinopora lamellosa*, *Montastrea curta* and *Cyphastrea serailia* (Crossland, 1952 has already mentioned the example of *Cyphastrea*). The reverse is the rule in the western or central Pacific.

The Faviidae is a very old group, extending back to the middle Jurassic (Fig. 3) and clearly this long, relatively stable history is an important factor in its modern zoogeographical and habitat distribution.

The present volume is the second part of *Scleractinia of eastern Australia*. It is based on a study of approximately 3600 specimens combined with extensive field studies throughout

the region. The reader is referred to the first volume for the general introduction, methods and listing of the principal collecting stations 1-60, all of which are applicable to the present volume.

Except where noted in the text, synonymies listed are based on extensive re-examination of all available type material affecting the validity of species names used, including all available junior synonyms considered valid in taxonomic publications of this century. Older type specimens which do not have taxonomic validity were studied only where questions of historical significance were involved. The synonymies of the nominal species given in this paper are therefore largely based on the researches of earlier taxonomists and, where indicated, contemporary studies.

II

Principal Collecting Stations

Principal collecting stations used in the present study are those listed in Part I of *Scleractinia of eastern Australia*, together with those listed below. As noted in Part I, one or several biotopes are present at any one collecting station. Individual biotopes are not described.

All collections from the stations below were made with SCUBA.

OUTER REEFS INCLUDING BARRIER REEFS

Further detail of these collecting stations is given in Veron & Hudson (1977) and Veron (1977).

Biotopes of reef fronts

1-4. *see Part I*

61. *Jewell Reef* (Fig. 2); outer slope, exposed to strong wave action, steeply sloping, cemented reef rock substrate; two collections at 1-6m and two at 10-20m below reef front.

Biotopes of reef flats and very shallow lagoons

5, 6. *see Part I*

62. *Waining Reef* (Fig. 2); reef flat, exposed to tidal currents and slight wave action, sand and rubble substrate; one collection, 2-5m.

63. *Ribbon Reef* (Fig. 2); reef flat lagoon, protected from currents and wave action, substrate of reef rock on sand; one collection, 1-5m.

Biotopes of reef backs

7-10. *see Part I*

64. *A plug reef S of Ribbon Reef, N side* (Fig. 2); back reef margin, partly exposed to currents and wave action, substrate of reef rock; one collection, 2-10m.

65. *Ribbon Reef, S end* (Fig. 2); back reef margin, partly exposed to currents and wave action, substrate of reef rock; one collection, 5-15m.

66. *Jewell Reef* (Fig. 2); back reef margin, well protected, substrate of reef rock and sand, one collection, 12m.

INNER REEFS AND ASSOCIATED CAYS AND LAGOONS

Biotopes of semi-enclosed lagoons

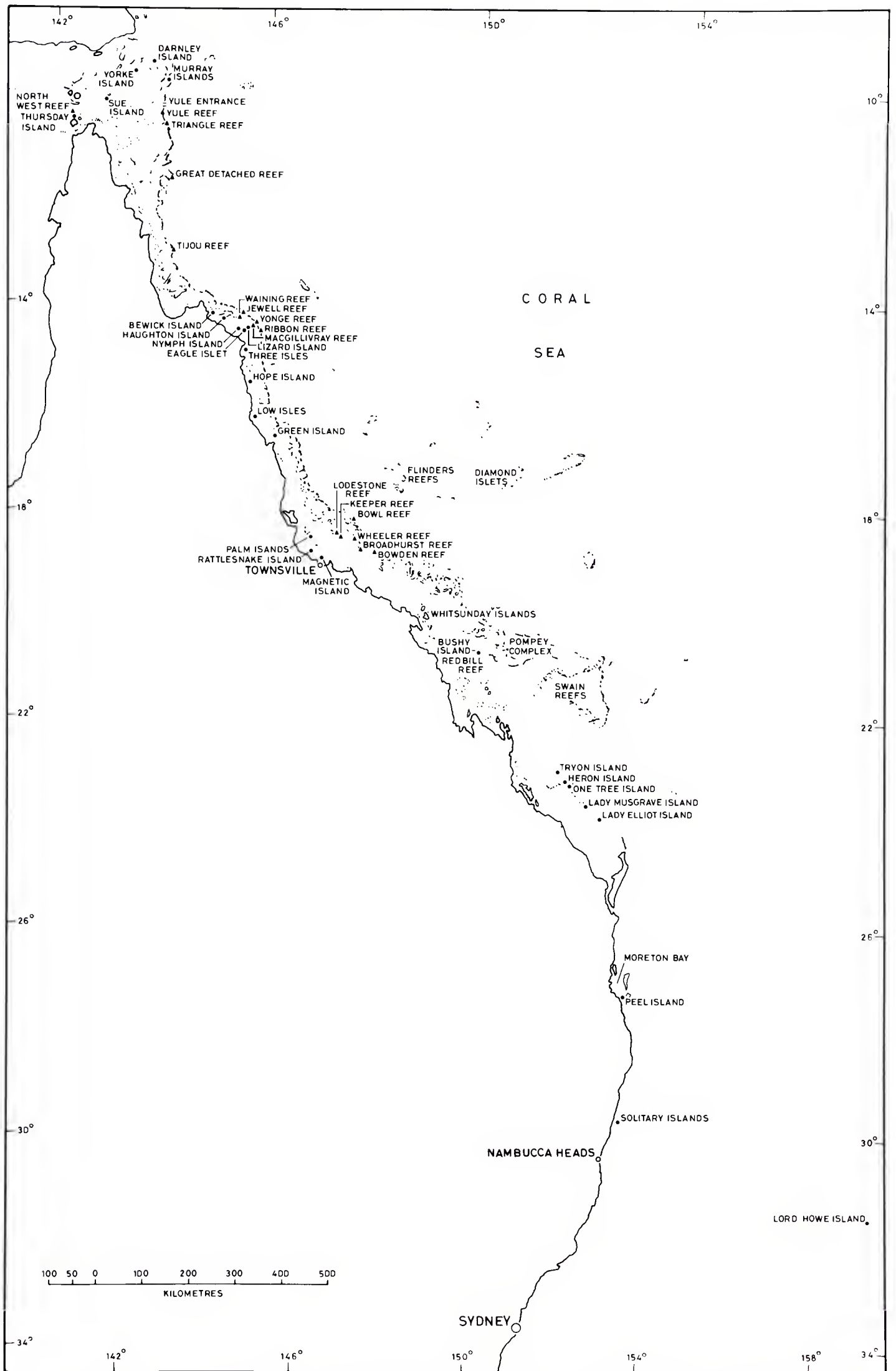
11, 12. *see Part I*

67. *Swain Reefs, 21° 30' S lat. 152° 25' E long.*; protected, substrate of reef rock merging onto sandy floor; one collection, 3-8m.

68. *Swain Reefs, 21° 30' S lat. 152° 25' E long.*; protected, substrate of soft sand; one collection, 3-10m.

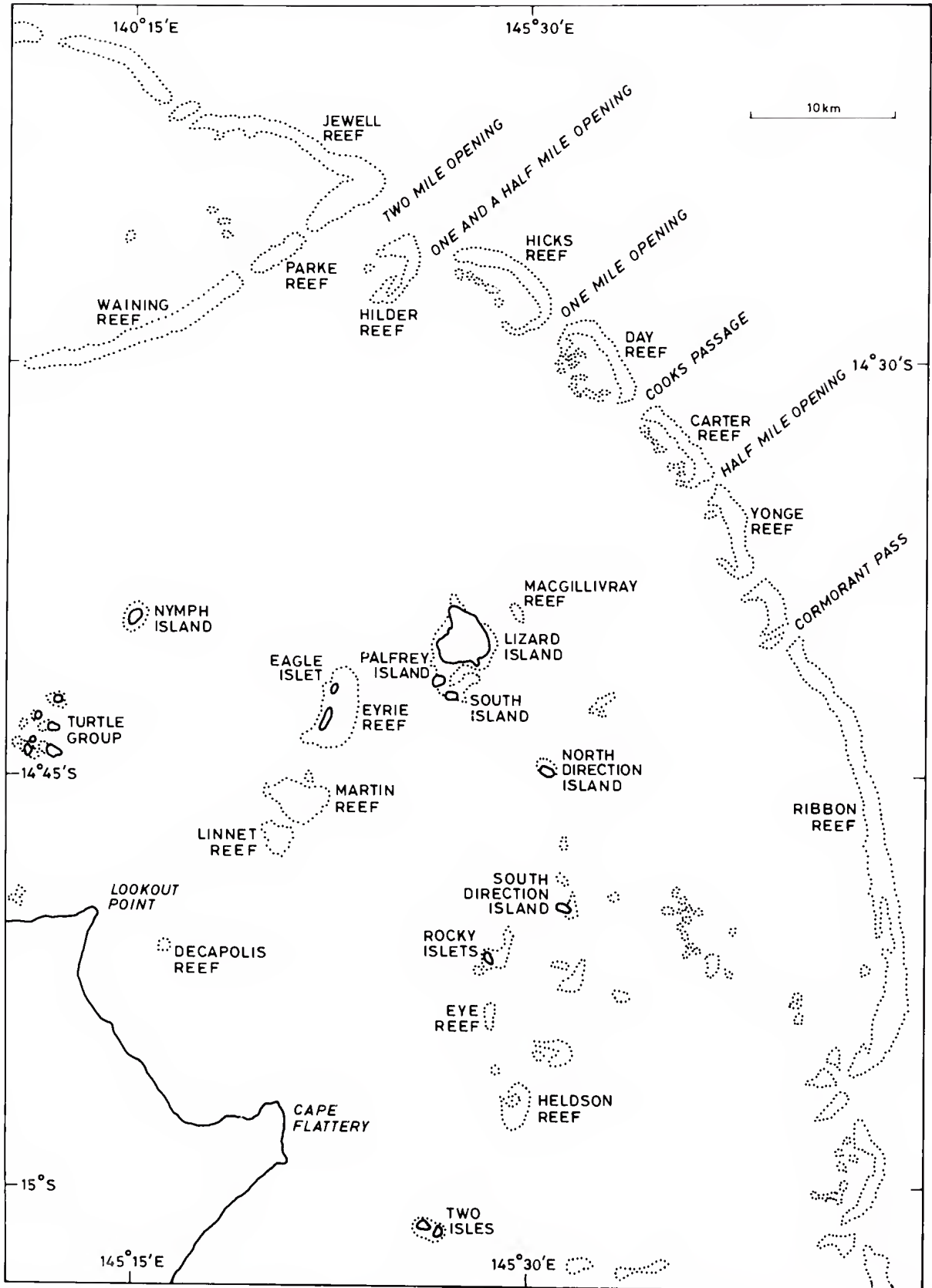
69. *Swain Reefs, 21° 50' S lat. 151° 48' E long.*; partly protected entrance to lagoon, exposed to currents, substrate of reef rock; two collections, 5-14m.

70. *Pompey Complex, SE end*; protected lagoon, substrate of sand; one collection, 2-5m.



71. *Pompey Complex*; partly protected lagoon, exposed to tidal currents, reef rock and sand substrate; two collections, 5-10m.
72. *Pompey Complex*; small, partly protected circular lagoon, exposed to tidal currents, substrate of sand and mud; one collection, 2-20m.
73. *Bushy Island-Redbill Reef*; large, protected lagoon, substrate of reef rock and soft sand; two collections, 2-5m.

Fig. 2 Lizard Island and surrounding islands and reefs.



Biotopes of sloping reef areas

13-16. *see Part I*

Biotopes of reef backs

17-22. *see Part I*

74. *MacGillivray Reef* (Fig. 2); semi-protected, substrate of broken reef rock merging onto sand; one collection, 3-12m.

75. *Reef 8 km W of Pompey Reef*; semi-protected, substrate of reef rock merging onto sand; one collection, 5-10m.

76. *Swain Reefs, 21° 12' S lat. 152° 34' E long., NW side*; protected back reef margin; one collection, 5-15m.

77. *Swain Reefs, 21° 07' S lat. 142° 46' E long.*; protected back reef margin; one collection, 2-8m.

78. *Swain Reefs, same reef as 77, W end*; semi-protected, substrate of reef rock merging onto sand; one collection, 5-16m.

79. *Swain Reefs, 21° 30' S lat. 152° 25' E long.*; semi-protected back reef margin, substrate of reef rock merging onto sand; two collections, 3-12 and 3-10m.

80. *Bushy Island-Redbill Reef, N end*; dissected back reef margin with associated small reef patches, exposed to strong tidal currents, adjacent to deep water, protected from strong wave action; three collections, 5-12m.

81. *Frigate Cay, Swain Reefs, NW side*; back reef margin, exposed to strong tidal currents, protected from strong wave action; four collections, 3-10m (x 3), 10-25m.

HIGH ISLANDS

Biotopes of sandy or partly sandy flat ocean floor

23-25. *see Part I*

Biotopes of the front of fringing reefs

26-40. *see Part I*

82. *Between Bird Islet and South Island* (Fig. 2); fully exposed to trade winds, substrate of steeply sloping reef rock merging onto sand; two collections, 4-5m and 10m.

83. *Barber Islet, Palm Islands, NE side*; exposed to trade winds, substrate of reef rock merging onto sand; one collection, 5-22m.

Biotopes of intertidal and sub-intertidal mud flats

41-43. *see Part I*

84. *Maude Bay, Magnetic Island*; intertidal mud flat; one collection.

85. *Florence Bay, Magnetic Island*; sub-intertidal mud flat; one collection

86. *Bushy Island-Redbill Reef*; intertidal mud flat; one collection.

Biotopes of the zone of coral growth on the protected side of high islands

41-43. *see Part I*

87. *Nymph Island* (Fig. 2); partly protected, substrate of reef rock and soft sand; one collection, 2-8m.

88. *Chinaman's Head, Lizard Island* (Fig. 2); protected, substrate of reef rock and sand; two collections, 2-5m.

89. *Headland between Watson's Beach and Aborigine Beach, Lizard Island* (Fig. 2); protected, substrate of reef rock and sand; one collection, 0-15m.

90. *Pelorus Island, Palm Islands, W side*; protected, substrate of reef rock merging onto soft sand; two collections, 3-15m.

91. *Pioneer Bay, Orpheus Island, Palm Islands, N end*; very protected, substrate of reef rock merging onto mud; two collections, 2-12m.

92. *Great Palm Island, NW side*; very protected, substrate of reef rock merging onto soft sand; two collections, 2-5m.
93. *Barber Islet, Palm Islands, NE side*; protected, substrate of reef rock merging onto soft sand and mud; one collection, 5-20m.
94. *Between Haslewood and Whitsunday Islands*; protected from wave action but exposed to very strong tidal currents; one collection, 3-8m.
95. *Whitehaven Bay, Whitsunday Island*; protected, substrate of sand and mud; two collections, 5-20m.
96. *Cateran Bay, Border Island, Whitsunday Islands*; protected, vertical reef face undercut with caves; two collections, 2-20m.
97. *Nara Inlet, Hook Island, Whitsunday Islands, S side of entrance*; partly protected, substrate of coral, reef rock and sand; nine collections, 3-12m.
98. *Butterfly Bay, Hook Island, Whitsunday Islands*; protected, irregular reef face with caves; four collections, 2-14m.

Lagoons of high islands

99. *Lizard Island lagoon, between South Island and Palfrey Island (Fig. 2)*; protected, substrate of reef rock and coral rubble merging onto sand; three collections, 0-7m.
100. *Lizard Island lagoon, SW entrance near Bird Islet (Fig. 2)*; protected, substrate of reef rock and coral rubble merging onto soft sand and mud; two collections, 2-15m.

Biotores of muddy ocean floors

44-46. *see Part I*

101. *Cateran Bay, Border Island, Whitsunday Islands*; very protected, soft mud; one collection, 6-12m.
102. *Happy Bay, Long Island, Whitsunday Islands*; very protected, soft mud; two collections, 3-7m.

The upper continental slope

47, 48. *see Part I*

Tidal channels between reefs exposed to currents

49-52. *see Part I*

94. *see above*

103. *Pompey Complex, SW side*; protected from wave action, exposed to moderate tidal currents, substrate of reef rock and sand; one collection, 5-10m.
104. *Pompey Complex, W side of a major channel*; protected from wave action, exposed to very strong tidal currents; substrate of consolidated reef rock; two collections, 1-15m.
105. *Pompey Complex, W side of a major channel near seaward exit*; partly protected from wave action, exposed to very strong tidal currents, substrate of consolidated reef rock and coarse sand; one collection, 5-10m.

Sea-grass beds; rugged walls of high islands; semi-protected sand and rubble banks; miscellaneous.

53-60. *see Part I*

III

Family Faviidae Gregory, 1900

GENUS *CAULASTREA* DANA, 1846

Generic synonymy

Caulastrea (*pars*) Dana, 1846; Edwards & Haime (1848); Matthai (1928); Yabe, Sugiyama & Eguchi (1936); Crossland (1952); Nemenzo (1959); Wijsman-Best (1972)

Dasyphyllia Edwards & Haime (1849).

Type species *Caulastrea furcata* Dana, 1846.

Ever since the genus *Caulastrea* was described by Dana, there has been some confusion concerning its limits and relations, in particular with *Eusmilia* and *Euphyllia*, and with the Mussidae. Dana himself, in his original description, included the species *Caulastrea undulata*, which is certainly a *Eusmilia*, and in consequence, subsequent authors such as Edwards & Haime (1848), Duncan (1884), Quelch (1886) and Ortmann (1888) did not gain a clear understanding of the genus *Caulastrea*.

Excellent reviews of the question by Matthai (1928) and Yabe & Sugiyama (1931), together with Vaughan & Wells' revision (1943), clarified the situation in a definitive manner. However, Crossland (1952) described a new species of *Caulastrea* from the Great Barrier Reef, which certainly does not belong to this genus, and he himself pointed out its affinities with the family Mussidae and with *Parasmilia*, thus reverting to the confusion prior to Matthai (1928). Despite Crossland's opinion, it is considered that, in the light of the above-mentioned studies, *Caulastrea* appears to be a well-defined genus and the question of its relationships with genera of other families is not relevant.

As far as growth form is concerned, Wells (1954) mentioned that within the Subfamily Faviinae (as it was originally understood by Vaughan & Wells, 1943), there is a continuous series, composed of the following genera: *Caulastrea* (phaceloid), *Bikiniastrea* (subdendroid), *Barabattoia* (subplocoid), *Plesiastrea* (plocoid).

This situation is now considered to be artificial, the subdendroid and subplocoid forms being largely environmentally-induced ecomorphs of species which normally have a plocoid growth form (discussed below p. 32). Thus, *Caulastrea* stands well apart from all other Faviidae, with no genera clearly representing growth forms intermediate between phaceloid and plocoid.

Within the Family Faviidae, as it stands at present, *Caulastrea* (and in particular *Caulastrea tumida* Matthai, the type of which comes from N.W. Australia) has strong affinities with *Astraeosmilia* Ortmann, which is typically subplocoid.

Caulastrea echinulata (Edwards & Haime, 1849)

Synonymy

Dasyphyllia echinulata Edwards & Haime, 1849; Edwards & Haime (1857); Ortmann (1888).

Caulastrea echinulata (Edwards & Haime, 1849); Matthai (1928); Nemenzo (1959); Wijsman-Best (1972).

Caulastrea aiharai Yabe & Sugiyama, 1935; Yabe, Sugiyama & Eguchi (1936).

Material studied

Yonge Reef, Palm Islands (4 specimens).

These localities include collecting stations 9, 36, 90.

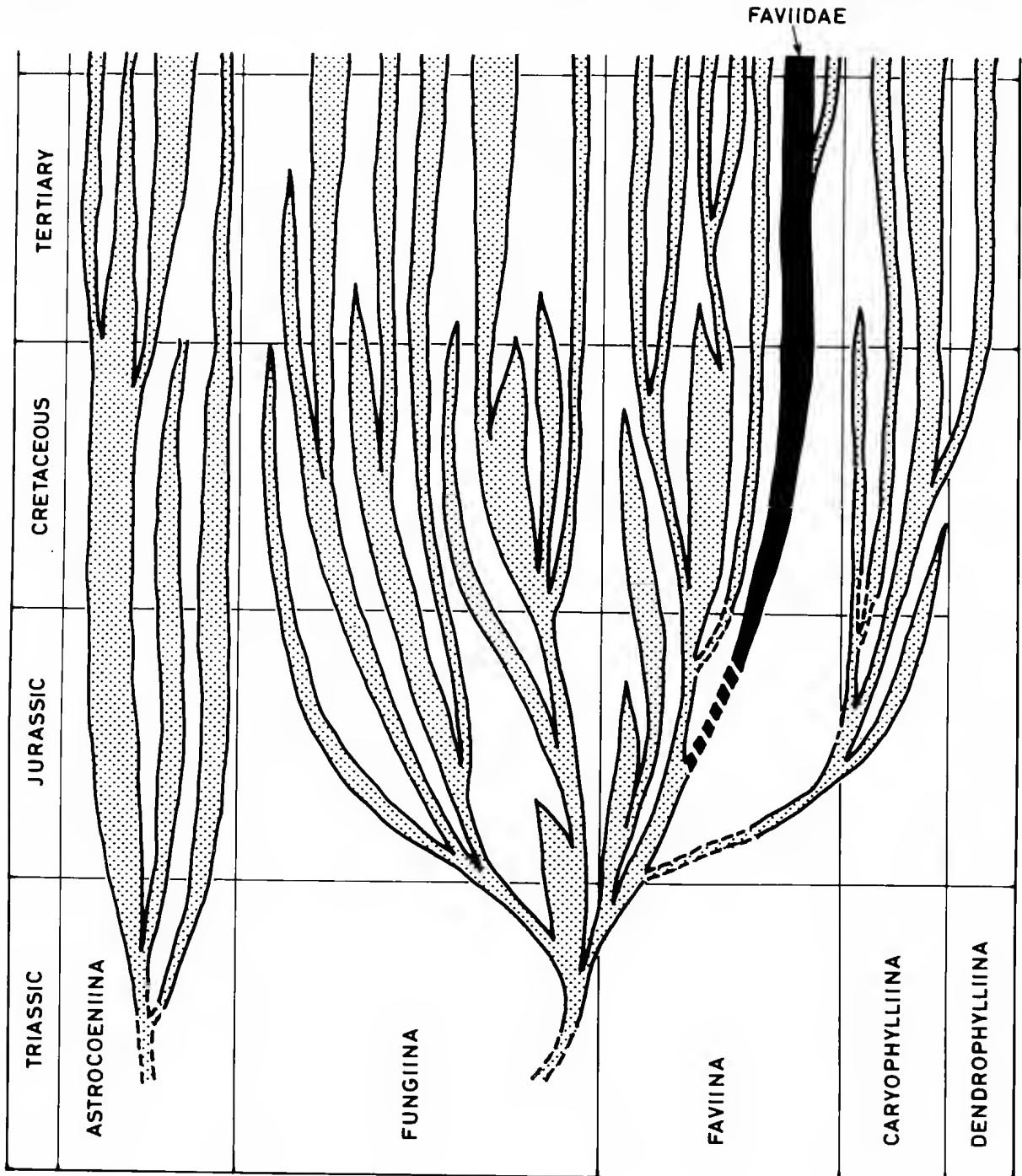
Previous records from Eastern Australia

Not previously recorded.

Characters

The growth form is typically phaceloid, with parallel branches remaining close to each other (6-8mm apart, on average) (Figs. 4, 5). The corallites are mostly monocentric, although some in the process of division are dicentric. Monocentric corallites are generally oval in outline, with an average diameter of 10-12mm. Some are laterally compressed, with flattened sides giving a triangular appearance.

Fig. 3 Evolutionary pattern of the Scleractina after Wells, 1956 with the family Faviidae indicated in black.



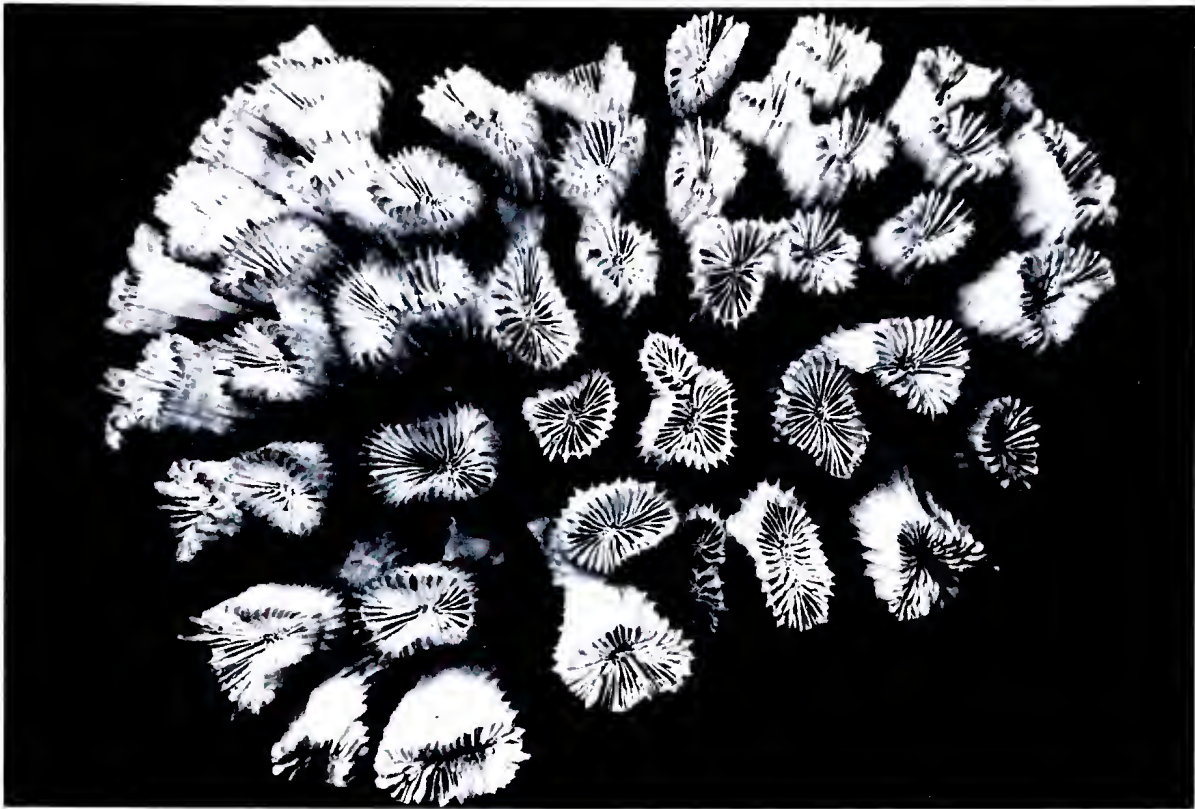


Fig. 4 *Caulastrea echinulata* from Electra Head, Great Palm Island, collecting station 36 ($\times 1.0$), a general view of a corallum from above showing branches close together and the division of the corallites.

Fig. 5 *Caulastrea echinulata* from the Palm Islands.





Fig. 6



Fig. 7



Fig. 8



Fig. 9

The corallite wall is thin. The number of septa ranges from twenty-four to thirty-six, depending upon the size of the corallites. Septa are markedly exsert (up to 2mm) above the common wall. Up to eighteen septa reach the columella. In some cases, the inner margins of the secondary septa meet with the sides of the primary ones. The septal margin is irregularly lobed, covered with minute, acute dentations. The lower and innermost septal lobe sometimes takes the appearance of a paliform lobe. The sides of the septa bear scattered conical spines. The columella is composed of a few flattened, twisted trabeculae. Uneven, irregular costae are present, bearing small, irregular spines.

Affinities

Only four specimens in the present collection are attributed to this species. Both are close to the type and are distinguished from *C. furcata* primarily by their compact mode of branching. However, *C. echinulata* has not been recognised as a distinct species underwater and its validity has yet to be clearly established.

Distribution

Recorded from Straits of Malacca, Singapore, Philippines, Ryukyu, New Caledonia, Great Barrier Reef.

Figs. 6-10 *Caulastrea furcata*

- Figs. 6, 7 From Sue Island, collecting station 17, showing side and top views of the same corallum respectively. Compare with *C. curvata* (Fig. 12) from the same biotope ($\times 1.0$).
- Figs. 8, 9 From Elk Cliff, Great Palm Island, collecting station 37, showing side and top views of the same corallum respectively ($\times 1.0$).
- Fig. 10 From Frigate Cay, collecting station 81, showing appearance of polyps when expanded and contracted ($\times 2.0$)



Caulastrea furcata Dana, 1846

Synonymy

Caulastrea furcata Dana, 1846; Edwards & Haime (1857); Matthai (1928); Yabe & Sugiyama (1932, 1935); Eguchi (1935); Yabe, Sugiyama & Eguchi (1936); Crossland (1952); Stephenson & Wells (1955); Nemenzo (1959); Wijsman-Best (1972); Pillai, Vine & Scheer (1973).

Caulastrea distorta Dana, 1846; Edwards & Haime (1857); Quelch (1886); Ortmann (1888).

Material studied

Yorke Island, Murray Islands (2 specimens), **Sue Island** (2 specimens), **Palm Islands** (19 specimens), **Whitsunday Islands** (6 specimens), **Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex, Swain Reefs** (13 specimens).

These localities include collecting stations 13, 17, 22, 27, 28, 34, 35, 36, 37, 42, 55, 56, 67, 68, 69, 71, 76, 79, 80, 81, 97, 98, 102.

Previous records from Eastern Australia

Lizard Island, Yonge (1930); **Low Isles**, Yonge, Yonge & Nicholls (1932), Crossland (1952), Stephenson & Wells (1955); **Palm Islands**, Matthai (1928).

Characters

Colonies are phaceloid, with branches generally diverging (Figs. 6-10). The branches are 10 to 15mm apart at their extremities. Most corallites are monocentric, circular or oval in outline, with an average diameter of 9.5mm. During division, the corallites tend to have a triangular shape, with flattened sides. The walls are thin, with first order septa very exsert (up to 2-3mm for the principal ones). There are about thirty-two septa in single corallites, of which sixteen to eighteen reach the columella. Septal margins are irregularly dentate. The costae are strongly developed, particularly in the upper edge zone, but can be followed downwards along the branches for some distance. The columella is generally well developed, and is composed of twisted trabeculae.

Living colonies are brown with bright green centres (Fig. 414).

Skeletal variation

Although colonies remain typically phaceloid, there are continuous variations in the angle of branching, in the length of branches before division, and in the distance between branches. There is also variation in the shape of the terminal branches, which can be dilated, cylindrical or even slightly constricted.

Corallites may be shallow, almost superficial, to about 6mm deep. The inner margins of the septa in some specimens (particularly those with shallow corallites) slope regularly and gently towards the columella. In others, the inner margin is vertical down to about half the height of the septa, then joins the columella.

The length of the edge zone is highly variable, from 1 to 5cm, and *C. furcata* is not therefore necessarily characterised by its large edge zone, as has frequently been suggested. Indeed, Matthai (1928) wrote about Dana's holotype, 'The edge zone seems to have extended down to 10 to 12mm', and the same author even quotes 8mm as the edge zone length for a specimen from Fiji in the Museum of Comparative Zoology, Harvard University.

Distribution

Seychelles Islands, Maldives Islands, China Sea, Great Barrier Reef, New Caledonia, Solomon Islands, Philippines, Palau, Ryukyu, Fiji, Tongatabu.

Caulastrea curvata Wijsman-Best, 1972

Synonymy

Caulastrea curvata Wijsman-Best, 1972.

Material studied

Sue Island (2 specimens), **Ribbon Reef, Low Isles, Lodestone Reef, Palm Islands** (9 specimens), **Whitsunday Islands** (4 specimens).

These localities include collecting stations 12, 17, 34, 42, 43, 45, 57, 59, 65, 90, 93, 97, 102.

Previous records from Eastern Australia

Not previously recorded.

Characters

The corallum is phaceloid, with branches diverging, 10 to 20mm apart. The average diameter of the branches is 8mm at most. These conditions give the corallum a lax appearance (Fig. 11) contrasting with the more compact habit of *C. echinulata* and *C. furcata*. In some colonies, the extremities of a few branches, particularly at the periphery of the corallum, are curved upwards, inwards or sideways (Fig. 12).

The corallites have thin walls. The number of septa varies from 14 to 31 (with an average of 24) in single corallites. Septa are about 2mm exsert above the wall (up to 4mm for the principal ones). Their inner margin is dentate, sometimes with a well marked paliform lobe in the lower part. The septal sides bear small scattered granules. The columella is not well developed, being composed of loosely twisted trabeculae. The edge zone is variable in length, but is generally well developed. It can be only 15-20mm in some specimens or extend below the junction of adjacent branches in others. Costae are well marked over the whole length

Figs. 11-12 *Caulastrea curvata* ($\times 1.0$).

Fig. 11 From Pelorus Island (Palm Islands), collecting station 90, showing a corallum with a characteristically lax branching pattern.

Fig. 12 From Sue Island, collecting station 17, showing curving of branches at the corallum periphery.



Fig. 11

Fig. 12

of the edge zone, and are covered with minute, acute spines. Intercostal ridges are distinctly present in some specimens.

Living colonies are pale brown, sometimes with green oral discs. They are usually less brightly coloured than those of *C. furcata*.

Affinities

As pointed out by Wijsman-Best (1972), *C. curvata* has strong affinities with *C. furcata*. In particular, colonies of *C. curvata* with thicker branches come close, in general aspect, to those specimens of *C. furcata* which have branches relatively far apart and of relatively small diameter. The two species can still be separated, however, by the average diameter of the corallites and the number of septa (both smaller in *C. curvata*) and to a certain extent by the costae, uniformly developed along the branches, but less prominent in *C. curvata*. The other distinctive characters mentioned by Wijsman-Best (curved end of the branches, more exsert septa and colour of the polyps) seem less reliable. The two former are not constant, and the colour pattern described for *C. curvata* also exists in *C. furcata*.

Distribution

New Caledonia, Great Barrier Reef.

***Caulastrea tumida* Matthai, 1928**

Synonymy

Caulastrea tumida Matthai, 1928; Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936).

Caulastrea yokoyamai Yabe & Sugiyama, 1931.

Caulastrea multiseptata Yabe & Sugiyama, 1931.

Caulastrea tumida multiseptata Yabe & Sugiyama, 1935; Yabe, Sugiyama & Eguchi (1936).

Caulastrea tumida conglobata Yabe & Sugiyama, 1935; Yabe, Sugiyama & Eguchi (1936).

Material studied

Yonge Reef (2 specimens), collecting station 9, **Lizard Island, Palm Islands.**

Previous records from Eastern Australia

Not previously recorded.

Characters

The growth form is phaceloid, as in the other species of this genus. All four specimens of the present series have comparatively short, thick branches (Figs 13-15). The younger and smaller corallites are circular in outline, but fully developed ones tend to be oval or even triangular. A number of them are in the process of division, showing mono- to tristomodaeal budding conditions. Circular corallites have a diameter of 10 to 12mm, and the dimensions of oval ones average 10 to 12 x 15mm. Walls are 1.5 to 2mm thick. The number of septa varies from thirty-two to sixty with an average of forty-two per corallite. Septa are slightly exsert (up to 2mm for the principal ones). These are markedly thickened close to the wall. Septal dentations are well developed, in particular in the lower half of the septal inner margin. The columella is trabecular and well developed. The edge zone varies from 10 to 35mm in length, although the present specimens are all short-branched and thus the probable length of the edge zone is not indicated. Costae tend to be more developed towards the extremities of branches. They are smooth or finely dentate.

The colour of the polyp is brown, with a green oral disc.

Affinities

Matthai (1928) pointed out the following distinctive characters of *C. tumida*: 'Comparatively heavy corallum, large corallites, especially well developed columella

and costae of a uniform nature'. This description applies largely to specimens of the present series, although these do not have uniform costae.

By their number of septa, the specimens of the present series come very close to *C. tumida multiseptata* Yabe & Sugiyama from Honshu and Kyushu (Japan). They also resemble *C. tumida conglobata* Yabe & Sugiyama, which has distinctively short corallites, this latter subspecies being itself close to *C. tumida multiseptata*, as mentioned by Yabe, Sugiyama & Eguchi (1936). Judging from the description and figures of these authors, their subdivision into three subspecies (*gracilis* (or *gracillis*), *multiseptata* and *conglobata*) seems hardly justified. The lack of relevant ecological data does not indicate whether these supposed 'subspecies' represent distinct ecomorphs or not.

Distribution

Madagascar, Maldive Islands, N.W. Australia, Japan (Honshu, Sikoku, Kyushu), Bonin Islands, ? New Caledonia.

Fig. 13-15 *Caulastrea tumida* from Yonge Reef, collecting station 9, ($\times 1.75$), Figs. 13 and 14 showing the side and top views of the same corallum, Fig. 15 the top view of another corallum showing variation in septal arrangement and ornamentation.



GENUS *FAVIA* OKEN, 1815

Generic synonymy

Favia Oken, 1815; Edwards & Haime (1857); Matthai (1914); Vaughan (1918); Vaughan & Wells (1943); Alloiteau (1957); Wells (1956).

Type species *Madrepora fragum* Esper, 1795.

Affinities

Delineation of the genera *Favites* and *Favia* as shown on p. 3 is not at all distinct. Vaughan & Wells (1943) simply noted that *Favites* is 'like *Favia* but cerioid, walls usually septo-thecal' and Wells (1956) that *Favites* is 'like *Favia* but cerioid'. This distinction has been followed by most subsequent authors with the exception of Matthai (1914, 1924), who considered the two genera synonymous, but gave little discussion of them. Several studies, the present one included, have shown that several species of *Favites*, notably *F. rotundata* and *F. complanata*, frequently have cerio-plocoid growth forms and in the present collection some specimens of every *Favites* species show some tendency towards a plocoid habit. Conversely, some *Favia* species, e.g. *F. pallida* and *F. rotumana*, may be completely cerioid. Thus it must be emphasised that the generic designation of *Favia* and *Favites* species is somewhat arbitrary and is likely to lack a true phylogenetic basis. Perhaps the most consistent difference is the nature of the budding, which is usually equal or near-equal in *Favia* and markedly circumferential in *Favites*.

The same may be true of *Goniastrea*, which is separated from *Favites* and *Favia* firstly on the basis that some species show some tendency to meander, and secondly on the basis that purely cerioid species have similar calicular structures to meandroid ones. These calicular structures are mainly septa with fine, regular dentations, and paliform lobes which form a conspicuous crown. Also, *Favia* is characterised by having paliform lobes and septa made up of one uniform fan system, rather than by separate or divided fan systems as in *Goniastrea* (Chevalier, 1971). Wells' (1956) additional characters, i.e. a permanently monocentric corallite and feeble columella, do not apply to several species. Species which show a tendency to have a sub-plocoid growth form are placed in *Favia*; those which do not have conspicuously *Goniastrea*-like septal structures are usually placed in *Favites*. These delineations are not always clear and as the synonymies show, the generic status of many species of *Goniastrea*/*Favites*/*Favia* has been changed one or more times by recent authors.

It may be noted that approximately ten specimens of the present collection cannot be placed in any of the eleven species discussed below. It is possible that these specimens include both *F. speciosa* (Dana) and *F. cf. danae* Verrill. However, neither of these species have been distinguished underwater and it is concluded that if present, they are rare or have a very limited distribution.

***Favia stelligera* (Dana, 1846)**

Synonymy

Madrepora acropora Linnaeus, 1767.

Orbicella stelligera Dana, 1846.

Orbicella orion Dana, 1846.

Parastrea lobata Edwards & Haime, 1850.

Parastrea hombroni Rousseau, 1854.

Favia lobata (Edwards & Haime); Edwards & Haime (1857); Klunzinger (1879); Ortmann (1888).

Favia hombroni (Rousseau); Edwards & Haime (1857); Gardiner (1904); Vaughan (1907); Matthai (1914); Chevalier (1968).

Heliastrea acropora (Linnaeus); Edwards & Haime (1857); Gardiner (1899).

Heliastrea orion (Dana); Gardiner (1899).

Plesiastrea armata Verrill, 1872 = *Astraea (Fissicella) intersepta* Dana, 1846.

Favia acropora (Linnaeus); Matthai (1914, 1948).

Favia stelligera (Dana); Vaughan (1918); Hoffmeister (1925); Crossland (1931, 1935, 1952); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1939, 1940); Wells (1954, 1955b); Ma (1959); Pichon (1964); Scheer (1967); Chevalier (1968, 1971); Rosen (1971); Wijsman-Best (1972, 1974); Scheer & Pillai (1974).

Favia pseudostelligera Hoffmeister 1932; Chevalier (1971).

Vaughan (1918) p. 101 noted that *M. acropora* is not determinable; therefore this name is not available for this species as supposed by Matthai (1914).

In the present series, *F. pseudostelligera* and *F. stelligera* fall into the same range of variations, calicular structures of the former being found at the base of large colonies of the latter or in other situations where corallites have become heavily calcified.

Material studied

Yorke Island, reef NE from **Murray Islands**, **Murray Islands** (4 specimens), **Sue Island** (2 specimens), **Thursday Island**, **Great Detached Reef** (14 specimens), **Tijou Reef** (7 specimens), **Bewick Island** (3 specimens), **Yonge Reef** (9 specimens), **Lizard Island** (3 specimens), **Eagle Reef** (2 specimens), **Low Isles** (4 specimens), **Palm Islands** (7 specimens), **Lodestone Reef**, **Keeper Reef**, **Wheeler Reef** (5 specimens), **Whitsunday Islands**, **Bushy Island-Redbill Reef**, **Pompey Complex** (3 specimens), **Swain Reefs** (7 specimens).

These localities include collecting stations 1, 2, 3, 5, 6, 7, 9, 13, 17, 18, 19, 26, 27, 30, 32, 34, 35, 53, 55, 56, 68, 69, 75, 77, 80, 81, 98, 100, 104.

Fig. 16 A characteristic growth form of *Favia stelligera* ($\times 0.5$).



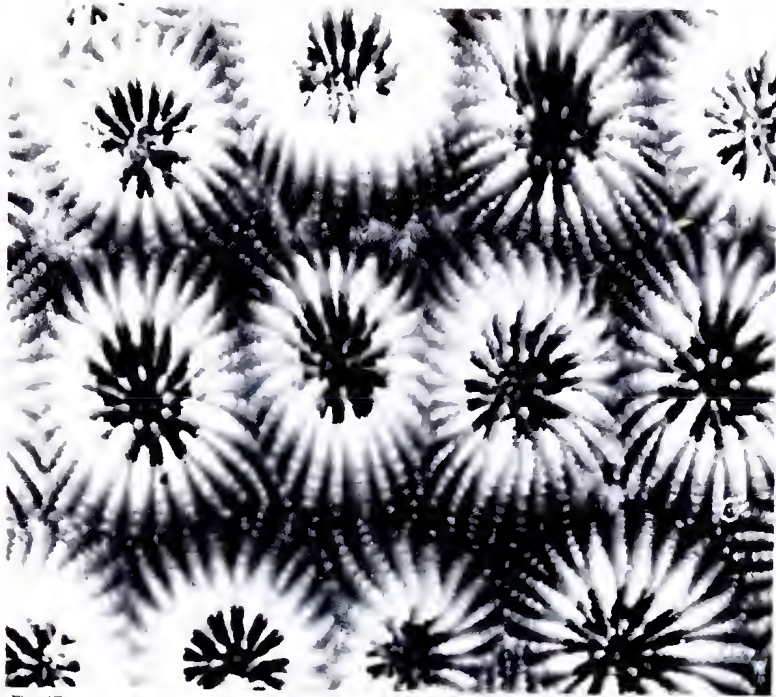


Fig. 17▲

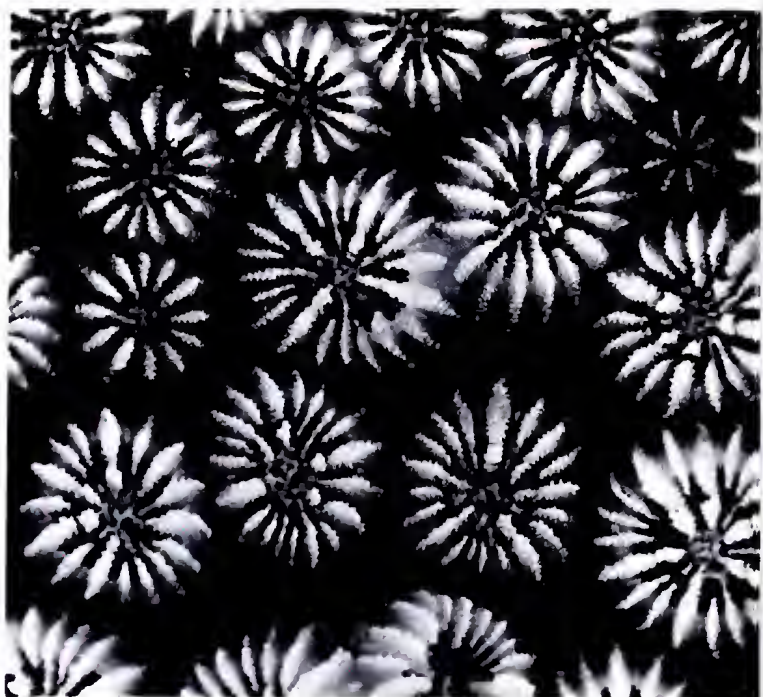


Fig. 18▲

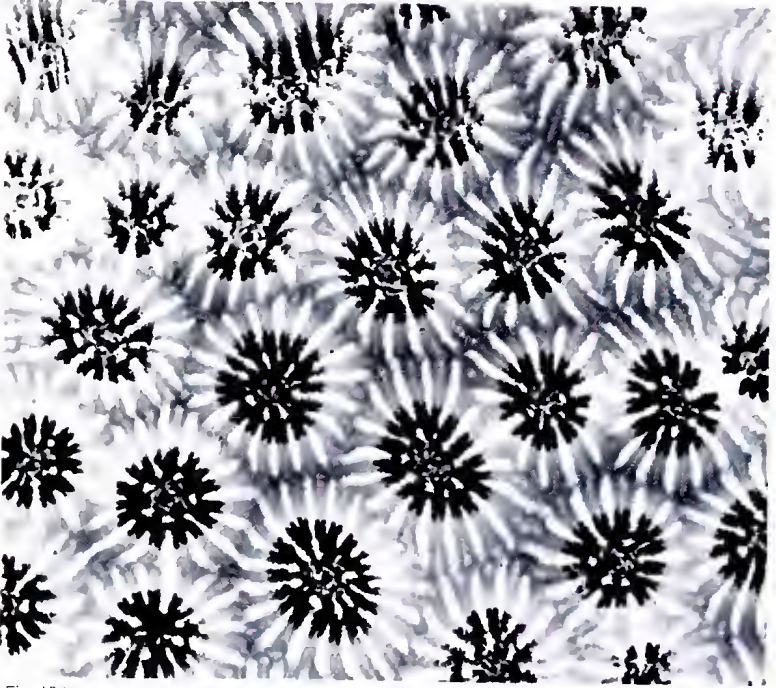


Fig. 19▲



Fig. 20▲

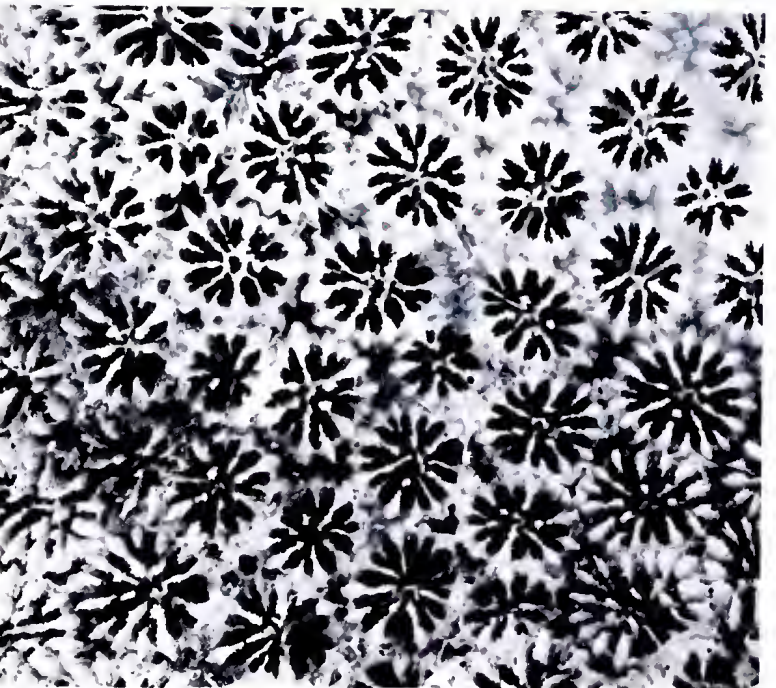


Fig. 21▲

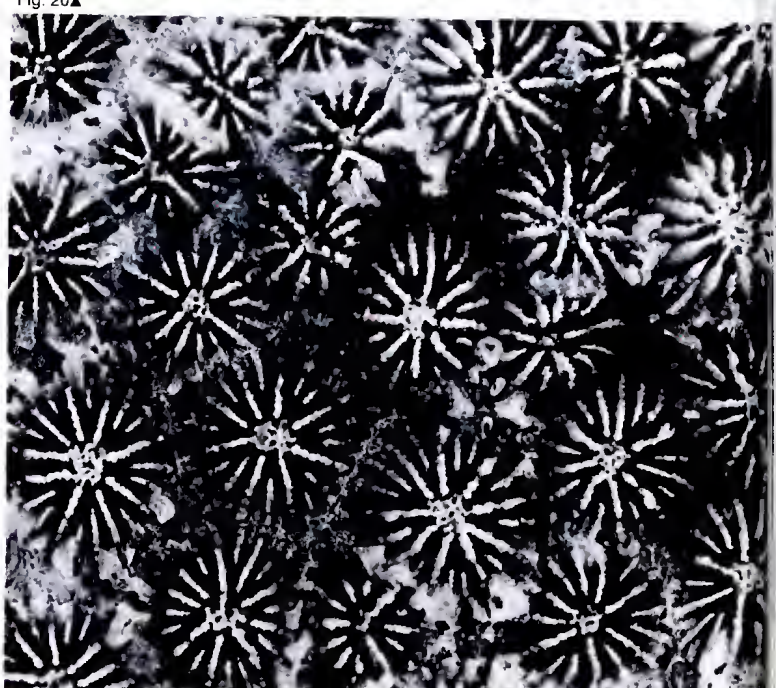


Fig. 22▲

Previous records from Eastern Australia

Low Isles, Manton (1932), Crossland (1952); **Heron Island**, Salter (1954); **Moreton Bay** (subfossil), Wells (1955b); **Solitary Islands**, Veron *et al.* (1974).

Characters

This common species is one of the most readily recognised of the Faviidae. Colonies are massive or sub-massive, either spherical, columnar, hillocky or flat (Fig. 16). They are smooth and even, sometimes containing large numbers of parasites. Colonies several metres across are common in reef biotopes; coralla are usually hard, dense and brittle. Coralla are plocoid. Septa are in two (sometimes indistinct) orders; a third order of very small septa sometimes occurs in large calices. First order septa are irregular in length; those reaching the columella usually have large paliform lobes of irregular length and number. Septa are usually moderately exsert; they are dentate and granulated on their sides. The columella are trabecular and usually inconspicuous. Except for very actively dividing calices (Fig. 20), the theca is thick. Septa over the theca are thickened and usually equal or subequal, as are the costae. Small intercostal ridges (or septo-costae of the third order) are frequently formed at the base of corallites. The coenosteum is smooth and frequently blistered.

Skeletal variation

Favia stelligera from exposed biotopes (ecomorph *pseudostelligera*) (Figs. 17, 18).

The principal distinctive features of this ecomorph are larger calices, 2.5-3.5mm diameter, and more heavily calcified calicular structures. Septa are usually in three distinct orders. First order septa reach the columella and have conspicuous paliform lobes. second order septa may reach the columella but do not have paliform lobes. Third order septa consist only of a ridge running down the endotheca. The columella is trabecular but more calcified than that of *F. laxa*. Costae of the first two orders are equal, those of the third order are reduced at their upper margins. Many specimens show evidence of predominantly extratentacular budding.

Favia stelligera from partly protected biotopes (Figs. 19-22).

Coralla from most reef or island biotopes have the full range of skeletal variation indicated above but have relatively constant calicular characters, as described.

Distribution

Widely distributed from the Red Sea to Hawaii.

Favia laxa (Klunzinger, 1879)

Synonymy

Orbicella laxa Klunzinger, 1879; Gardiner (1904); von Marenzeller (1907).

Favia laxa (Klunzinger); Matthai (1914); Nemenzo (1959); Scheer (1972).

This species is similar to *Favia helianthoides* Wells, the paratypes of which are close to some specimens of the present series but differ in having thick walled conical corallites with more abundant septa and a more conspicuous paliform crown. These species are not synonymous, as indicated by Wijsman-Best (1972).

Figs. 17-22 *Favia stelligera* ($\times 5.0$).

Fig. 17 From Thursday Island, collecting station 53, showing heavily calcified calices.

Fig. 18 From Swain Reefs, collecting station 69.

Figs. 19, 20 Same corallum from barrier reefs NE of Murray Islands, collecting station 7. Fig. 20 shows corallites in process of rapid division.

Fig. 21 From NE Curaçoa Island, Palm Islands, collecting station 56.

Fig. 22 Calices near the base of the corallum illustrated in Fig. 17, showing pronounced development of vesicular exothecal dissepiments.

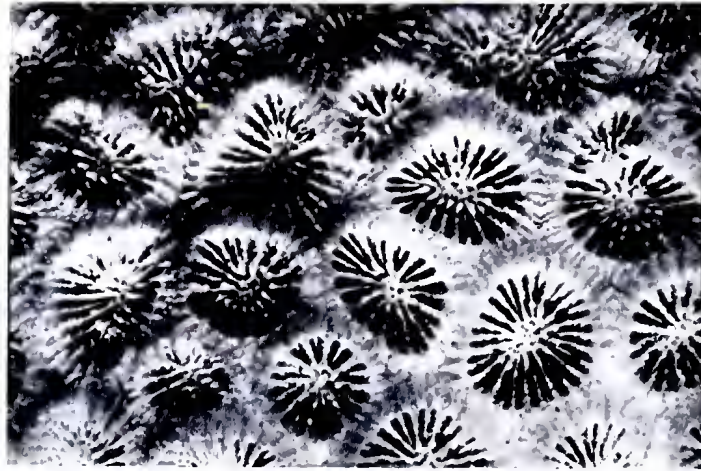


Fig. 23 Holotype of *Favia laxa* ($\times 2.5$).

Material studied

Yorke Island (2 specimens), **Jewell Reef**, **Lizard Island** (2 specimens), **Low Isles**, **Bowl Reef**, **Palm Islands** (16 specimens), **Whitsunday Islands** (5 specimens), **Pompey Complex** (3 specimens), **Swain Reefs** (12 specimens).

These localities include collecting stations 10, 12, 13, 35, 41, 43, 45, 55, 67, 68, 69, 72, 75, 79, 90, 91, 97, 98, 100, 102, 103.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are massive, flattened or rounded. They are plocoid, with mature calices, 3-6mm in diameter. Septa are in two distinct orders. First order septa are relatively thick and have well developed paliform lobes which form a conspicuous crown around the columella. Second order septa are thinner and shorter and descend abruptly down the endotheca without reaching the columella. The columella is small and trabecular. The septa and paliform lobes are conspicuously dentate along their margins and granulated on their sides. First order septa are regularly exsert and dentate above the theca. Costae are usually equal, elongated and conspicuous. They are finely dentate. The coenosteum is not otherwise ornamented and is either smooth or blistered. Budding is mostly intratentacular.

Colonies are uniform in colour, usually pale brown or pinkish-brown (Fig. 415). Colonies from shaded environments are darker and many colonies have darker sides than tops.

Skeletal variation

The range of growth forms of the present series is illustrated in Figs. 24-27. This species is readily recognised underwater but is not common in most reef biotopes.

Distribution

Widely distributed from the Red Sea to New Caledonia and the Great Barrier Reef.

***Favia fava* (Forskål, 1775)**

Synonymy (partly after Chevalier, 1971 and Wijsman-Best, 1972)

Madrepora fava (*pars*) Forskål, 1775.

Madrepora cavernosa Forskål, 1775.

Madrepora denticulata Ellis & Solander, 1786.

Parastrea denticulata Edwards & Haime, 1849.

Parastrea affinis Edwards & Haime, 1849.

Parastrea savignyi Edwards & Haime, 1849.

Parastrea deformata Edwards & Haime, 1849.

Favia affinis (Edwards & Haime); Edwards & Haime (1857); Studer (1881); Ortmann (1888); von Marenzeller (1901); Gardiner (1904); Chevalier (1968).

Figs. 24-27 *Favia laxa* Fig. 24 ($\times 0.75$), Figs. 25-27 ($\times 1.75$).

Figs. 24, 25 From Yorke Island, collecting station 13.

Fig. 26 From Bullumbooroo Bay, Great Palm Island, collecting station 35.

Fig. 27 From Low Isles, collecting station 12.



Fig. 24▲

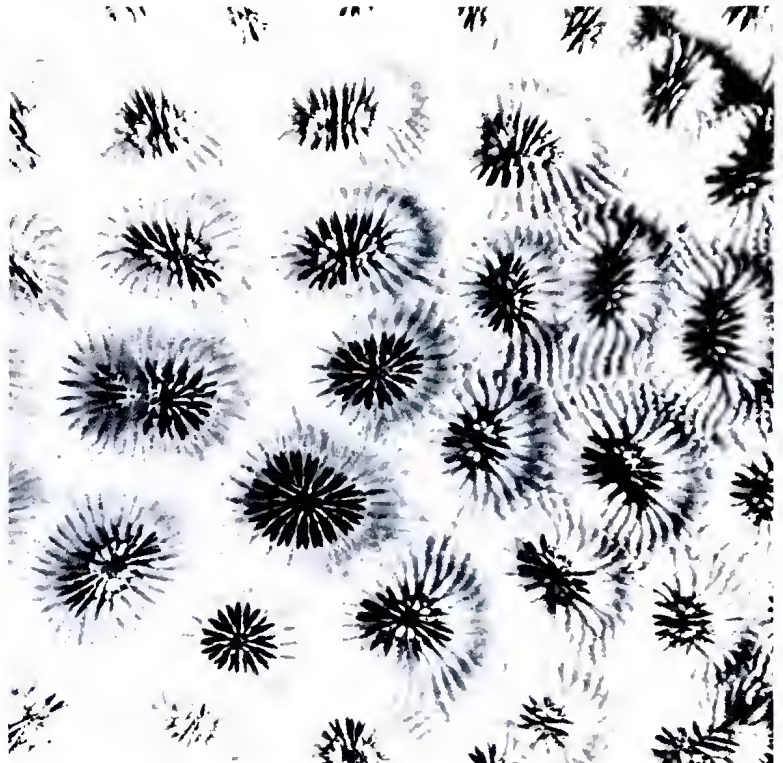


Fig. 25▲



Fig. 26▲

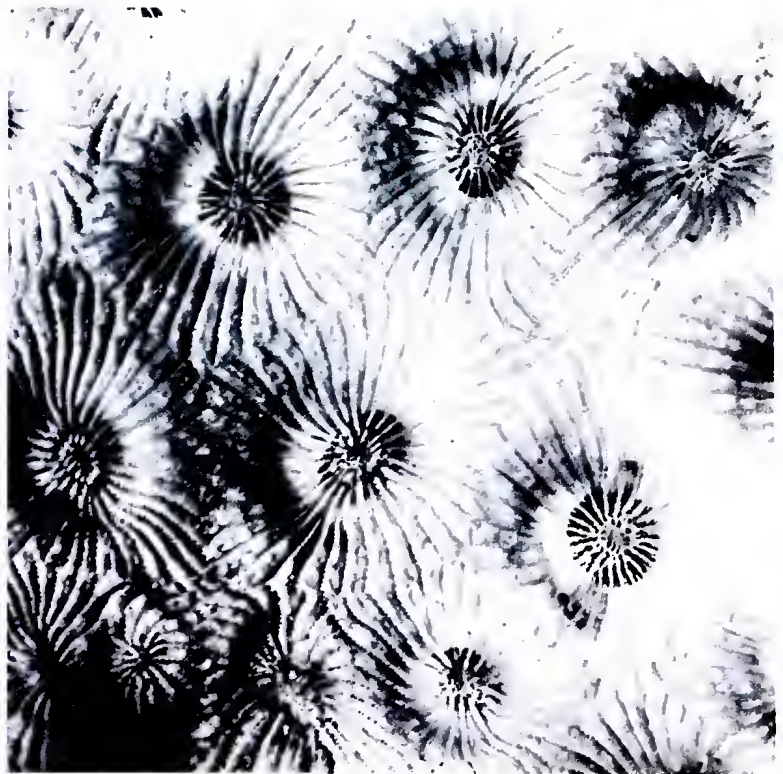


Fig. 27▲

Favia jacquinoti Edwards & Haime, 1857.

Favia geoffroyi Edwards & Haime, 1857.

Favia deformata Edwards & Haime, 1857.

Favia savignyi Edwards & Haime, 1857; von Marenzeller (1907); Gravier (1907, 1911).

Favia aspera Edwards & Haime, 1857.

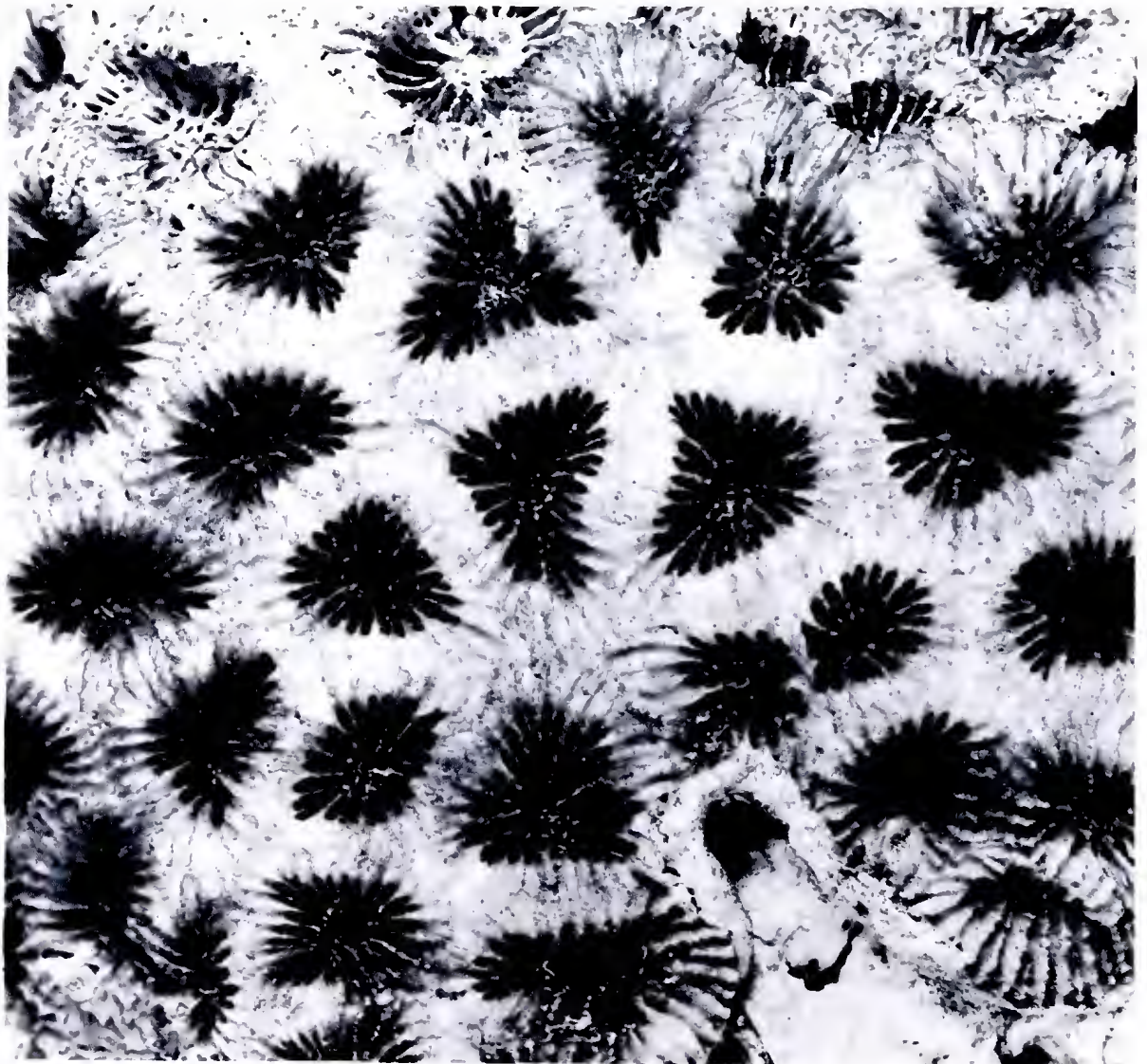
Favia ehrenbergi Klunzinger, 1879; Ortmann (1888, 1889, 1892); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938).

Orbicella borradailei Gardiner, 1904

Favia fava (Forskål); Matthai (1914, 1923, 1924); Hoffmeister (1925); Faustino (1927); Crossland (1952); Rossi (1954); Wells (1954); Nemenzo (1959); Ma (1959); Scheer (1964, 1967); Rosen (1968, 1971); Chevalier (1971); Wijsman-Best (1972, 1974); Scheer & Pillai (1974).

Favia fava Forskål No. 28 from Universitetes Zoologiske Museum, Danmark, is designated lectotype of this species (Fig. 28).

Fig. 28 Designated lectotype of *Favia fava* ($\times 2.5$).



Material studied

Yorke Island (4 specimens), **Murray Islands** (3 specimens), **Sue Island** (3 specimens), **North West Reef**, **Thursday Island**, **Great Detached Reef** (2 specimens), **Tijou Reef** (2 specimens), **Bewick Island**, **Houghton Island**, **Jewell Reef** (3 specimens), **Lizard Island** (17 specimens), **Ribbon Reef**, **Three Isles**, **Hope Island** (5 specimens), **Low Isles** (7 specimens), **Bowl Reef**, **Palm Islands** (147 specimens), **Magnetic Island**, **Whitsunday Islands** (39 specimens), **Bushy Island-Redbill Reef**, **Pompey Complex** (4 specimens), **Swain Reefs** (12 specimens).

These localities include collecting stations 1, 2, 6, 10, 12, 13, 14, 17, 18, 27, 29, 30, 32, 33, 34, 35, 37, 38, 39, 40, 41, 42, 43, 45, 53, 55, 57, 58, 59, 60, 65, 66, 67, 69, 70, 75, 79, 80, 81, 84, 90, 91, 92, 97, 98, 99, 102.

Previous records from Eastern Australia

Low Isles, Yonge (1940), Crossland (1952).

Characters

Colonies are massive, rounded, sometimes flattened. Skeletal structures are very variable both within and between biotopes and to a much lesser extent, within individual coralla. Coralla are plocoid, with corallites 12-20mm in diameter. They may be up to 5mm exsert with broad bases (Figs. 29-31). Conical corallites are usually circular, although those of rapidly growing colonies may be irregular in shape. The surface of the endotheca is almost always cylindrical. Calices may be deep or (as in corallites where the theca is not exsert) shallow. As with *F. matthaii* and *F. pallida*, septa do not usually form distinct orders. They always have elongated, irregular, inwardly sloping dentations. These dentations are themselves finely serrated, especially at their tips, which frequently form minute horizontal fans. Septa have granulated sides. They are normally thickened above the theca, are regularly exsert and frequently vary in thickness within the one corallite. The formation of paliform lobes is extremely variable among different coralla; in some they are hardly recognizable, in others they form a single, distinct crown. Usually all septa reaching the columella tend to form some sort of paliform lobe. The columella is small and trabecular. Costae are equal; intercostal ridges (e.g. Fig. 33) are rare. Those of adjacent corallites are frequently aligned. They always have regular rows of fine dentations. The coenosteum is usually blistered with exothecal dissepiments.

Individual colonies are usually relatively uniform in colour and most colonies within the one biotope have similar colours. These are usually dull browns, greys and greens (Fig. 418). Sometimes the oral disc is more brightly coloured than the coenosarc. Some colonies are mottled brown and light grey (Figs. 417, 419). This colouration usually distinguishes *F. favus* from *F. pallida*, the latter having distinctly dark centres (Fig. 423).

Skeletal variation

The great abundance of this species in a wide variety of biotopes greatly facilitates study of intra-biotope growth form variation. Even under very uniform environmental conditions, different colonies may have substantially differing corallite structures that are readily observable underwater. Thus, as with some *Platygyra* and *Goniastrea* species, there appears to be a major genotypic component in growth form variation which permits only loose correlations between calice structure and environmental parameters.

Calice structure in coralla from most reef biotopes appears to be partly related to the rate or degree of calcification. Thus coralla from biotopes where coral growth is abundant have thick, conical-shaped thecae and well-formed skeletal structures. However, the variability illustrated in Figs. 29-34 appears to be more genotypic than phenotypic.

Affinities

This is one of the most abundant of the *Favia* species and also one of the most variable. Consequently, it is readily confused with less abundant species in large collections. This study indicates that *Barabattoia mirabilis*, *Favia amicornum*, *Favia favus*, *Favia* sp.1 and possibly

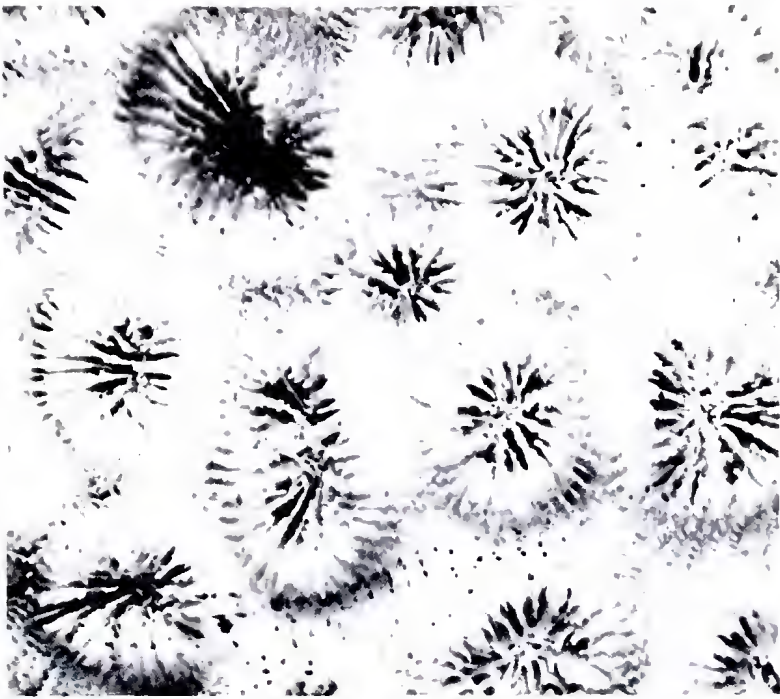


Fig. 29▲

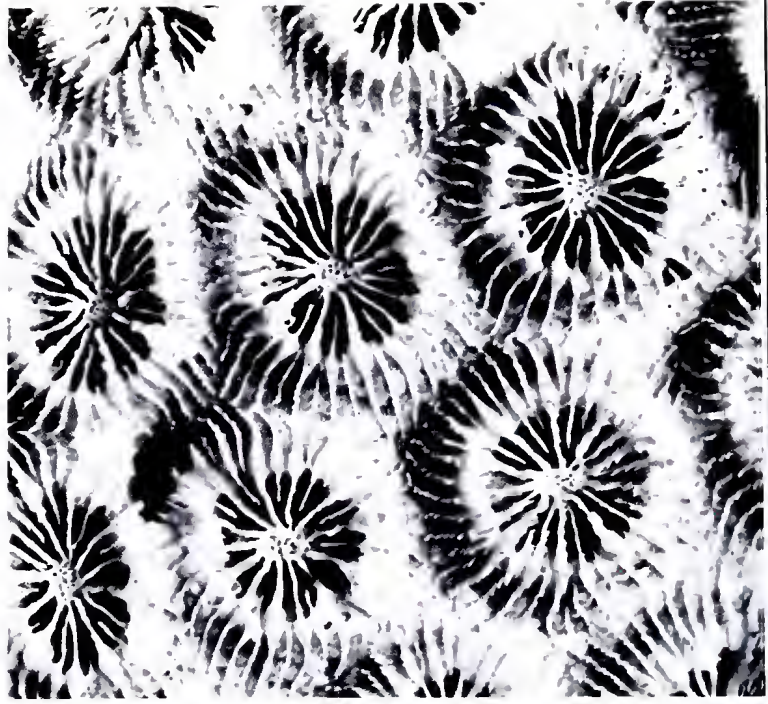


Fig. 30▲



Fig. 31▲

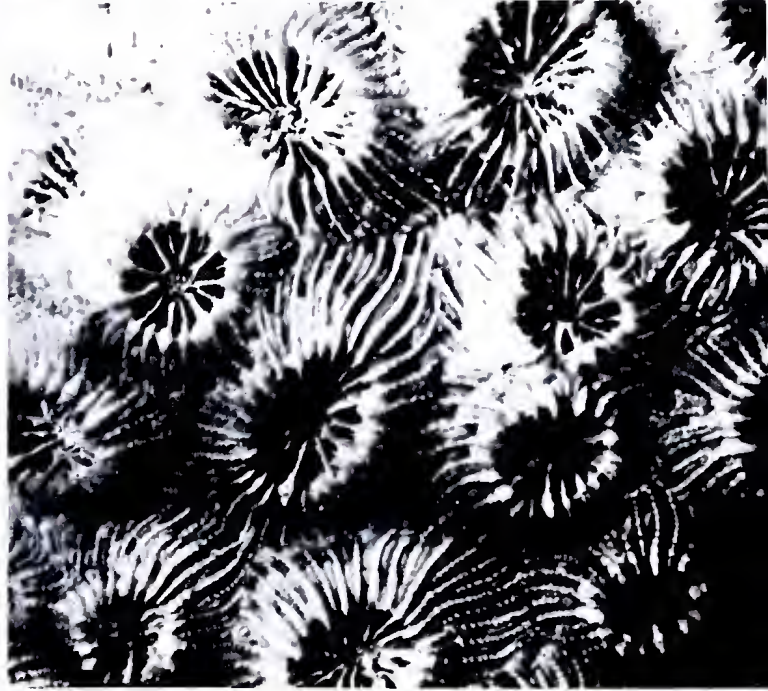


Fig. 32▲



Fig. 33▲

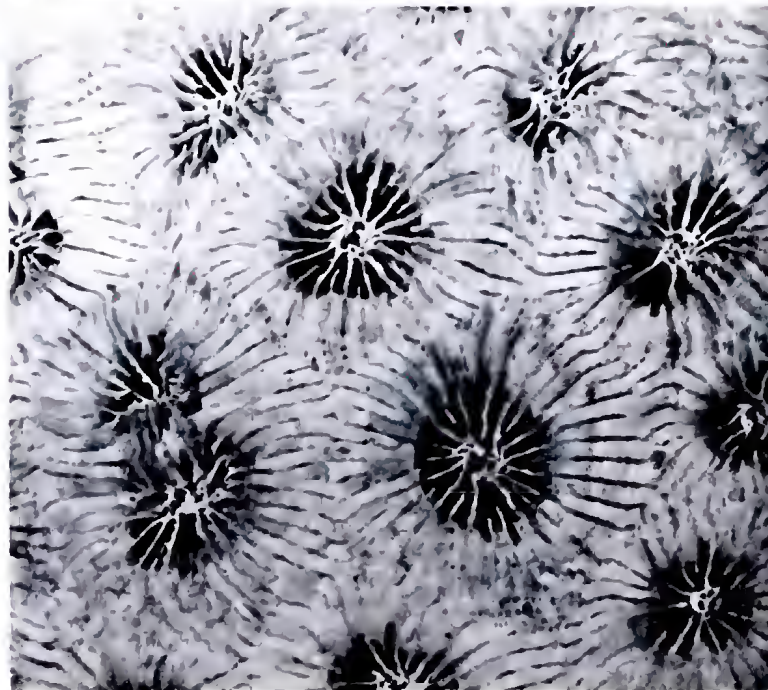


Fig. 34▲

Bikiniastrea laddi form a broad complex that is essentially divisible into three species or groups: cf. *amicorum*, *favus* and *Favia* sp.1.

Favia cf. *amicorum*, itself a heterogeneous complex including *Barabattoia mirabilis* and possibly *Bikiniastrea laddi* (see p.32), cannot clearly be differentiated from *F. favus* in large collections. Underwater and in collections from similar biotopes, it is readily distinguished from *F. favus* by its relatively small, very exsert corallites with thin thecae. Adjacent colonies of these two species can be compared in Fig. 420. However, the range of calicular structures is so great in both species that they overlap completely in heterogeneous collections. The range of variation of *Favia* sp.1 is not known, but it is normally distinguished from *F. favus* by

Figs. 29-34 *Favia favus* ($\times 2.5$).

- Fig. 29 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91.
- Fig. 30 From Falcon Island, Palm Islands, collecting station 41.
- Fig. 31 From Bullumbooroo Bay, Great Palm Island, collecting station 35.
- Fig. 32 From Hazard Bay, Orpheus Island, Palm Islands, collecting station 45.
- Fig. 33 From Elk Cliff, Great Palm Island, collecting station 37.
- Fig. 34 From Bewick Island, collecting station 39.

Figs. 35, 36 *Favia favus*, in situ, Fig. 35 at the Palm Islands, Fig. 36 at Lizard Island, with polyps expanded at night ($\times 2.0$).

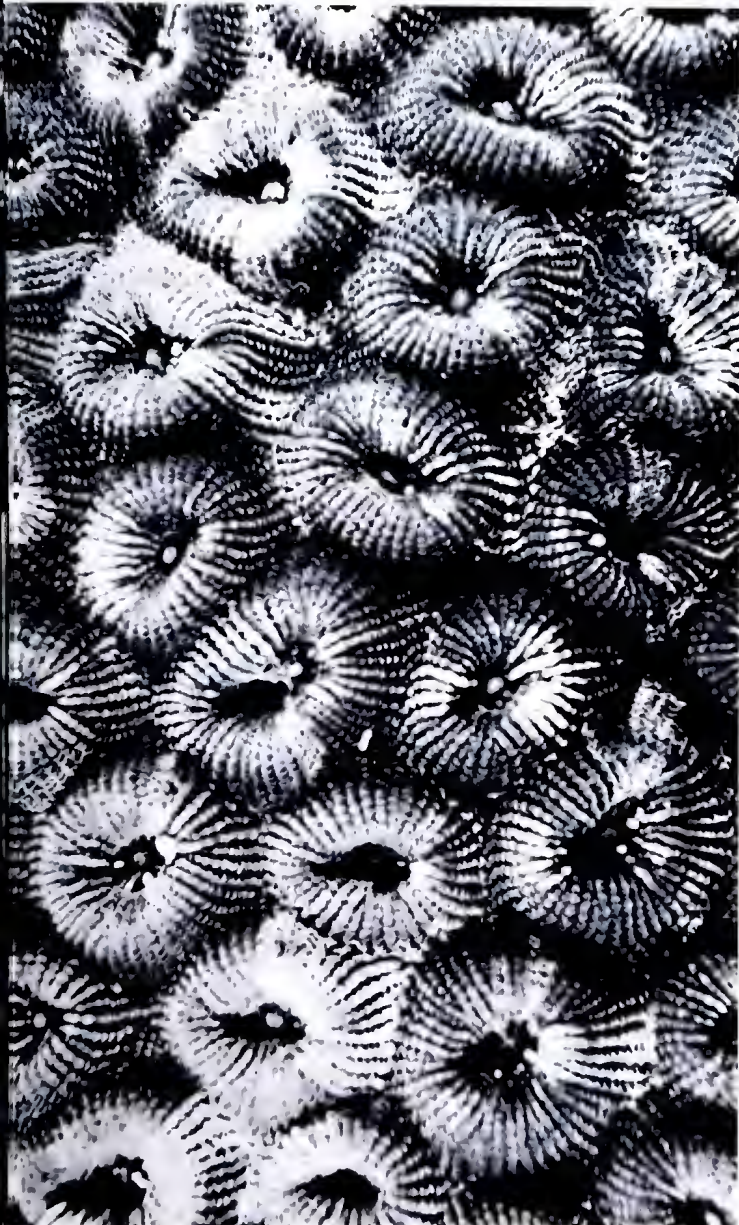




Fig. 37A

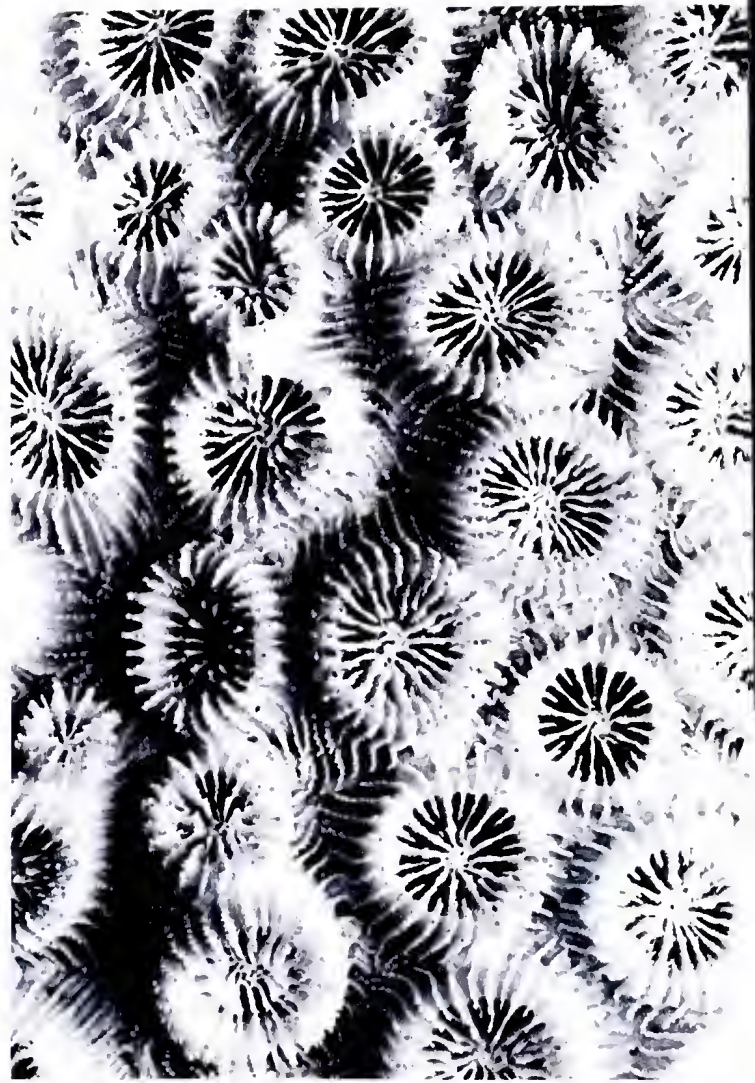


Fig. 38A

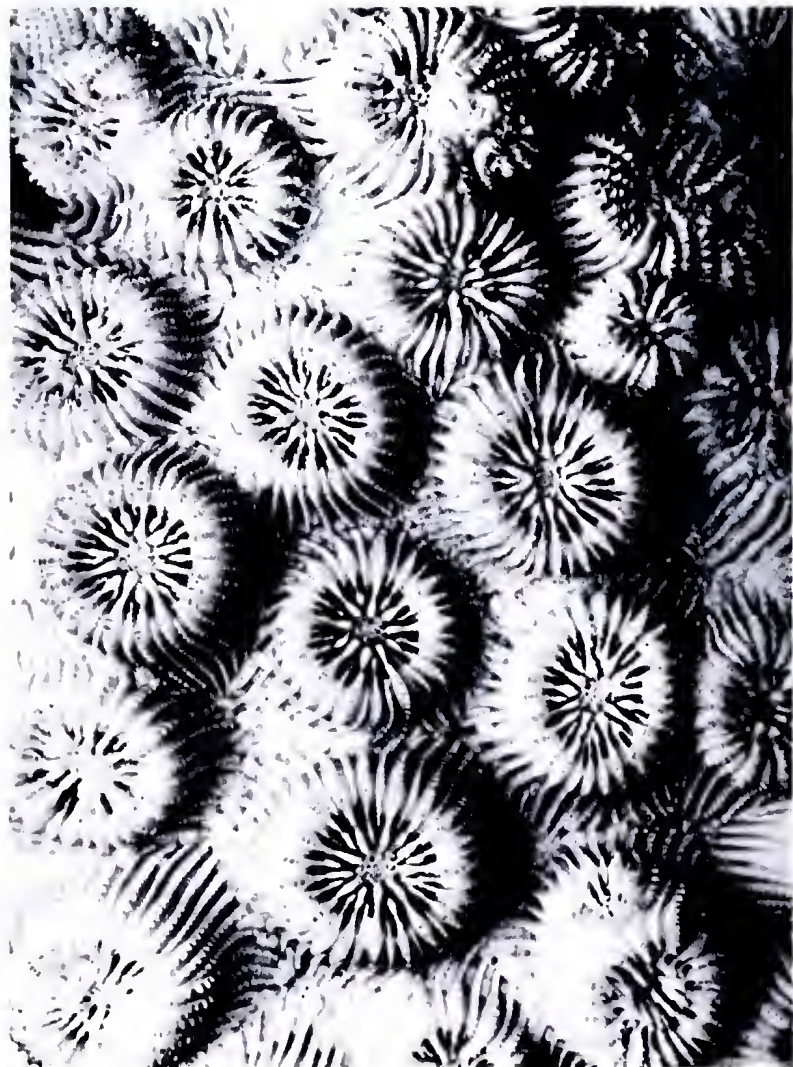


Fig. 39A

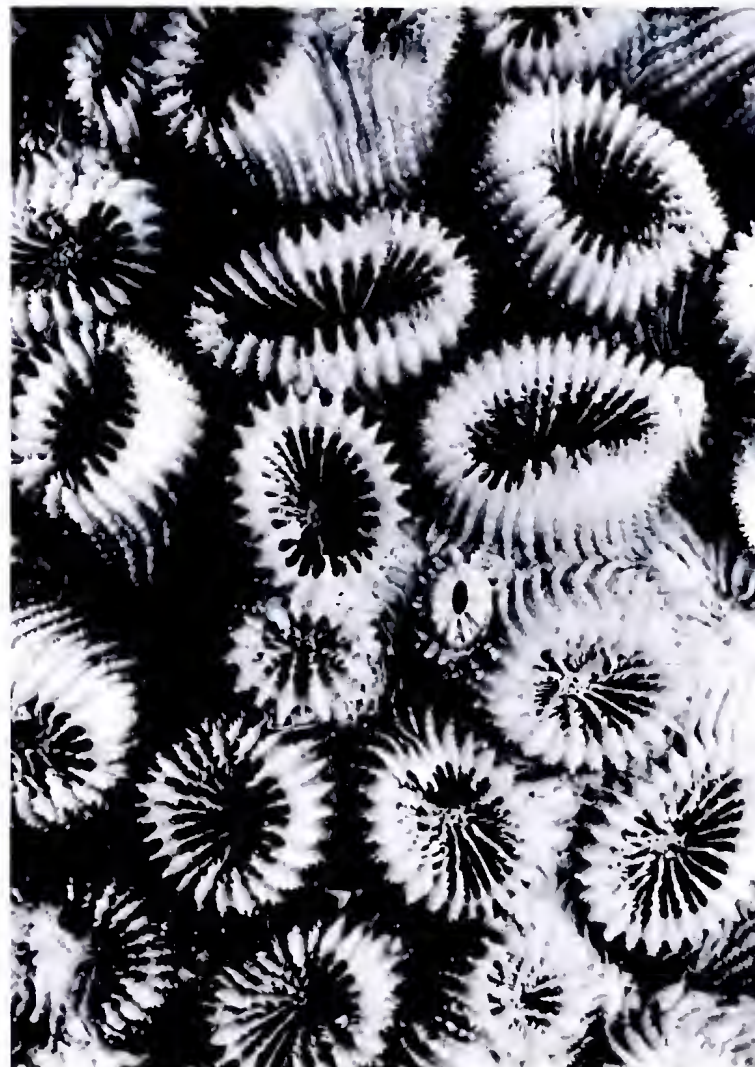


Fig. 40A

Fig. 41



Fig. 42



Fig. 44



Fig. 43



its larger corallites with very exsert thecae and by the septal dentations which are fine and regular. Adjacent colonies of these two species can be compared in Fig. 416.

Favia favus is also close to *F. lizardensis*. These species are readily distinguished underwater and in collections from similar biotopes (see p.46) but can be confused in heterogeneous collections, especially when ecological data is lacking.

Distribution

Widely distributed from the Red Sea to Japan, the Marshall Islands and Samoa.

Favia amicorum complex

This complex involves the following genera and species:

Parastrea amicorum Edwards & Haime, 1850 (new name for *Astraea ananas* Quoy & Gaimard, 1833, non *Astraea ananas* Lamarck, 1816).

Barabattoia mirabilis Yabe & Sugiyama, 1941.

Barabattoia goroensis Yabe & Sugiyama, 1941.

Bikiniastrea laddi Wells, 1954.

Favia amicorum (Edwards & Haime); Wijsman-Best (1972, 1974).

Barabattoia modesta Nemenzo, 1971.

Material studied

Murray Islands, Bewick Island, Lizard Island (13 specimens), **Palm Islands** (21 specimens), **Whitsunday Islands** (7 specimens), **Bushy Island-Redbill Reef**.

These localities include collecting stations 30, 32, 34, 35, 37, 39, 41, 45, 55, 86, 89, 91, 97, 98, 99, 100.

Previous records from Eastern Australia

None of this group has been previously recorded.

Common characters

Coralla are sub-massive or encrusting, with exsert corallites tending to become sub-ramose and anastomosing. The latter growth form appears to be largely a result of deposition of sediment within and around colonies, allowing only exsert corallites and protruding parts of colonies to grow. Thus these colonies are usually found only in close proximity to sediments, usually in turbid water, and therefore have a very irregular appearance. Budding is intratentacular, mono- to tristomodaeal, with daughter corallites projecting at a sharp angle. In sub-ramose coralla, these corallites tend to anastomose where they meet, forming in extreme cases an interlocking network. Such colonies are usually small because they exist only in very marginal environmental conditions.

Septa are in two indistinct, alternating orders. They have strongly dentate inner margins. The columella is usually small, usually trabecular. Costae are always prominent, equal and strongly dentate or beaded. Paliform lobes may form a distinct, prominent crown or may

Figs. 37-44 *Favia amicorum* complex ($\times 2.5$).

Fig. 37 Holotype of *Favia amicorum*.

Fig. 38 From Elk Cliff, Great Palm Island, collecting station 37, showing thin, exsert thecae and well developed paliform lobes.

Fig. 39 From Wyer Island, Murray Islands, collecting station 30, showing more heavily calcified calicular structures, otherwise similar to Fig. 38.

Fig. 40 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97, showing *mirabilis*-like calicular structures and a sub-dendroid growth form.

Fig. 41 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91, showing a ramose growth form with anastomosing branches and *laddi*-like calicular structures.

Fig. 42 Holotype of *Barabattoia mirabilis*.

Fig. 43 Holotype of *Bikiniastrea laddi*.

Fig. 44 Partly expanded polyps of the corallum illustrated in Fig. 41.

be almost absent. There is a high degree of correlation between the degree of calcification of calicular structures and growth form, more heavily calcified coralla occurring in more exposed biotopes and having more compact, massive growth forms.

Affinities

Coralla included in this complex make a very heterogeneous group, different ones showing close affinity with the type specimens of *Barabattoia mirabilis*, *Bikiniastrea laddi* and *Favia amicornum* (Figs. 41, 43 & 37 respectively). Conclusions from this study are that these three forms are either closely related species or, as claimed by Wijsman-Best (1972), all the one species. The present series, however, is not adequate to resolve these questions.

Distribution

This complex is recorded only from the western Pacific, including Tonga (type locality of *Favia amicornum*), Yap (type locality of *Barabattoia mirabilis*), New Caledonia (type locality of *Barabattoia goroensis* and locality of *Favia amicornum* (Wijsman-Best, 1972)), Marshall Islands (type locality of *Bikiniastrea laddi*) and the Great Barrier Reef (present study).

Favia pallida (Dana, 1846)

Synonymy (partly after Vaughan, 1918, Chevalier, 1971 and Wijsman-Best, 1972.)

Parastraea urvilleana Edwards & Haime, 1850.

Parastraea amplior Edwards & Haime, 1850.

Favia doreyensis Edwards & Haime, 1850; Edwards & Haime (1857); Matthai (1914, 1924); Gravely (1927); Crossland (1952); Chevalier (1968).

Favia amplior (Edwards & Haime); Edwards & Haime (1857); Ortmann (1889); Yabe & Sugiyama (cf.) (1935).

Favia okeni Edwards & Haime, 1857; Bedot (1907); von Marenzeller (1907); Gravier (1907, 1911); Harrison & Poole (1909); Yabe & Sugiyama (1935).

Astraea ordinata Verrill, 1866.

Astraea cellulosa Verrill, 1872 = *Astraea (Fissicella) denticulata* Dana, 1846.

Favia tubulifera Klunzinger, 1879.

Goniastrea serrata Ortmann, 1889.

Favia laccadivica Gardiner, 1904.

Favia denticulata Gardiner, 1904.

Heliastrea borradailei Gardiner, 1904.

Favia pallida (Dana); Vaughan (1918); Mayor (1918); Matthai (1923); Hoffmeister (1925); Faustino (1927); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1940); Wells (1954); Stephenson & Wells (1955); Nemenzo (1959); Pichon (1964); Chevalier (1968, 1971); Utinomi (1971); Rosen (1971); Wijsman-Best (1972-1974); Scheer (1972); Pillai, Vine & Scheer (1973); Pillai & Scheer (1973); Scheer & Pillai (1974).

Fig. 45 Holotype of *Favia speciosa* ($\times 2.5$).

Figs. 46-53 *Favia pallida* ($\times 2.5$).

Fig. 46 From Lizard Island, showing close similarity with the type of *Favia pallida*.

Figs. 47-49 From Houghton Island; Fig. 47 collected from near low water level, Figs. 48 and 49 from adjacent, deeper water, all collecting station 16.

Figs. 50, 52 From Three Isles.

Fig. 51 From Hope Island.

Fig. 53 Holotype of *Favia pallida*.

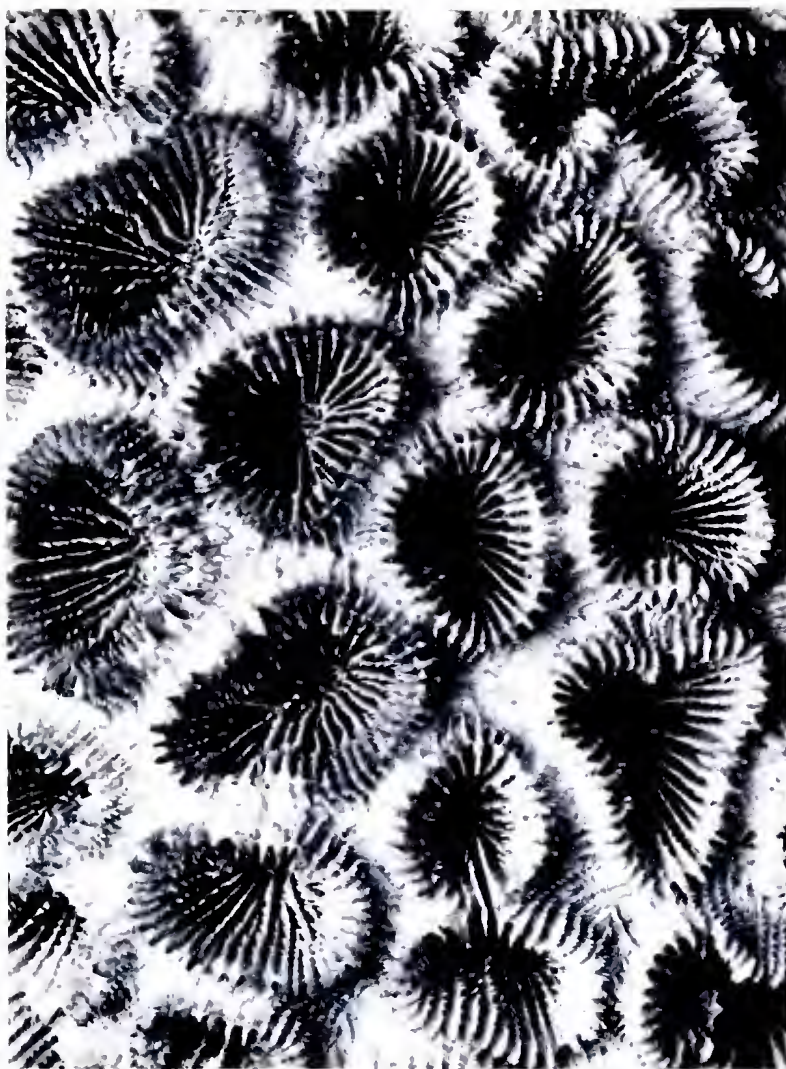


Fig. 45▲

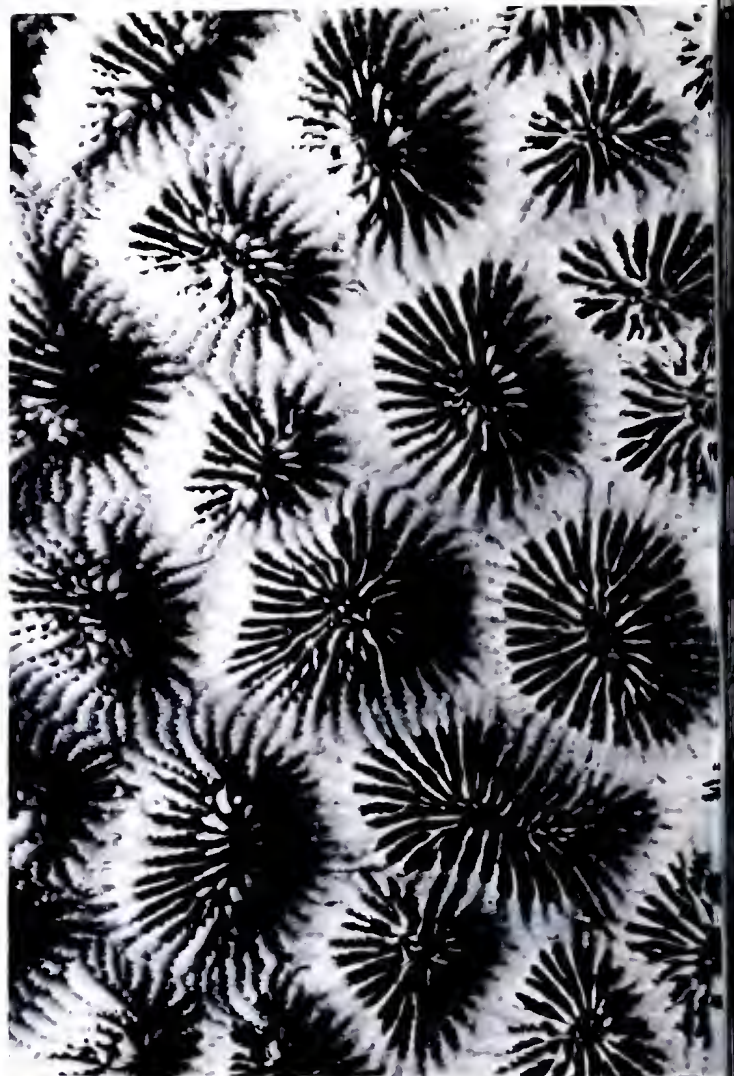


Fig. 46▲

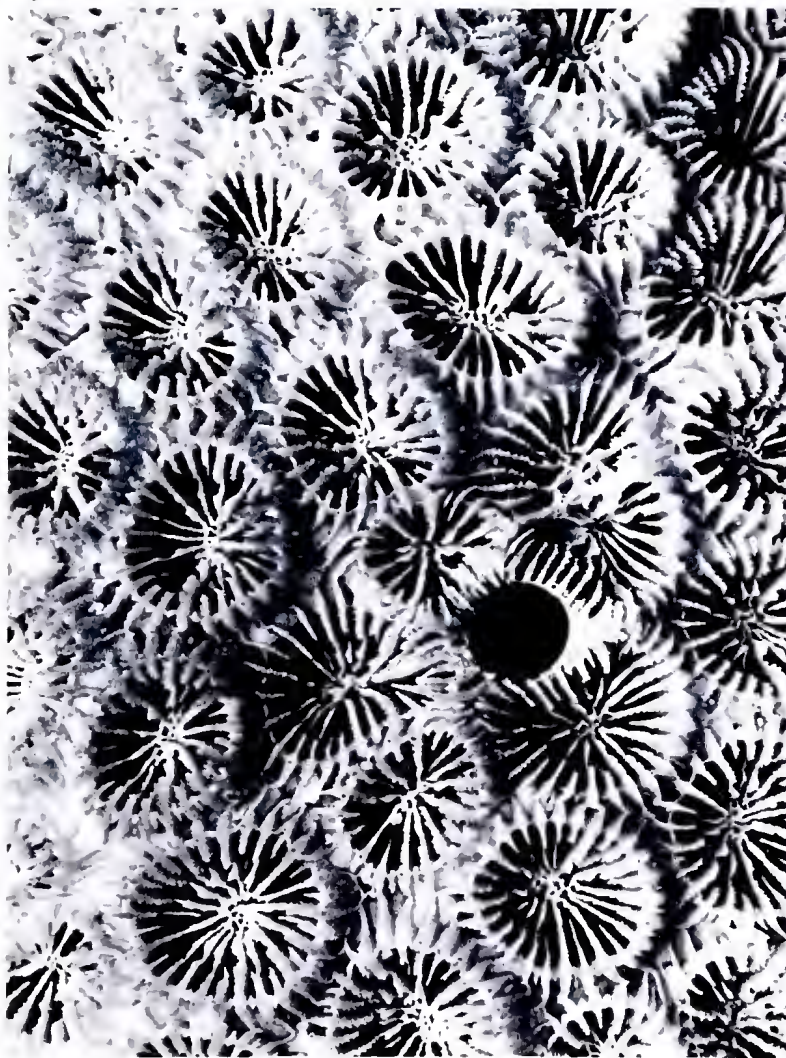


Fig. 47▲

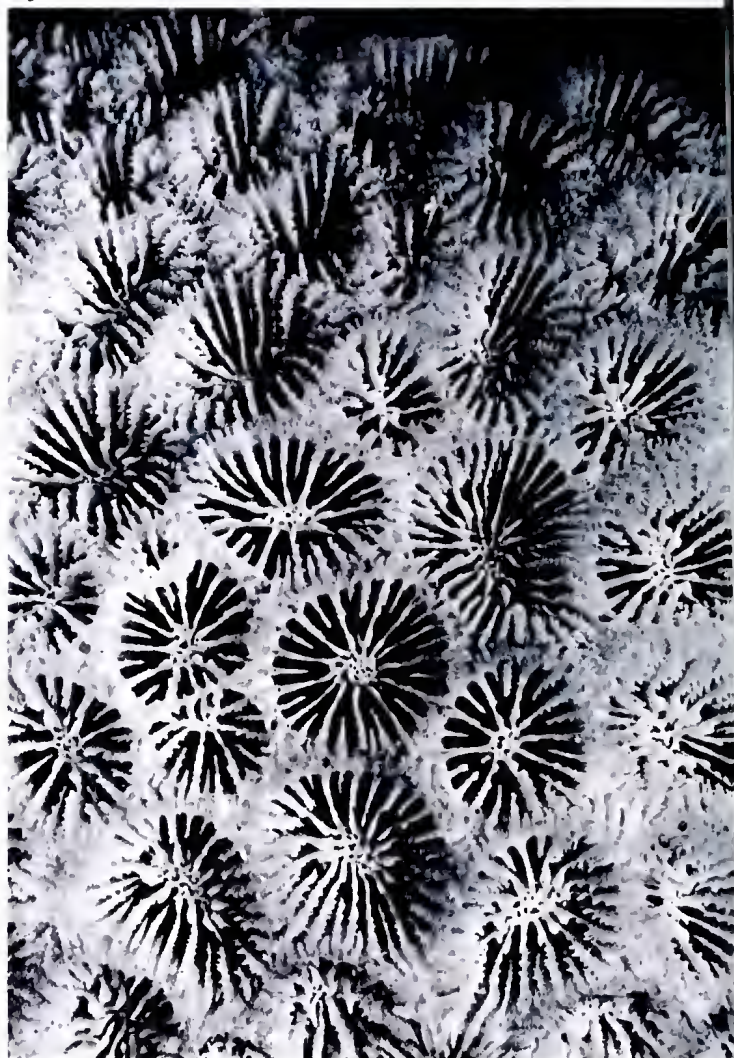


Fig. 48▲

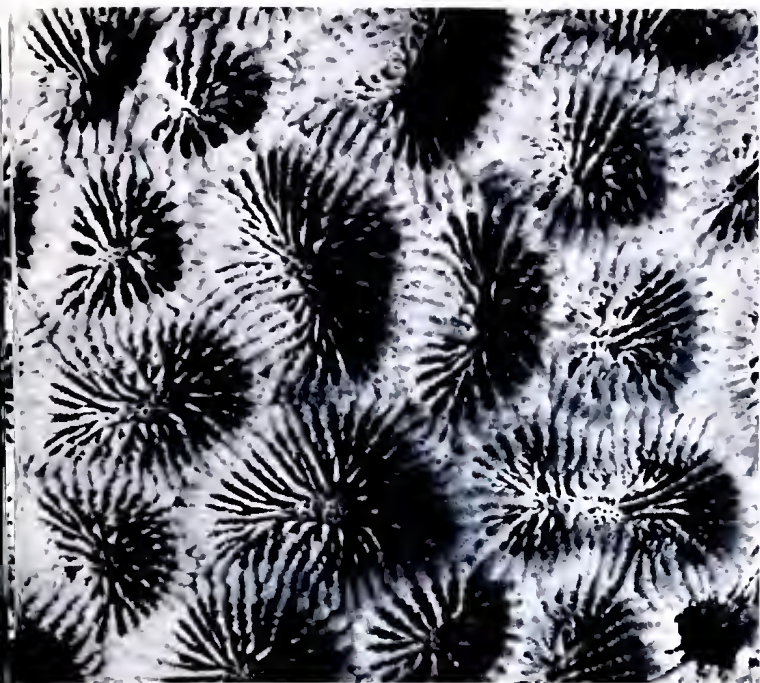


Fig. 49▲

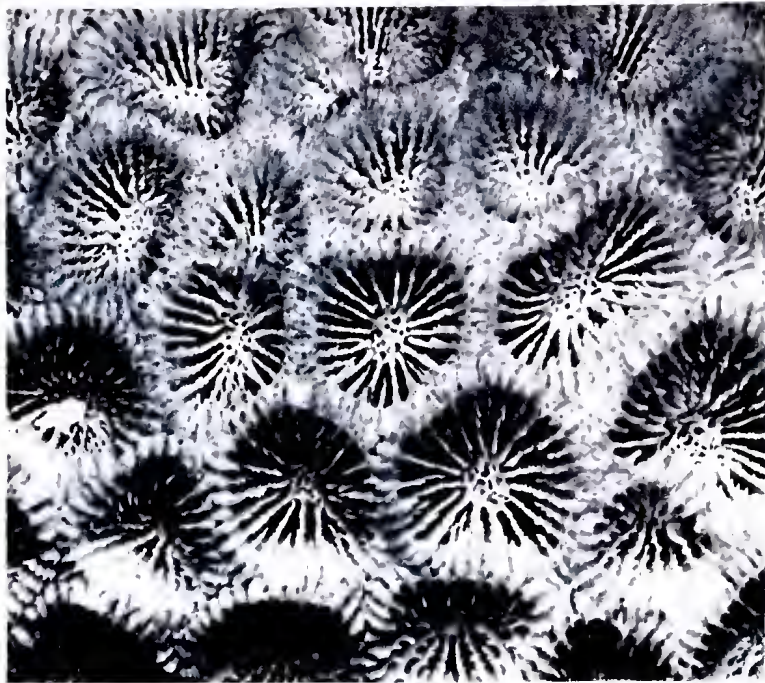


Fig. 50▲

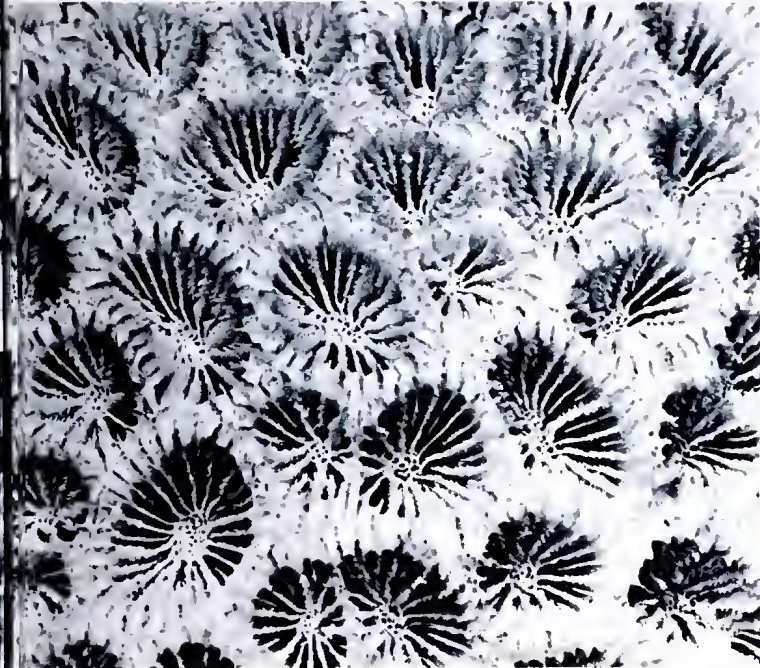
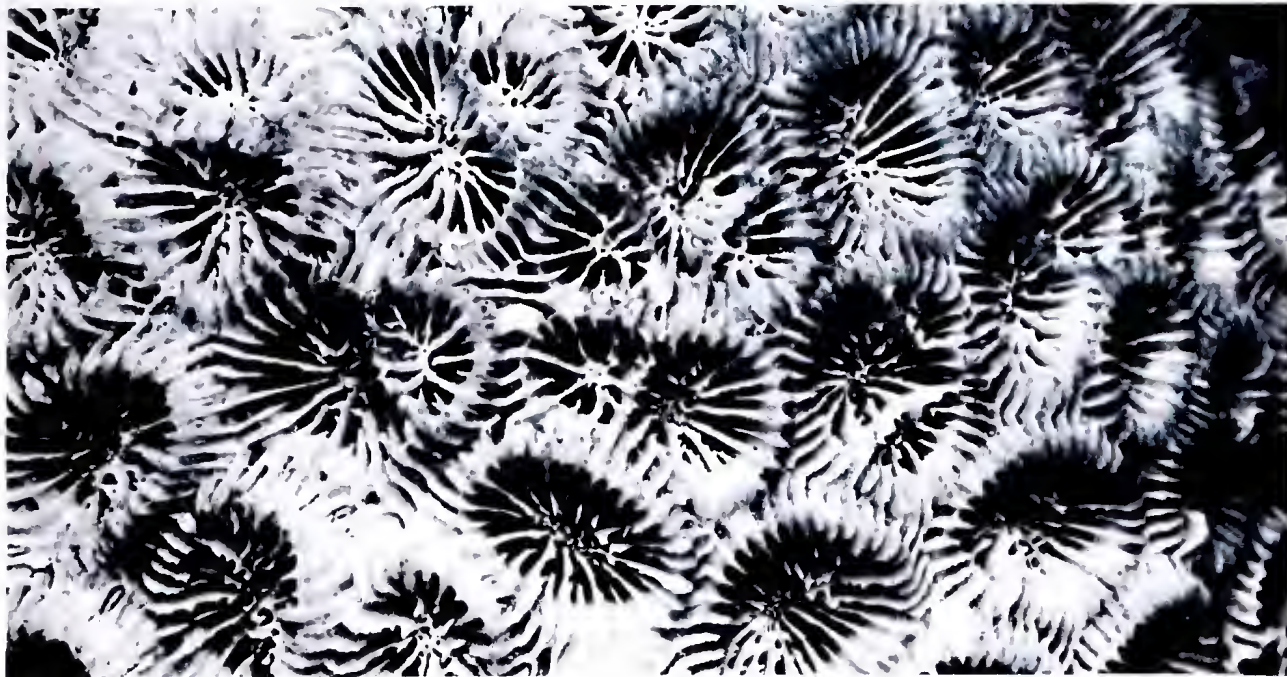


Fig. 51▲



Fig. 52▲



◀ Fig. 53

Favia pallida is the most common and one of the most variable species of *Favia* of the Great Barrier Reef and occurs widely throughout the Indo-Pacific where it has, to a large extent, been confused with *F. speciosa*.

Although these two species have been distinguished by the authors elsewhere in the Indo-Pacific, no such distinction has been made on the Great Barrier Reef where clearly there is a single common species, *F. pallida*. However, as previously noted (p.20) there remains a possibility that *F. speciosa* is present – as a rare species of the Northern Region, where three specimens resembling the type were collected from a single shallow exposed biotope. The holotypes of both species are illustrated with the present series for comparison. Vaughan gave a lengthy account of the synonymy of Dana's species, placing *Astraea pandanus*, *A. puteolina* and *A. fragilis* with *A. speciosa*, and *A. versipora*, *A. denticulata* and *A. cellulosa* with *A. pallida*. Yet he completely omitted any mention of how these species groups differ. Chevalier, however commented that they are close, but differentiated between them on the following bases:

1. In *F. speciosa* calices are crowded and unequal whereas in *F. pallida* they are circular or elliptical, less crowded and less deep.
2. In *F. speciosa* the septa are thinner, more numerous, less even, have longer dentations and better developed paliform lobes than in *F. pallida*. The latter species has more numerous costae.
3. The exothecal dissepiments of *F. speciosa* are finer than those of *F. pallida*.
4. The wall may be partly septothecal in the case of *F. pallida*, but not in *F. speciosa*.

Because of the wide variation of *F. pallida*, some difficulty remains with these points of distinction. The first and third have been observed in whole or in part within single large colonies of *F. pallida* and all except the second are attributable to intra-biotope growth form variation. Further, it appears that Chevalier has included specimens of *F. fava*, as described in this paper, in his illustration of *F. pallida* and *F. speciosa*. *Favia speciosa* var. *exserta* (Plate X, Fig. 5) in particular appears to be a *F. fava*. Thus, some of his distinctions between *F. pallida* and *F. speciosa* may in fact be distinctions between *F. pallida* and *F. fava*; this would certainly account for the separation of septal characters indicated in '2'.

Material studied

Darnley Island, Yorke Island, Murray Islands (3 specimens), **Sue Island** (4 specimens), **North West Reef** (3 specimens), **Great Detached Reef** (62 specimens), **Tijou Reef** (11 specimens), **Bewick Island** (15 specimens), **Houghton Island** (6 specimens), **Jewell Reef, Yonge Reef** (5 specimens), **Eagle Reef** (2 specimens), **Lizard Island** (13 specimens), **MacGillivray Reef, Ribbon Reef** (2 specimens), **Three Isles** (42 specimens), **Hope Island** (26 specimens), **Low Isles** (32 specimens), **Bowl Reef** (2 specimens), **Palm Islands** (70 specimens), **Keeper Reef** (2 specimens), **Wheeler Reef** (3 specimens), **Magnetic Island, Whitsunday Islands** (21 specimens), **Pompey Complex** (2 specimens), **Lord Howe Island** and vicinity.

These localities include collecting stations 1, 2, 5, 6, 9, 10, 12, 13, 14, 15, 17, 18, 19, 27, 30, 31; 32, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 45, 55, 57, 60, 65, 74, 90, 91, 97, 98, 99, 100, 102, 103.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918), Mayor (1918); **Low Isles**, Yonge (1930), (as *F. doreyensis*) Stephenson & Stephenson (1933), Marshall & Stephenson (1933), Manton (1935), Yonge (1940), Crossland (1952), Stephenson & Wells (1955); **Heron Island**, Salter (1954); **Moreton Bay**, Wells (1955a); **Solitary Islands**, Veron *et al.* (1974); **Lord Howe Island**, Veron (1974).

Characters

Large collections of *Favia* specimens from within one biotope are normally readily divisible into species units, each of which falls into a clearly defined range of variation. With *F. pallida*, this intra-biotope variation usually includes a wide range of corallite shapes and sizes, a wide range of septal characteristics (including number, thickness, development of dentations, development of paliform lobes, degree to which they are exsert) and some variation in the structure and appearance of the thecae. Similar collections from other biotopes may have different ranges of skeletal variation, which readily allow confusion with other species, notably *F. favius* and *F. matthaii*. Large collections from a wide range of different biotopes may therefore have a very heterogeneous appearance.

The following descriptions and illustrations apply to the species as a whole. This range of variability is not found within single or similar biotopes, nor does this species normally appear very heterogeneous underwater.

Colonies are massive and rounded, plocoid or plococerioid, with corallites averaging 6-10mm diameter. They are circular or irregularly squashed together, circular corallites

Figs. 54-55 *Favia pallida* ($\times 2.5$).

Fig. 54 From Houghton Island, collecting station 40 (adjacent to collecting station 16, Figs. 47-49 above), exposed to strong tidal currents in very shallow water.

Fig. 55 From Great Detached Reef, collecting station 1, exposed to extreme wave action.

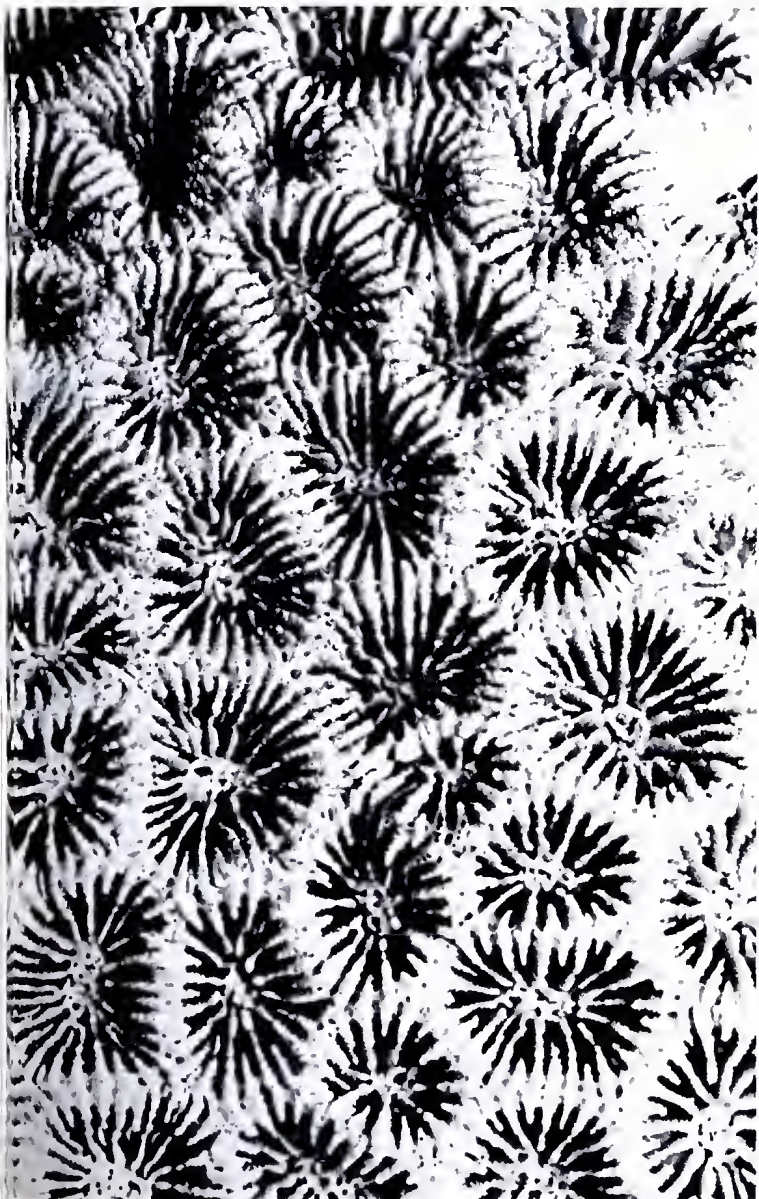


Fig. 54▲

Fig. 55▲

usually being found at the sides of large coralla and on coralla from protected water. They are seldom more than 2mm exsert. Ploco-ceroid corallites usually have thin thecae and correspondingly thin septa. The septa may appear to be in one, two or three orders, with these combinations sometimes occurring in the one corallum. They may be of uniform thickness, tapered towards the centre or very thickened over the thecae. Second and third order septa, when present, are slightly (occasionally markedly) thinner than those of the first order. Similarly, first order septa are usually more exsert. All septa descend abruptly inside the thecae. Those which reach the columella usually have paliform lobes. These may form a well defined crown, or may be inconspicuous or absent. This variation appears to be largely genotypic in origin as there is little association between paliform structure and biotope type, neither is there much variation between corallites of the same corallum. All septa are regularly dentate but, unlike *F. favus*, the dentations are always relatively short. Costae, when present, are regularly dentate or beaded, and are usually equal. The coenosteum is smooth or slightly blistered.

The species can be almost any colour underwater. Usually the coenosarc is a pale yellow, cream or green, the oral disc dark brown or green (see Fig. 423).

Skeletal variation

Intra-biotope variation is minimal in exposed localities such as outer reef fronts, and (as with many species) increases with increasing water turbidity and protection from wave action. The full range of variation in the species is illustrated in Figs. 46-55.

Favia pallida from exposed biotopes.

Corallites are irregular in shape and moderately exsert. Septa, conspicuously exsert, are thickened along their outer margins and over the thecal rim. A conspicuous, sometimes wide intercorallite groove is invariably present. The coenosteum is smooth. Costae are well developed and an intercostal ridge may be present. The columella is well developed. The skeleton is always dense and hard.

Favia pallida from turbid water.

Corallites are usually circular and have thin skeletal structures including septa, thecae and costae. The columella may be very reduced. The coenosteum is usually blistered, as in other species from the same biotopes.

Affinities

This species shows close affinities with *F. speciosa* and *F. matthaii* as discussed on pp. 36 and 40.

Distribution

Widely distributed throughout the Indo-Pacific.

***Favia matthaii* Vaughan, 1918**

Synonymy

Favia matthaii Vaughan, 1918; Umbgrove (1940); (as *F. matthai*) Wijsman-Best (1972, 1974).

Figs. 56-61 *Favia matthaii* ($\times 2.5$).

Figs. 56, 57 Different coralla from Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97, Fig. 56 showing characteristically exsert septa.

Figs. 58, 59 Different coralla from Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91, Fig. 59 showing the highly irregular, dentate septa frequently associated with heavy infestation of boring organisms.

Fig. 60 From Fantome Island, Palm Islands, collecting station 34.

Fig. 61 From Dewar Island, Murray Islands, collecting station 29.



Fig. 56A

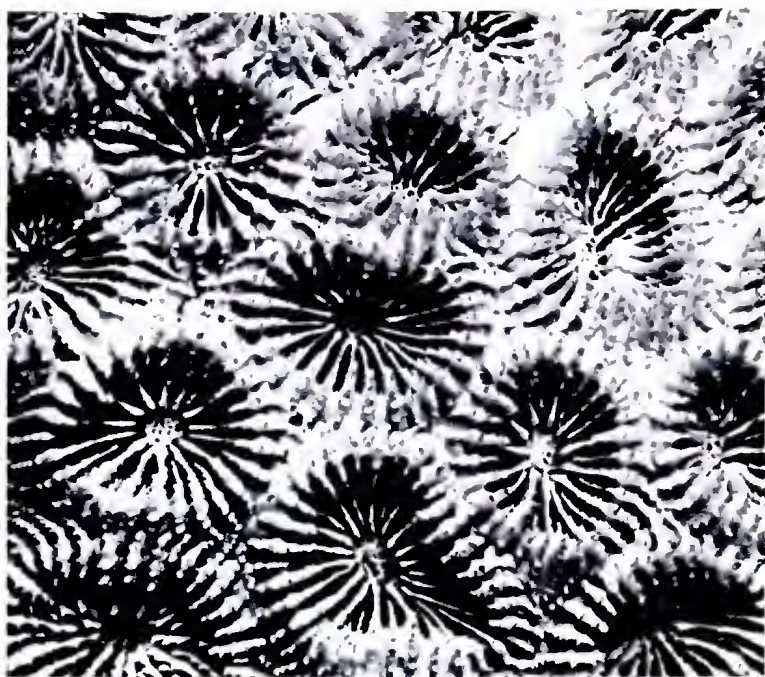


Fig. 57A

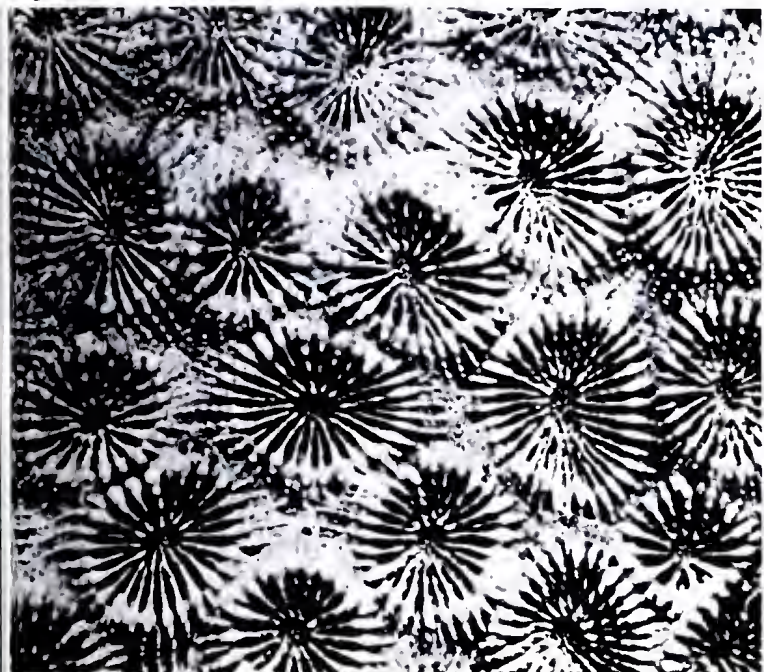


Fig. 58A

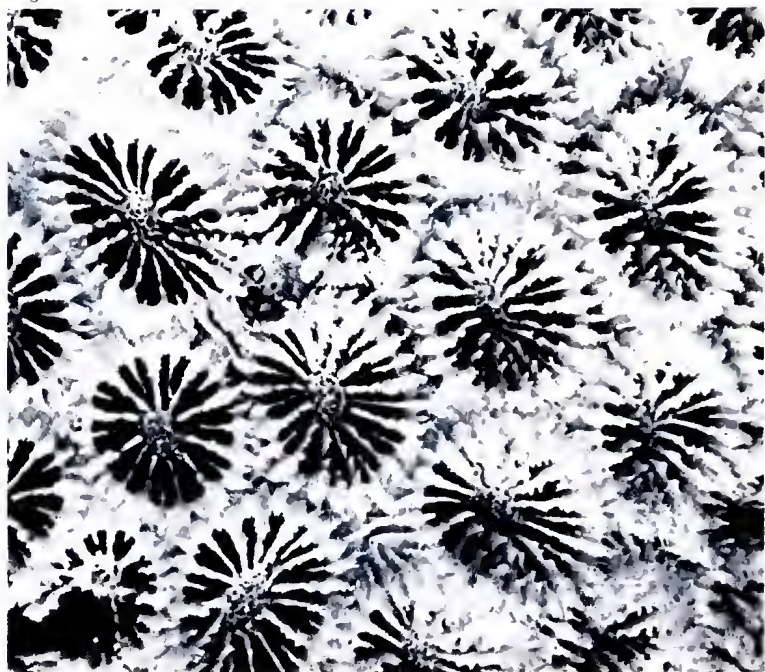


Fig. 59A

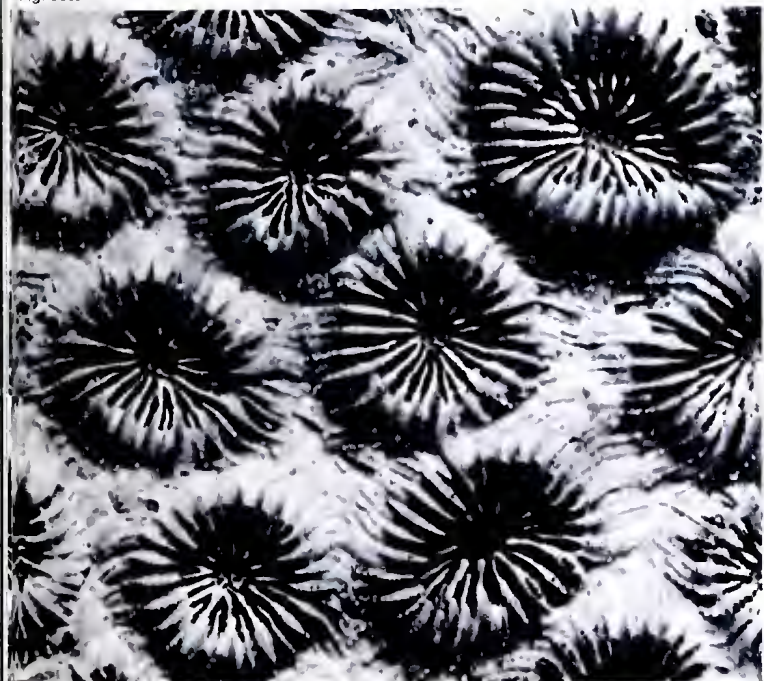


Fig. 60A

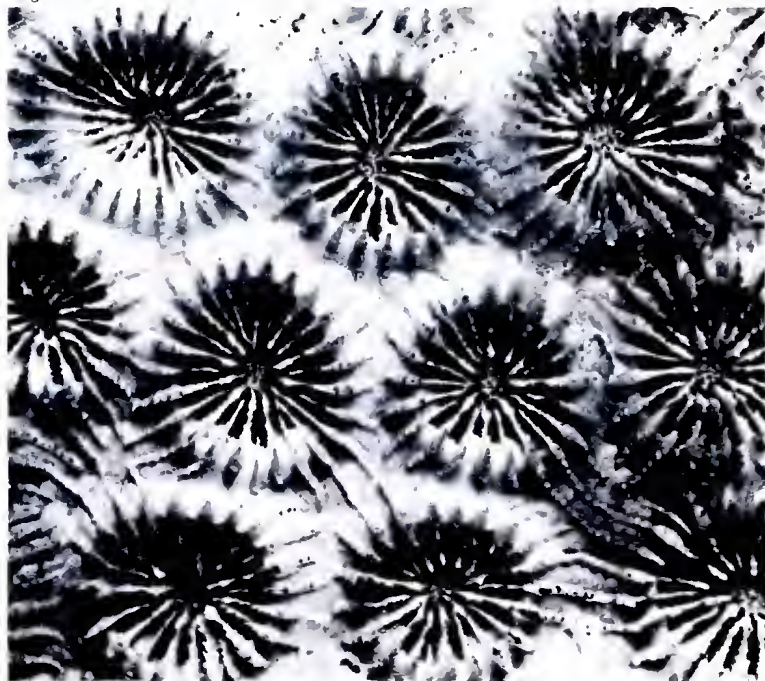


Fig. 61A

The relative lack of reference to this species in the literature appears to be a result of difficulties of recognition rather than restricted distribution or rarity.

Material studied

Murray Islands (2 specimens), **Sue Island**, **Tijou Reef**, **Jewell Reef** (2 specimens), **Yonge Reef**, **Lizard Island** (4 specimens), **MacGillivray Reef**, **Ribbon Reef** (2 specimens), **Hope Island**, **Low Isles**, **Palm Islands** (46 specimens), **Whitsunday Islands** (8 specimens), **Bushy Island-Redbill Reef**, **Swain Reefs**.

These localities include collecting stations 2, 9, 12, 17, 29, 34, 35, 36, 37, 38, 41, 43, 45, 55, 57, 60, 65, 73, 74, 83, 90, 91, 97, 99, 102.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are massive, rounded, occasionally flat or encrusting. They are plocoid, with circular corallites 9-15mm diameter. Septa are in three arbitrarily defined orders, the first forming a well defined, distinctive paliform crown around the columella. Sometimes there is more than one concentric circle. Second order septa do not reach the columella and do not have paliform lobes. Third order septa are abortive. All septa, especially those of the third order, have elongated inwardly projecting dentations which are usually arranged in concentric circles. They have granulated sides and finely serrated margins, the latter being particularly prominent on the inner margins of the paliform lobes of first order septa. The columella is compact and set deep in the calice. Costae are equal. They are prominently beaded, with beads of adjacent costae forming concentric circles which are clearly recognisable in living colonies with contracted polyps. Costae of adjacent corallites are not usually adjoined. The coenosteum between the costae is usually blistered. Budding is entirely intratentacular.

Living colonies (Figs. 424, 425) usually have a uniform colour, mostly brown or grey.

Skeletal variation

Corallite structure varies greatly within colonies, especially those from turbid biotopes which are frequently infested with *Lithophaga* and other boring organisms (Fig. 59). Colonies from such biotopes usually have wide, shallow calices and thin thecae. Septa usually have very elongated dentations and frequently the paliform crown is not as prominent as it is in coralla from most reef biotopes.

Affinities

Favia matthaii is close to *F. pallida* and may be confused with it in large collections with inadequate environmental descriptions. However, they are readily distinguished underwater and in collections from similar biotopes. *Favia matthaii* has shallower, more open calices with more exsert septa and a more prominent paliform crown or series of crowns. The concentric circles of elongated septo-costal dentations are readily recognisable underwater. The different colours of the oral disc and coenosarc of *F. pallida* (see p.38) usually distinguish it from *F. matthaii* and also from *F. favius*. The latter species has markedly larger, more protruding corallites than *F. matthaii* and substantially differing calicular structures.

Distribution

Previous reports of this species are from the western Indian Ocean, Madagascar, the Indonesian Archipelago and New Caledonia.

***Favia rotumana* (Gardiner, 1899)**

Synonymy

Astraea rotumana Gardiner, 1899.

Favia rotumana (Gardiner); Hoffmeister (1925); Yabe & Sugiyama (1935); Yabe,

Sugiyama & Eguchi (1936); Wells (1954); Nemenzo (1959); Ma (1959); Chevalier (1971); Wijsman-Best (1972, 1974); Scheer & Pillai (1974).

Chevalier (1971) listed three junior synonyms of *F. rotumana* used by Gardiner (1899): *Favia denticulata* Gardiner, *A. pallida* Dana and *A. affinis* Gardiner.

Favia rotumana Gardiner, Coel. 5686 of the Zoological Museum Amsterdam (figured, Wijsman-Best (1972) Plate III Fig. 2) is designated neotype of this species as the holotype is lost.

Material studied

Thursday Island, Great Detached Reef (12 specimens), **Tijou Reef, Lizard Island, Three Isles, Palm Islands** (6 specimens), **Bushy Island-Redbill Reef, Swain Reefs** (4 specimens).

These localities include collecting stations 1, 2, 5, 32, 34, 42, 54, 55, 60, 67, 76, 79, 80, 81, 90.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are massive, usually rounded, cerioid to sub-plocoid. Corallites are typically irregular in shape, usually being monocentric, but sometimes forming short irregular valleys containing up to three centres. The septa are usually thin and characteristically irregular in shape and appearance. All septa descend steeply inside the thecae. Those reaching the columella usually form paliform lobes which are seldom conspicuous. They have prominent dentations of irregular length, giving the septa a ragged appearance. The inner margins of the paliform lobes are especially prominently dentate. Many dentations form horizontal synapticular fans bordered with granulations. The sides of the septa and also the endotheca are granulated. The septa are usually irregularly exsert. Those of adjacent corallites are not usually adjoined. The columellae are compact. In many coralla (e.g. Fig. 64), the endotheca can be readily distinguished from the exotheca, and in most coralla, vesicular exothecal dissepiments are found.

Skeletal variation

The wide diversity of environments occupied by this species is reflected in the wide variation of its calicular structures. The present series contains three intergrading ecomorphs:

Favia rotumana from shallow, well-illuminated biotopes (Fig. 62).

Coralla collected from clear, shallow water where coral growth is abundant show thickening of all skeletal components and reduction in size of the columella. Septo-costae on either side and above the thecae, as well as the paliform lobes, may be very thick. Frequently there is a large amount of fusion between septa. All coralla are clearly plocoid.

Favia rotumana from biotopes exposed to strong wave action (Figs. 63, 64).

As with other species of *Favia*, coralla from exposed outer reef slopes have thickened thecae and septa. However, this is less apparent than in most *Favia* (e.g. the corallum illustrated in Fig. 64). Corallites are near circular and are always plocoid. The arrangement of the septa is relatively regular.

Favia rotumana from protected biotopes (Figs. 65, 66).

Coralla become cerioid with irregularly shaped corallites.

Septa are very exsert, have long, irregular dentations and a generally ragged appearance.

Fig 62 ▶

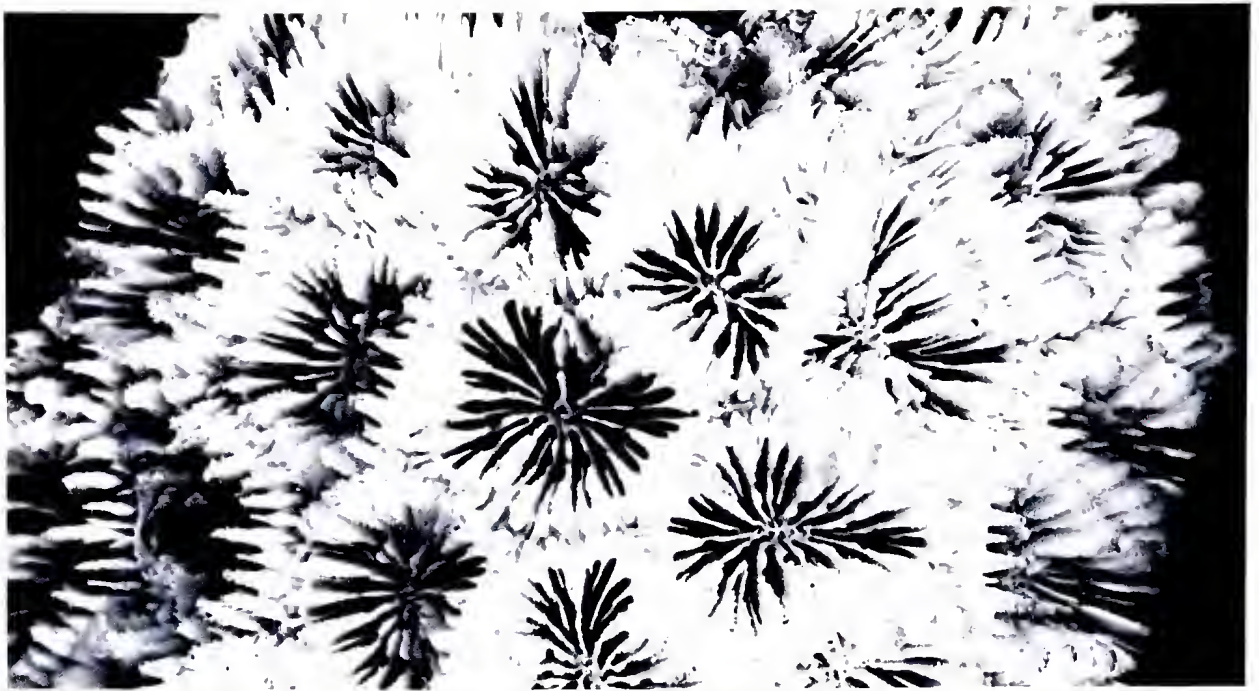


Fig 63 ▼

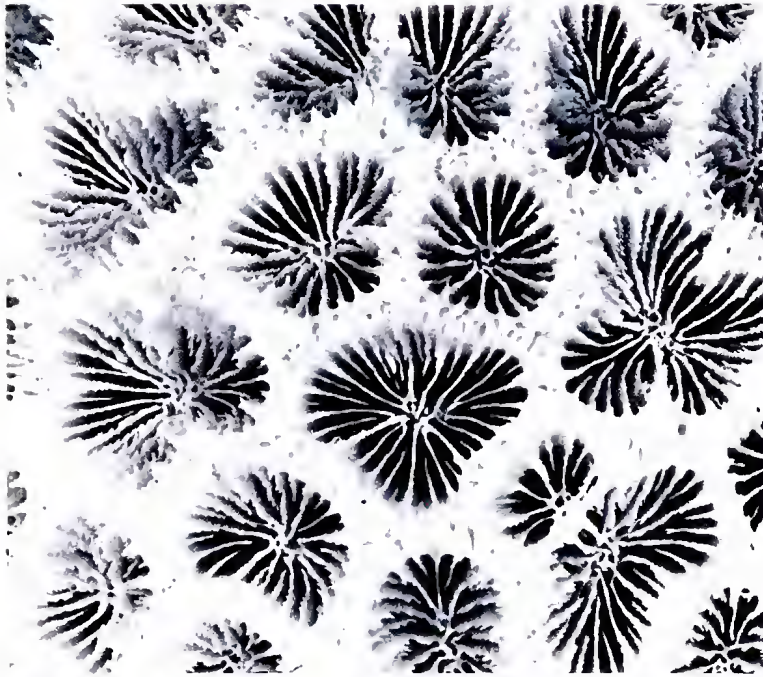


Fig 66 ▼

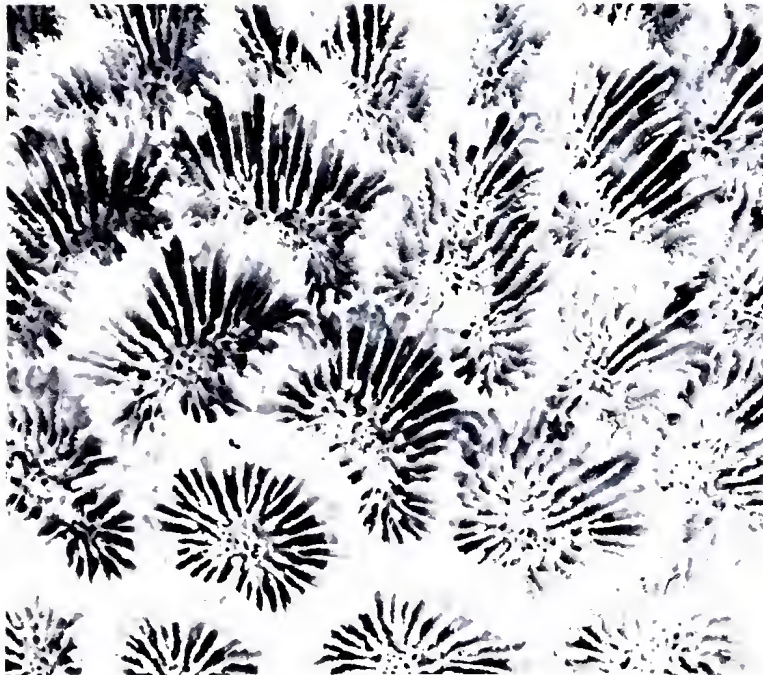


Fig 64 ▼

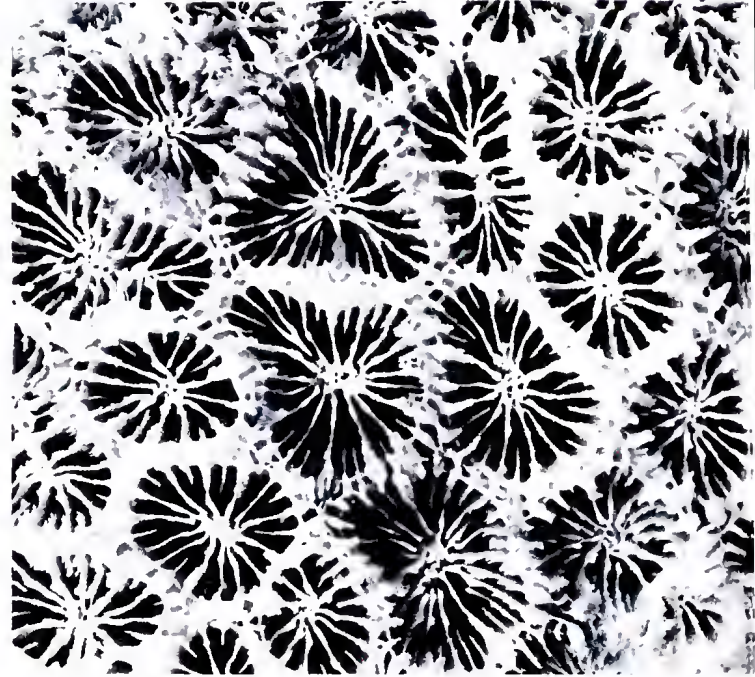
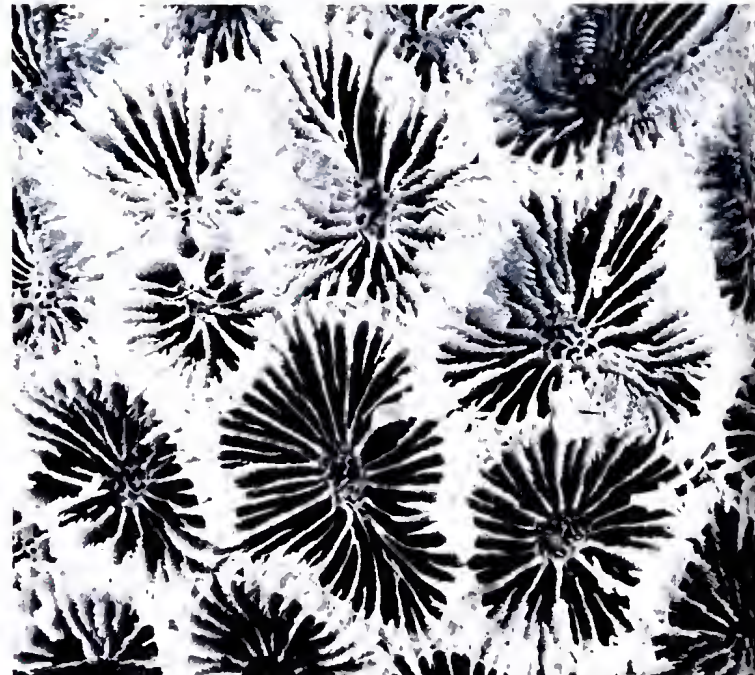


Fig 65 ▼



Distribution

This species appears to be restricted to the western Pacific: the China Sea in the north, the Philippines and the Marshall Islands, south to the Great Barrier Reef and east at least to Samoa.

Favia maxima n.sp.

Material studied

Murray Islands, Lizard Island, Ribbon Reef, Low Isles (2 specimens), **Palm Islands, Whitsunday Islands** (8 specimens), **Bushy Island-Redbill Reef, Swain Reefs** (2 specimens).

These localities include collecting stations 12, 31, 63, 80, 81, 91, 97, 98, 100.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are massive, with a flattened or near spherical growth form. They are plocoid, with very large calices (20-30mm diameter) which usually have distorted circular or oval outlines. They may be compressed closely together or widely separated (up to 9mm). Septa are not clearly arranged in orders. Those reaching the columella are usually thicker than the rest and have large paliform lobes which form a conspicuous crown around the columella. Other septa decrease in thickness as their radial length decreases, the smallest projecting inward only 1-2mm from the thecal rim. All septa are thickened over the theca and nearly evenly exsert. Costae are very conspicuous and are equal or sub-equal, those of adjacent corallites usually being adjoined. Inter-costal ridges are sometimes weakly developed. All septo-costae are regularly dentate; the inner margins of the paliform lobes may also be dentate. They are conspicuously granulated, the granules being arranged in rows running approximately normal to the margin. Sometimes these rows of granules are situated on shallow ridges. The endothecae are also granulated, the granules sometimes forming elongated spines. Budding is entirely intratentacular, in the manner characteristic of *Favia*.

Colonies are not brightly coloured (Figs. 427, 445), usually dull brown or yellow-brown. The oral discs are usually dull green. Polyps are large with elongated tentacles (Fig. 73).

Skeletal variation

Although the present series is too small to be reliably divided into ecomorphs, it does show that calice structures may vary greatly within the one locality or series of biotopes. As illustrated in Figs. 67-72, the degree of separation of the calices and the degree to which their structures are calcified provide the main sources of variation. Most colonies observed underwater closely resemble the holotype (Fig. 67); those growing in shaded environments tend to have the fine calicular structures indicated in Fig. 72.

Affinities

This is a distinctive species which does not closely resemble any other *Favia*. It most closely resembles *Favites rotundata*, which has similar sized corallites. However, these species

Figs. 62-66 *Favia rotumana* ($\times 2.5$)

Fig. 62 From Swain Reefs, collecting station 79, showing heavily calcified calicular structures.

Figs. 63, 64 From Great Detached Reef, collecting station 1, showing angular septal arrangement and reduction of paliform lobes. Endotheca of adjacent corallites are clearly distinguished in Fig. 64.

Fig. 65 From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.

Fig. 66 From Three Isles.

can readily be distinguished by their different modes of budding, which are characteristic of their respective genera, and by the various differences in calice structure, as illustrated.

Figs. 67-72 *Favia maxima*

Figs. 67, 68 Holotype from Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97 ($\times 0.6$ and 2.5 respectively).

Fig. 69 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98 ($\times 2.5$).

Fig. 70 From Lizard Island Lagoon, collecting station 100 ($\times 2.5$).

Fig. 71 From Ribbon Reef Lagoon, collecting station 63 ($\times 2.5$).

Fig. 72 From Frigate Cay, collecting station 81 ($\times 2.5$).

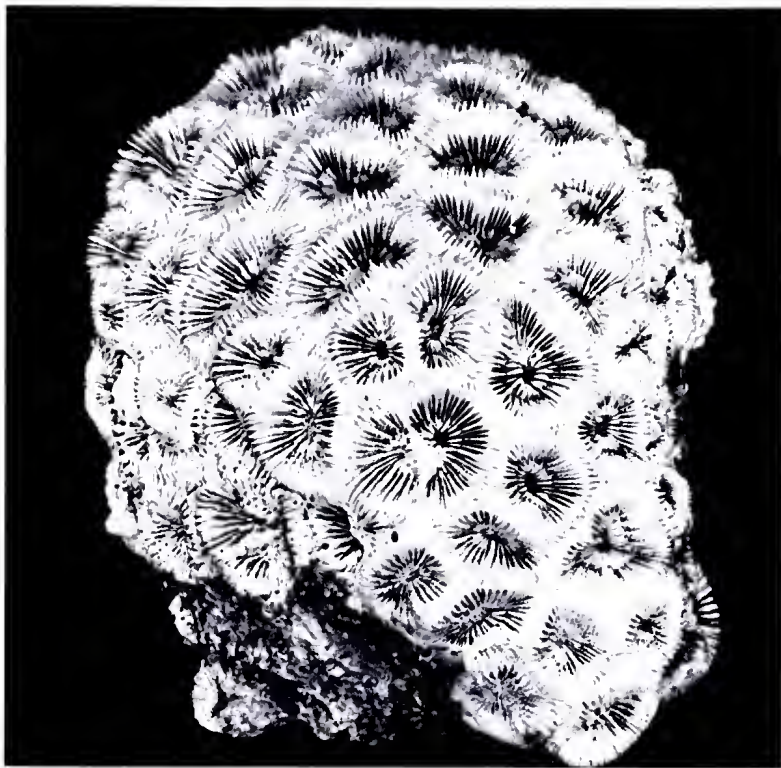


Fig. 67▲



Fig. 68▲



Fig. 69▲



Fig. 70▲

Etymology

Named *maxima* as this species is the largest described east Australian *Favia*.

Holotype (Fig. 67)

Dimensions: The maximum is 16cm, the minimum 12.2cm.

Locality: Nara Inlet, Hook Island, Whitsunday Islands (principal collecting station 97), Great Barrier Reef.

Depth: 5m.

Collector: J. E. N. Veron.

Holotype: British Museum (Natural History) 1977.1.1.1.

Paratypes

Australian Institute of Marine Science.

Queensland Museum, Australia.

Rijksmuseum van Natuurlijke Historie, Nederland, No. 10732.

Distribution

Great Barrier Reef and New Caledonia (recorded as *F. fava* 'ecotype from biotope 7', Fig 2, Plate II, Wijsman-Best, 1972).

Favia lizardensis n.sp.

Material studied

Waining Reef, Jewell Reef, Lizard Island (3 specimens), **MacGillivray Reef** (4 specimens), **Ribbon Reef** (2 specimens), **Low Isles, Palm Islands** (2 specimens), **Whitsunday Islands** (12 specimens), **Pompey Complex, Swain Reefs**.

These localities include collecting stations 62, 63, 65, 69, 70, 74, 97, 98, 99, 100.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are massive, tending towards a regular, spherical growth form. Corallites are circular or oval, 10-13mm in diameter and are very regularly spaced. Septa are not clearly arranged in orders. Those reaching the columella usually have weakly developed paliform



Fig. 71▲

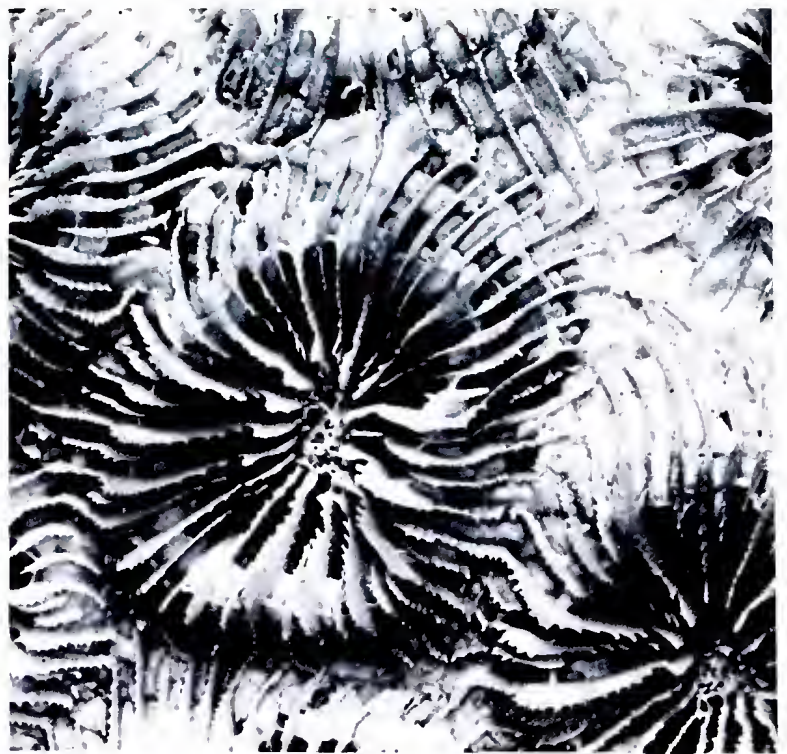


Fig. 72▲

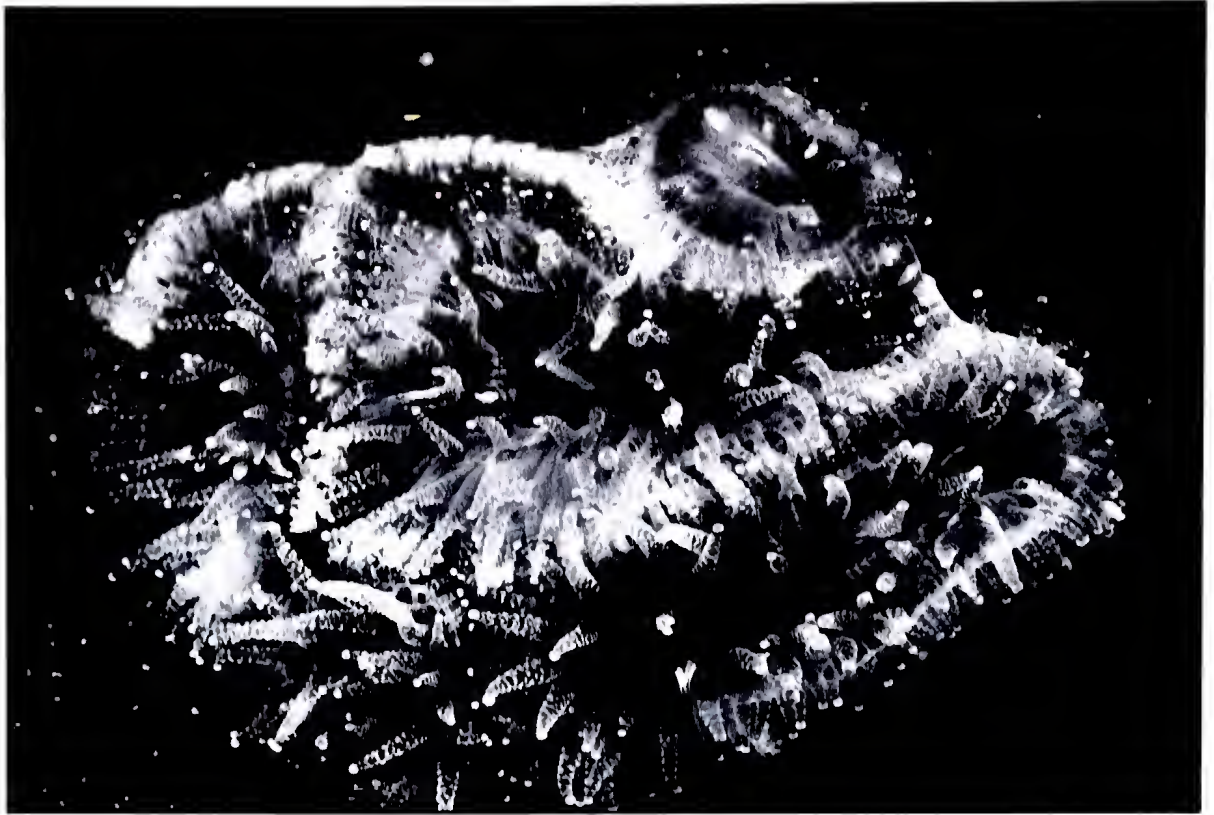


Fig. 73 *Favia maxima* from the Swain Reefs showing polyps expanded at night ($\times 2.0$).

lobes. All septa are thin and have fine, elongated dentations along their whole length and fine granules on their sides. They are evenly exsert and usually thickened above the thecae. Costae are even and very conspicuous. The endothecae are usually thin; the walls of the calices near vertical. The columellae are compact and usually small. The coenosteum is blistered in all but the most heavily calcified colonies. Budding is intratentacular, mono- to tristomadaeal.

This species can usually be recognised by its colour alone; the coenosarc being pale pink or brown and the oral disc green. This colour pattern is very uniform over the whole colony (Figs. 428-430).

Affinities

Although this species is very distinct underwater, it may be confused with other *Favia* species, especially *F. favus*, in large collections from diverse biotopes. It differs from *F. favus* in having more regular, shallower corallites with thinner septa and usually much thinner thecae. In the latter respect, *F. lizardensis* resembles *F. pallida* from protected biotopes but has larger corallites and septa which are more exsert and which have more elongated dentations.

This appears to be the same species as *Parastrea clouei*, named by Valenciennes (? 1846, unpublished manuscript) and redescribed as *Favia clouei* by Edwards & Haime (1857), who gave a description which fits the present series, but no holotype is designated. A new name is given to this species because it cannot be definitely associated with *F. clouei*. Matthai (1914) figured *F. clouei* (Plate 23, Figs. 1, 2 and 5; Plate 25, Fig. 2), clearly the present species, but he appeared partly to confuse it with *F. favus* (Plate 21, Fig. 1). Klunzinger's (1879) figure

Figs. 74-77 *Favia lizardensis* ($\times 2.5$).

Fig. 74 Holotype from MacGillivray Reef, collecting station 74.

Figs. 75, 76 (Same corallum) from Ribbon Reef, collecting station 63.

Fig. 77 From Lizard Island Lagoon, near Bird Island, collecting station 100.

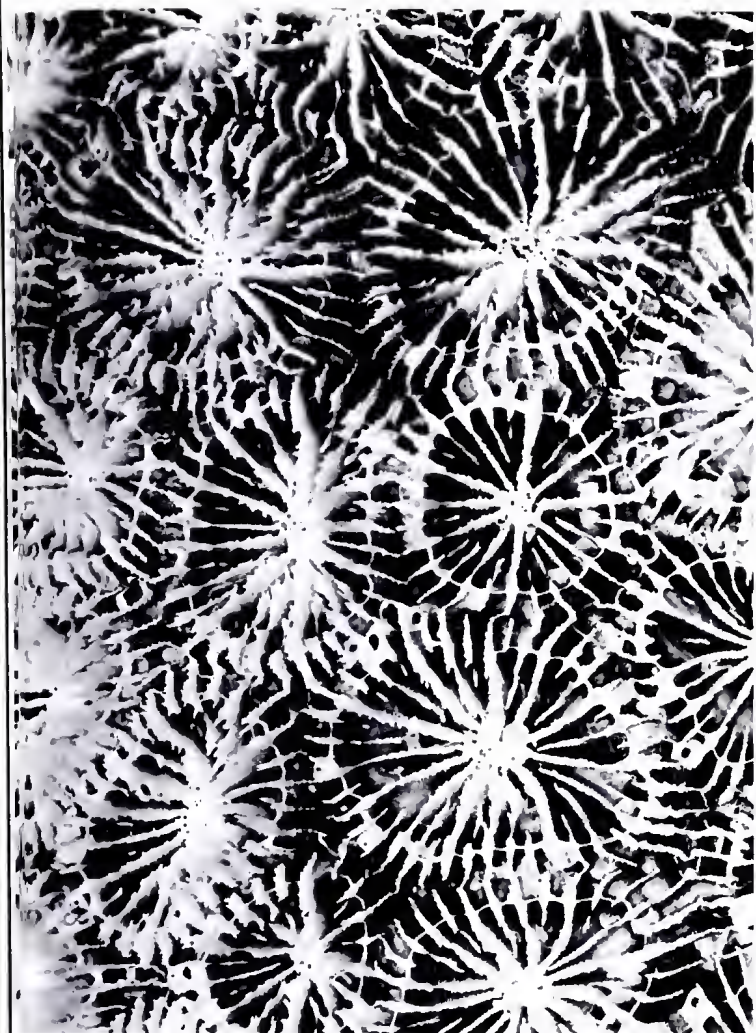


Fig. 74A



Fig. 75A



Fig. 76A

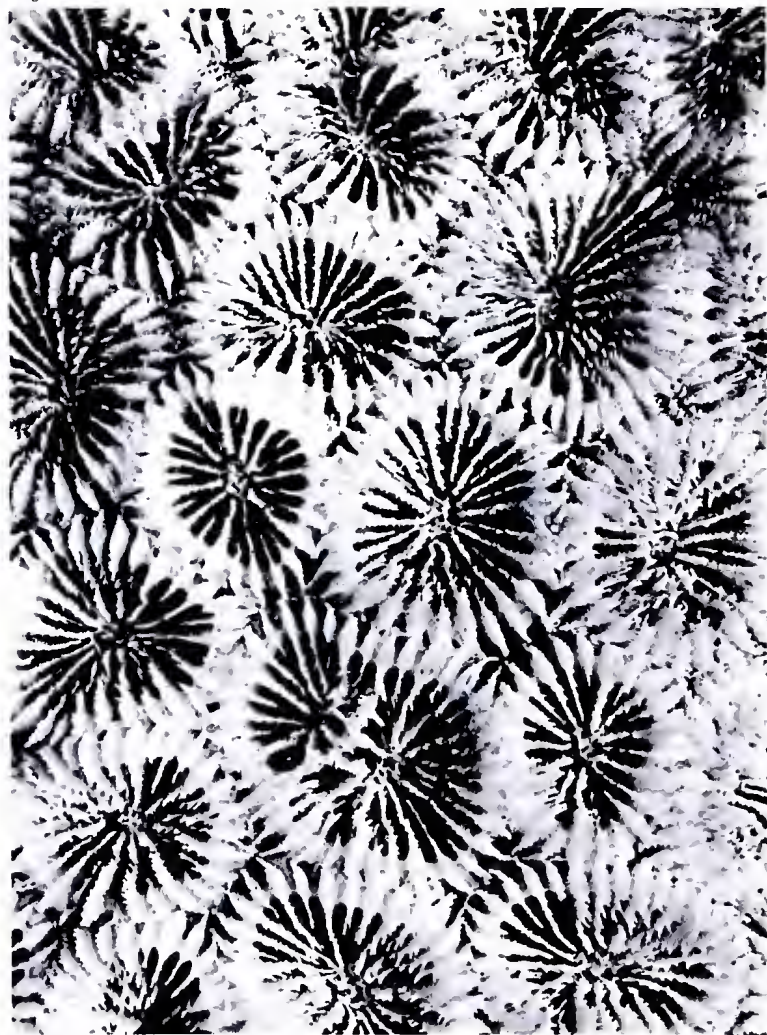


Fig. 77A

of *F. cavernosa* (Vol. III, Plate 3, Fig. 4) also appears to be *F. lizardensis*. Forskål's type of *F. cavernosa*, however, belongs to *F. fava*. There remains a possibility that *F. lizardensis* has a senior synonym but none has been positively associated with the present series, one of the most distinctive characters of which is the colour and appearance of the living colony.

Etymology

Named after Lizard Island, where this species was initially studied.

Holotype (Fig. 74)

Dimensions: The maximum is 12.7cm, the minimum 9.6cm.

Locality: McGillivray Reef near Lizard Island.

Depth: 7m.

Collector: J. E. N. Veron.

Holotype: British Museum (Natural History) 1977.1.1.2.

Paratypes

Australian Institute of Marine Science.

Queensland Museum, Australia.

Rijksmuseum van Natuurlijke Historie, Nederland, No. 10733.

Favia sp. 1

Material studied

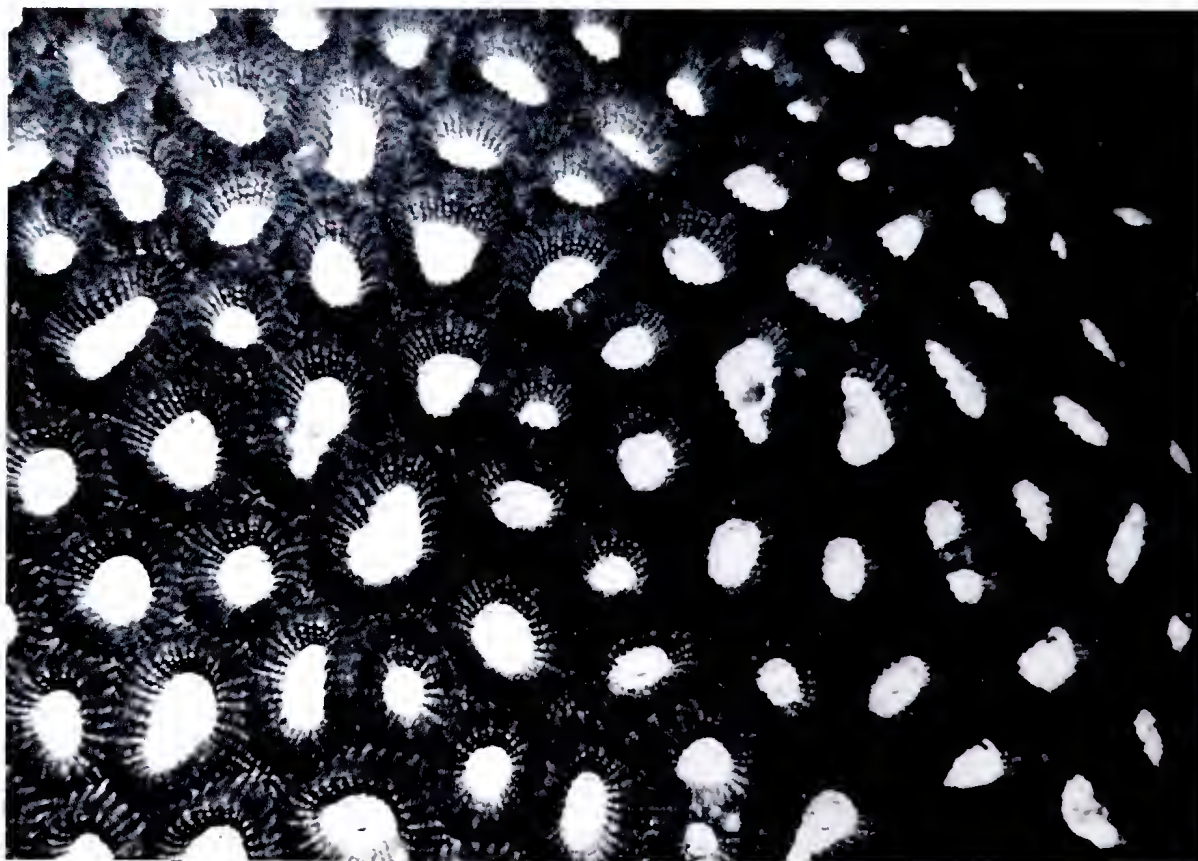
Palm Islands (4 specimens), **Magnetic Island**, **Whitsunday Islands** (2 specimens).

These localities include collecting stations 34, 38, 41, 45, 84, 97, 98.

Previous records from Eastern Australia

Not previously recorded.

Fig. 78 *Favia lizardensis* from Swain Reefs, collecting station 68, *in situ*.



Characters and affinities

This apparently rare species is close to *F. favus* (see p.27). It is usually distinguished from it by having larger corallites (up to 20mm diameter) with very exsert thecae. Septa have regular, relatively fine dentations. Paliform lobes are present in some coralla, although these are inconspicuous. Budding is equal, usually mono- to tri-stomodaeal.

There is little doubt that this is a valid species, although it is not always clearly distinct from *F. favus*. Figs. 79, 80 illustrate two specimens from widely differing biotopes, and Fig. 416 illustrates adjacent colonies of *Favia* sp.1 and *F. favus in situ*. It is close to, or the same as, *Bikiniastrea maritima* Nemenzo, 1971.

Favia sp. 2

Material studied

Whitsunday Islands, collecting station 97.

Previous records from Eastern Australia

Not previously recorded.

Figs. 79, 80 *Favia* sp. 1 ($\times 2.5$).

Fig. 79 From between Brisk and Falcon Islands, Palm Islands, collecting station 41.

Fig. 80 From Hazard Bay, Orpheus Island, Palm Islands, collecting station 45, showing the ecomorph from very protected biotopes.



Fig. 79▲



Fig. 80▲

Characters

This completely distinct species is represented in the present collection by only two coralla. Both are massive with very large corallites (up to 30mm across). They are closely compacted and have irregular outlines. Calices are up to 10mm deep and are very open with the septa remaining close to the endothecae. Septa are not arranged in cycles. They are finely serrated and tend to form rudimentary paliform lobes which are also serrated. The columellae are spongy. Coralla are sub-plocoid with septa of adjacent corallites adjoining in an irregular fashion and sometimes forming a fine intercalicular ridge. Budding is mono- or tri-stomodaeal.

GENUS *FAVITES* LINK, 1807

Generic synonymy

Favites Link, 1807; Vaughan (1907); Vaughan & Wells (1943); Wells (1956); Chevalier (1971).

Type species *Favites astrinus* Link, 1807 = *Madrepora abdita* Ellis & Solander, 1786.

Instability in the taxonomy of *Favites* has two main origins. Firstly, this genus can only be arbitrarily distinguished from other closely related genera, especially *Favia* and *Goniastrea* (see p.20). It was with good reason that Matthai (1924) placed all *Favites* species in *Favia*, and even in the most recent studies there is disagreement as to the best generic designation of some species. Secondly, delineation of species has led to confusion of synonymy especially of the *abdita/halicora/virens/vasta/flexuosa/rotundata* series (Fig. 82). Vaughan (1907) proposed the usage of *Favites* Link instead of *Prionastrea* Edwards & Haime, and in 1918 gave an account of the species within it with emphasis on this complex. He commented (p.111) that 'some specimens of *F. halicora* have a most perplexing resemblance to some specimens

Fig. 81 *Favia* sp. 2 from Darnley Island, collecting station 31 ($\times 2.5$).



of *F. abdita*.' He also commented (p.111) that 'the type of *Astraea virens* Dana . . . is so similar to Klunzinger's figure . . . of *Goniastrea halicora* that it might have served as the original'. Thus Vaughan appeared to have recognised the problems of synonymy of the types of these three species but nevertheless followed Matthai's (1914) opinion and partly confused these names in his own collections. According to Matthai (1924), Vaughan's *F. virens* is *F. vasta*;

Fig. 82 The synonymy of nominal species of *Favites*, and species of other genera previously placed in *Favites*, according to the authors indicated. Species names considered valid by each author are indicated by a cross. Synonyms are indicated by a dot and joining line. Generic designations are not indicated.

	Vaughan, 1918	Matthai, 1924	Yabe, Sugiyama & Eguchi, 1936	Umbgrove, 1939, 1940	Crossland, 1952	Wells, 1954, 1955b; Stephenson & Wells, 1955	Nemenzo, 1959	Chevalier, 1971	Wijsman-Best, 1972	Present study
abdita	x	x	x	x	x	x	x	x	x	x
halicora	x	x			x	x	x	x		x
virens	x		x	x	x	x	x	●	x	●
vasta	●	x			●	●		x	●	●
flexuosa	●		x	x	●	x	x	x	x	x
complanata			x					x		x
aspera					x	x				
favosa		x	x	x						
acuticollis								x	x	●
yamanarii			x	x			x	●	●	●
pentagona	x	x	x					x	x	x
melicerum	x							x	x	
rufa								x	x	●
chinensis								x	x	x
parvicella							x	●	●	
palauensis								x		
gailei								x		
spectabilis	x			x		x				
ruselli										x

according to Chevalier (1971), Vaughan's specimens from Murray Islands appear to be *F. flexuosa*. Stephenson & Wells (1955) (and later Nemenzo, 1959) call Vaughan's *F. abdita* (in part) *F. flexuosa* and comment that Matthai's *F. vasta* is *F. virens*. Crossland's (1952) inclusion of *F. flexuosa* and *F. vasta* in synonymy with his *F. virens* increases this confusion as his two figures of *F. virens* are clearly *F. rotundata*.

The conclusion of this study is that this complex is divisible into three discrete species which are readily recognisable underwater and in collections from diverse biotopes of the Great Barrier Reef. These species are:

1. *Favites abdita*, which appears to include the type of *F. virens* (Fig. 89) and some references to *F. halicora*.
2. *Favites flexuosa*, which has been given the name *F. virens* by many previous authors and *F. vasta* by others.

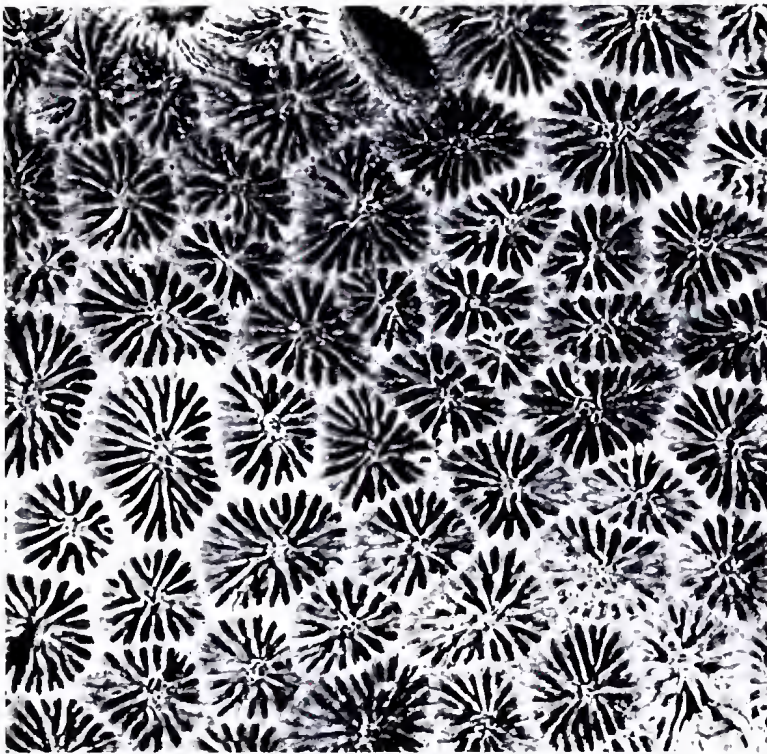


Fig. 83▲

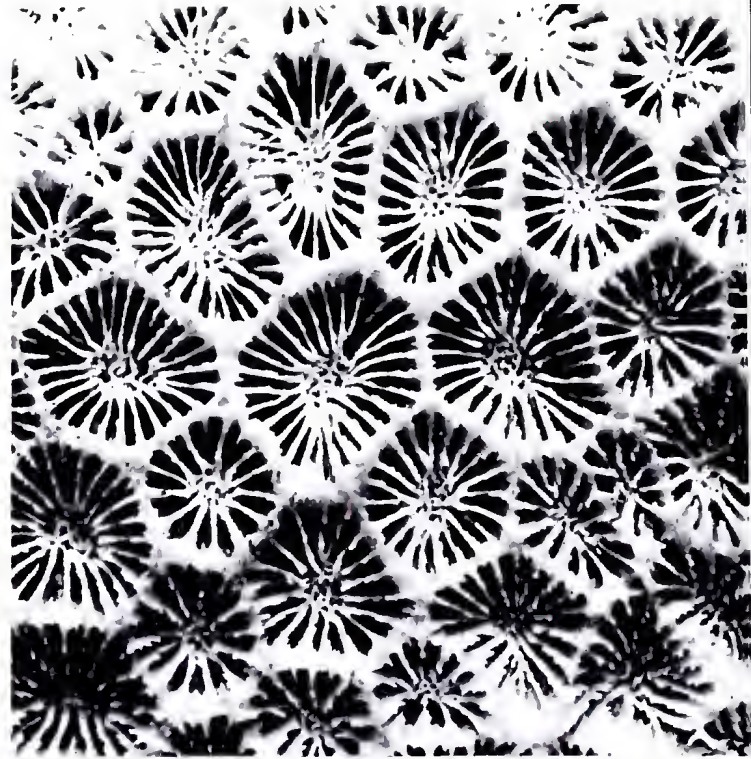


Fig. 84▲

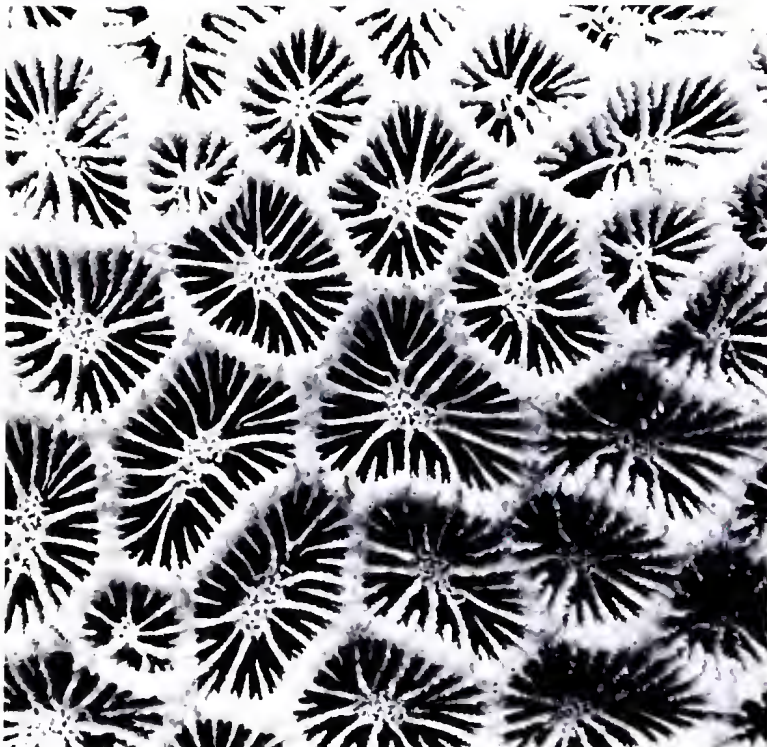


Fig. 85▲

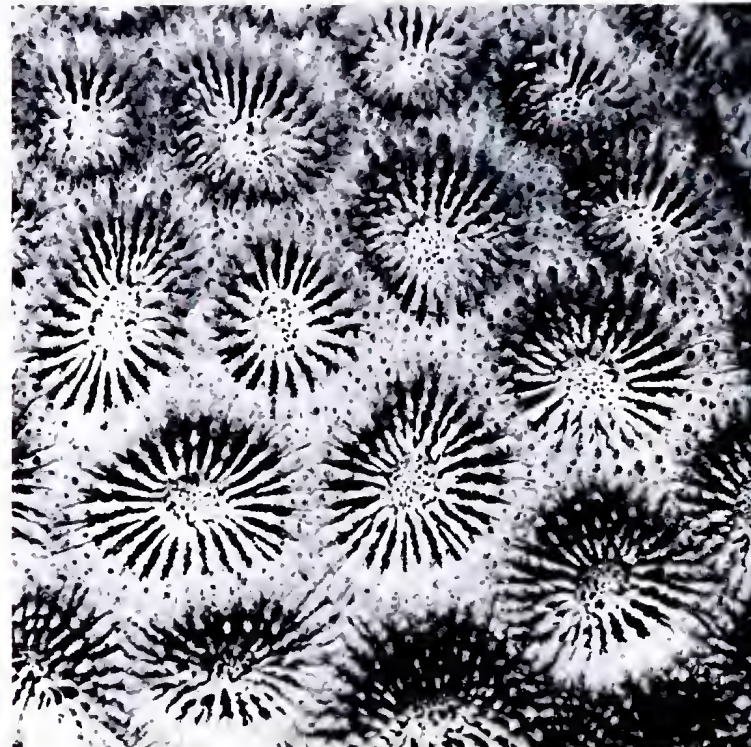


Fig. 86▲

3. *Favites rotundata*, a new name given to the species which some authors have, in part or in whole, called *F. flexuosa*. The identity of Dana's type of *F. flexuosa* (Fig. 102), however, very clearly belongs to species 2 above, not 3, and is the senior synonym of that species. The third species is given a new name as it appears to have no clear senior synonym.

Favites chinensis (Verrill, 1866)

Synonymy

Prionastraea chinensis Verrill, 1866

?*Favites melicerum* Ehrenberg, 1834; Matthai (1914); Vaughan (1918); Wijsman-Best (1972).

Prionastraea acuticollis Ortmann, 1889.

Favites yamanarii Yabe & Sugiyama, 1935; Yabe, Sugiyama & Eguchi (1936); Umbgrove (1940); Nemenzo (1959); Rosen (1971).

Favites acuticollis (Ortmann); Chevalier (1971); Wijsman-Best (1972).

non *Favites chinensis* (Verrill) Wijsman-Best (1972).

Favites melicerum was considered a synonym of *F. pentagona* by Matthai (1914) and a valid species by Vaughan (1918) and Wijsman-Best (1972). The type, figured by Matthai (1914) (pl. 36 Fig. 2), a small colony encrusting a *Lambis* shell, is now lost. It cannot clearly be attributed to the present species or to *F. pentagona*.

The holotype and paratype (Fig. 88) of *F. chinensis* are very close to many specimens in the present series while the holotype of *F. acuticollis* (Fig. 83) is close to others. The two types, although somewhat different, belong to the one monospecific series which has been given the name *F. acuticollis* by previous authors.

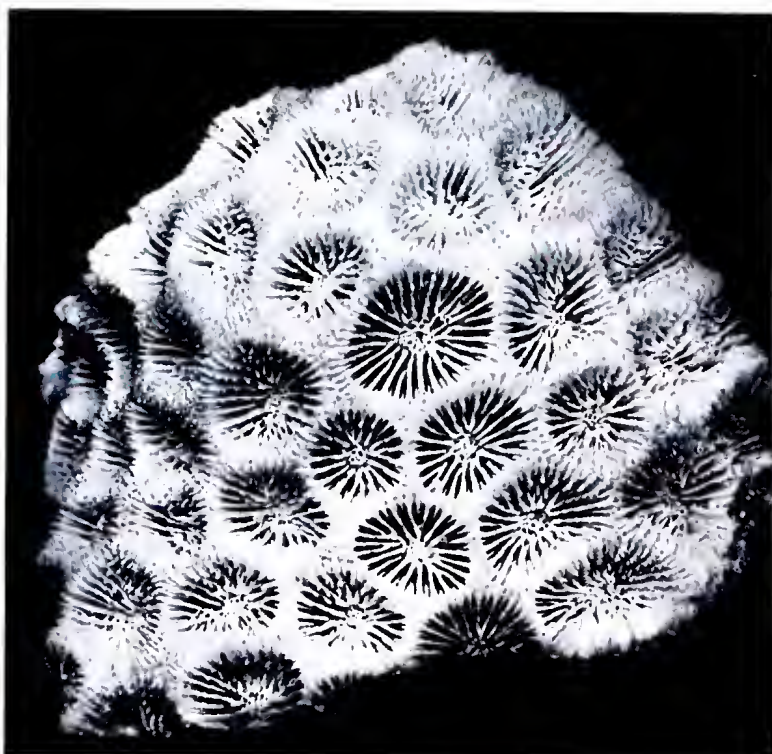
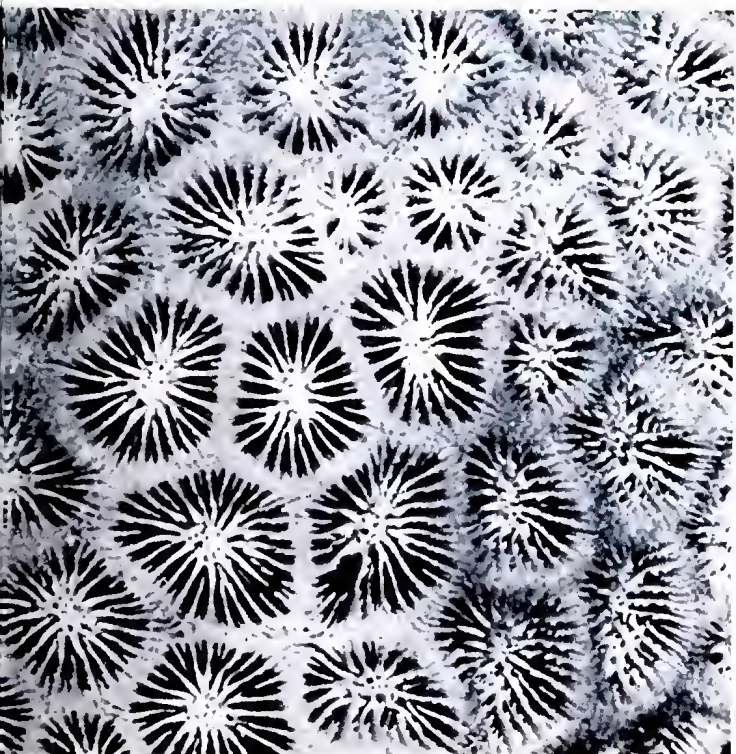
Figs. 83-88 *Favites chinensis* ($\times 2.5$)

Fig. 83 Holotype of *Favites acuticollis*.

Figs. 84, 85, 87 From Three Isles.

Fig. 86 From Houghton Island, collecting station 16.

Fig. 88 Holotype of *Favites chinensis*.



Material studied

Sue Island, Great Detached Reef (3 specimens), **Bewick Island, Houghton Island** (3 specimens), **Lizard Island** (3 specimens), **Three Isles** (5 specimens), **Hope Island** (4 specimens), **Low Isles** (3 specimens), **Bowl Reef, Palm Islands** (6 specimens), **Wheeler Reef**.

These localities include collecting stations 1, 5, 10, 17, 34, 36, 40, 41, 43, 45, 60, 91, 99.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are massive and rounded. Mature corallites are 10-13mm in diameter and tend to be angular or irregular in shape. Septa are in two or three indistinct orders; in some calices, all septa are equal. They vary in thickness but are usually spaced regularly and relatively widely. They have characteristically elongated dentations, especially on their upper margins where dentations of adjacent septa are frequently aligned in concentric rows. The dentations usually decrease in size towards the calice centre. Elongated dentations frequently have granulated tips which may form minute horizontal fans. Paliform lobes, if present, are short, rounded and inconspicuous. The columellae are well defined, compact, and seated deep within the calices. The thecae are thin and angular. Septa of adjacent corallites are usually aligned although in some plococerioid coralla there may be a deep inter-calicular groove.

Skeletal variation

This species is uncommon on the Great Barrier Reef, hence the range of growth form variation of the present series, illustrated in Figs. 84-87, is likely to be incomplete. There is little clear correlation between skeletal characteristics and environment other than, as with other *Favites*, the tendency of coralla from exposed biotopes to be heavily calcified with dense columellae and relatively thick septa. However, the thecae are usually thinner, the septa less numerous and less exsert, and the septal dentations shorter than in coralla from protected biotopes (e.g. Fig. 84).

Affinities

Favites chinensis is sometimes close to *F. abdita* but is distinguished by having smaller corallites which are usually angular, fewer septa and (less reliably) fewer but more elongated septal dentations. Chevalier (1971) notes that the endothecal dissepiments are much less developed in *F. acuticollis* (= *F. chinensis*).

Distribution

This species has been recorded from Ceylon, Indonesia, Japan, New Caledonia and the Great Barrier Reef. However it is likely to have a wider distribution than indicated in the present literature.

Favites abdita (Ellis & Solander, 1786)

Synonymy (partly after Wijsman-Best, 1972)

Madrepora abdita Ellis & Solander, 1786.

Favastrea magnifica de Blainville, 1830.

Astraea fusco-viridis Quoy & Gaimard, 1833.

?*Astraea hemprichii* Ehrenberg, 1834.

?*Astraea virens* Dana, 1846.

Astraea robusta Dana, 1846; Studer (1881); Quelch (1886); Gardiner (1904).

Prionastraea abdita (Ellis & Solander); Edwards & Haime (1857); Studer (1881); Gardiner (1899).

Prionastraea obtusata Edwards & Haime, 1849; Quelch (1886); Ortmann (1888)

Prionastraea quoyi Edwards & Haime, 1849; Quelch (1886).

Prionastraea sulfurea Edwards & Haime, 1857.

Prionastraea profundicella Edwards & Haime, 1849; Ridley (1883); Ortmann (1889).

Prionastraea crassior Edwards & Haime, 1849.

Prionastraea seychellensis Edwards & Haime, 1849; Ridley (1883).

Prionastraea gibbosa Klunzinger, 1879; Ridley (1883); Ortmann (1888, 1889).

Prionastraea magnifica (de Blainville); Studer (1881); Ridley (1883); Ortmann (1888, 1889).

Favia abdita (Ellis & Solander); Matthai (1914).

Favia hemprichii (Ehrenberg); Matthai (1914); Crossland (1931, 1935); Thiel (1932).

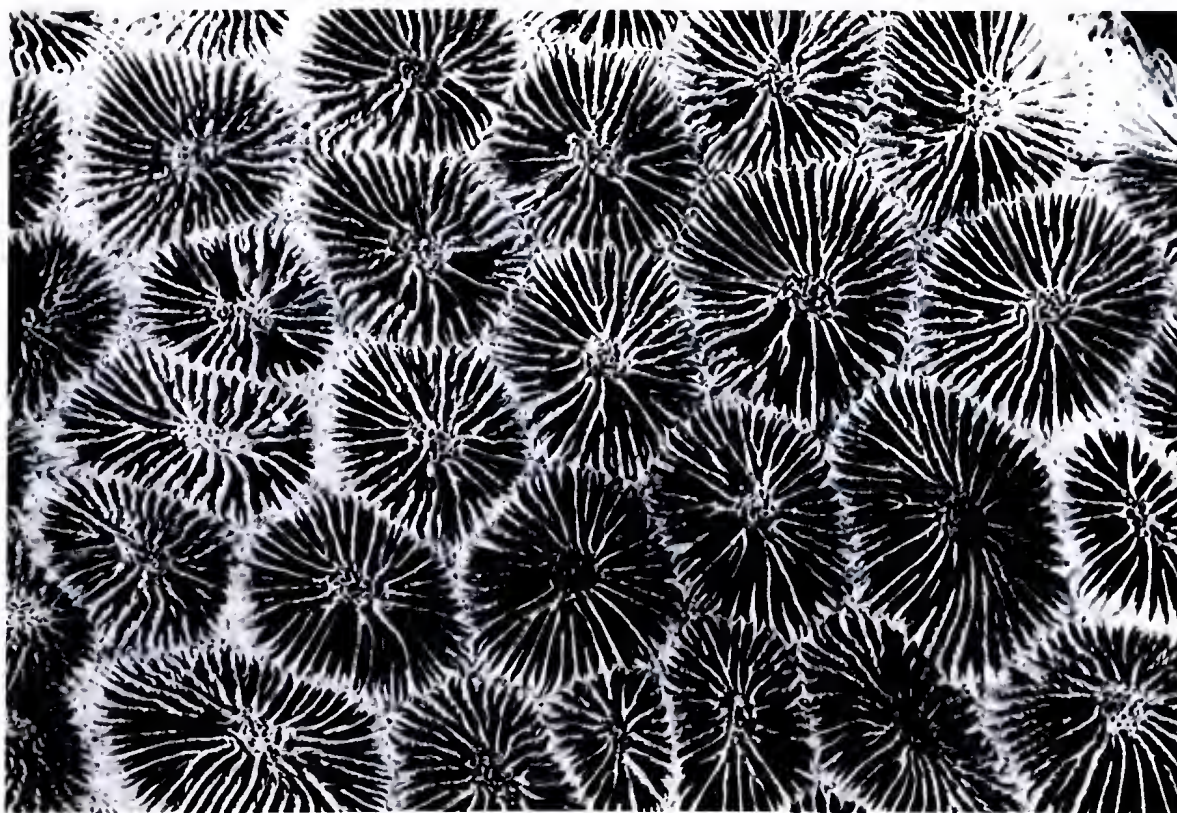
Favites abdita (Ellis & Solander); Vaughan (1918); Hoffmeister (1925); Faustino (1927); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1940); Crossland (1948, 1952); Wells (1954, 1955b); Stephenson & Wells (1955); Searle (1956); Nemenzo (1959); Ma (1959); Utinomi (1965, 1971); Chevalier (1968, 1971); Rosen (1971); Scheer (1972); Wijsman-Best (1972, 1976); Pillai & Scheer (1973, 1974).

The type of *F. virens* (Fig. 89) appears to be a *F. abdita*. The name *F. virens*, however, has most commonly been applied to *F. flexuosa* (see p.61).

Material studied

Thursday Island, Great Detached Reef (18 specimens), **Tijou Reef** (7 specimens), **Bewick Island** (3 specimens), **Houghton Island** (2 specimens), **Yonge Reef** (2 specimens), **Lizard Island** (5 specimens), **Eagle Reef** (2 specimens), **Three Isles**

Fig. 89 Holotype of *Favites virens* ($\times 2.5$).



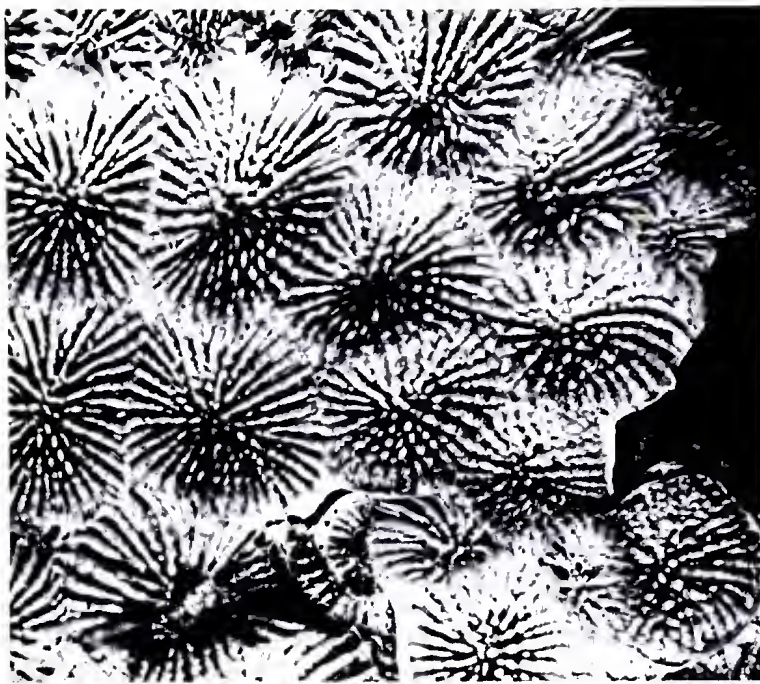


Fig. 90A

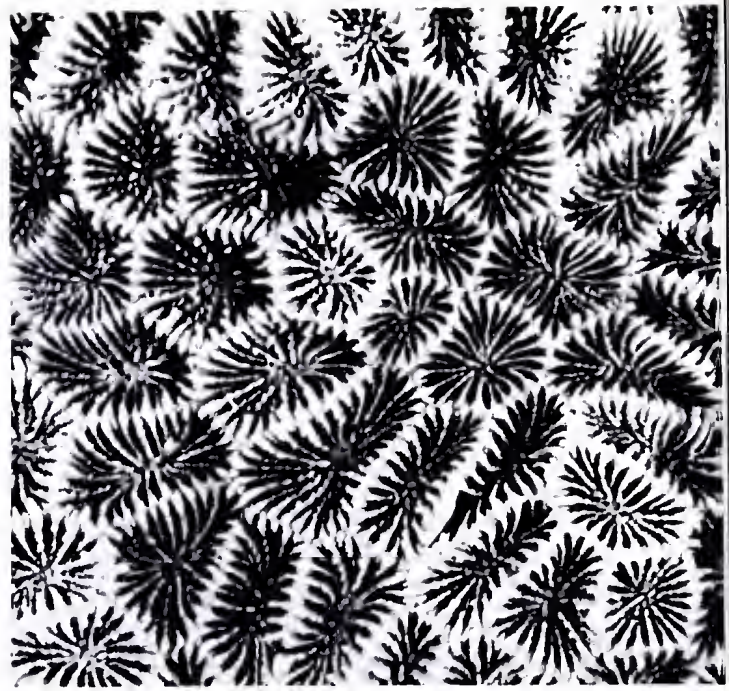


Fig. 91A



Fig. 92A

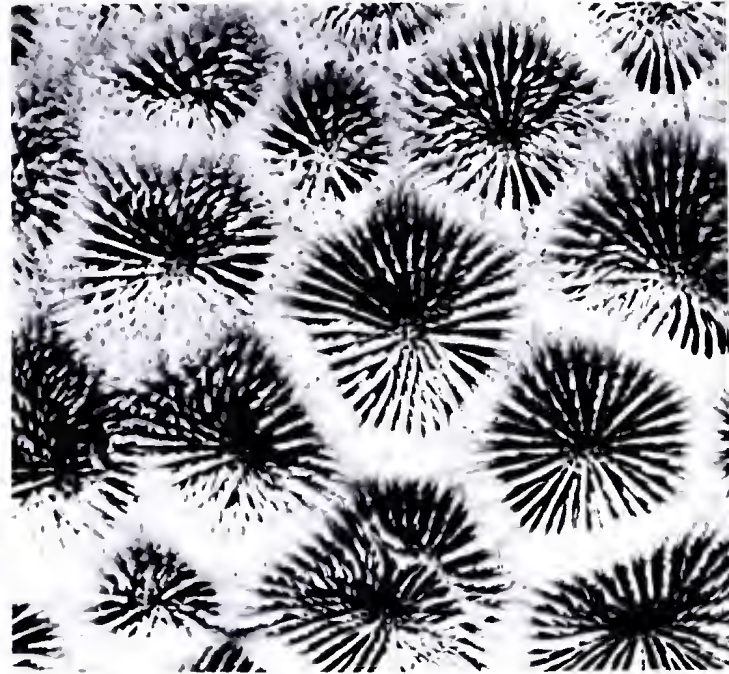


Fig. 93A

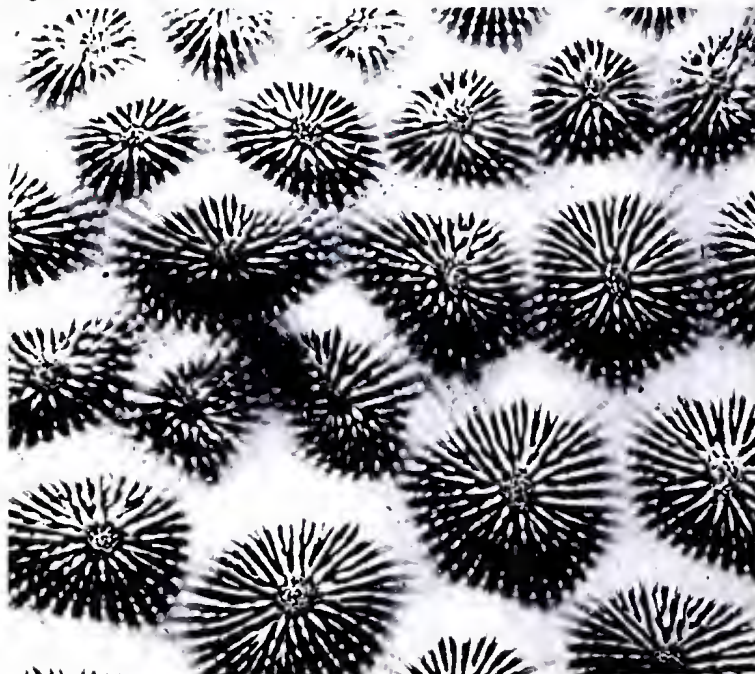


Fig. 94A



Fig. 95A

specimens), **Hope Island** (12 specimens), **Low Isles** (6 specimens), **Palm Islands** (36 specimens), **Magnetic Island**, **Whitsunday Islands**, **Solitary Island**.

These localities include collecting stations 1, 2, 5, 6, 9, 18, 19, 32, 33, 34, 35, 37, 40, 41, 43, 45, 54, 55, 57, 60, 85, 90, 92, 97, 99.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918), **Low Isles**, Manton (1935), Crossland (1952), Stephenson & Wells (1955); **Heron Island**, Salter (1954); **Moreton Bay**, Wells (1955a); **Solitary Islands**, Veron *et al.* (1974); **Lord Howe Island**, Veron (1974).

Characters

This is the most widespread of the Great Barrier Reef *Favites*, occurring at least as far south as Nambucca Heads and Lord Howe Island and is found in all biotopes normally occupied by hermatypic corals.

Colonies are massive, either rounded, flattened or hillocky (Fig. 432). Mature calices are usually 7-12mm in diameter and usually have a rounded rather than an angular appearance. The septa are moderately exsert, regularly spaced, and are usually uniform in thickness. Septal dentations are prominent along the length of the septal margin. Paliform lobes are either absent or weakly developed but do not form a conspicuous crown. The columellae are spongy and compact. The structure and appearance of the thecae often vary greatly from one part of a corallum to another. They are usually thin and irregular on hillocky parts and broad on flat sides where calices are shallow. Budding is always intratentacular and usually very unequal.

The colour of living colonies is variable. In deep or turbid biotopes they are usually dark; in well-illuminated areas they are usually various shades of pale brown, frequently with a bright green oral disc and/or stomodaeum (Fig. 433). Such colonies usually lose much of their colour during the summer wet season in the tropics. Those from southern localities are much more brightly coloured, usually various combinations of brown, green and red.

Skeletal variation

Coralla from far southern localities or from deep water tropical localities are flat, encrusting or plate like. Most Great Barrier Reef coralla tend to have a spherical growth form except in well-illuminated biotopes protected from strong wave action, where the hillocky growth form occurs.

In this species, calice structures vary with latitude almost as much as they do as a result of environmental extremes within a given region.

Favites abdita from temperate biotopes (Figs. 90, 91).

Coralla growing in very marginal conditions may be very thin with small, widely spaced calices which are frequently invaded by epitheca. Such calices are very shallow with skeletal structures very reduced. More massive coralla (e.g. Fig. 91) usually have much larger and deeper calices with angular outlines. The thecae are frequently very thin. The septa usually have very long, inwardly projecting dentations. Adjacent septa frequently fuse. The columellae are usually very reduced. Colour variations are noted above.

Favites abdita from protected, shallow biotopes (Figs. 94, 95).

Calices show little variation outside the general description above. Those on hillocky areas show many irregularities in shape but little variation otherwise.

Figs. 90-95 *Favites abdita* ($\times 2.5$).

Figs. 90, 91 From the Solitary Islands, showing extremes of variation. Fig. 90 shows a corallum with thin encrusting calices, Fig. 91 a corallum with deep calices and coarse calicular structures characteristic of temperate localities.

Fig. 92 From Juno Bay, Fantome Island, Palm Islands, collecting station 43.

Fig. 93 From Great Detached Reef, collecting station 1, showing a corallum with actively dividing calices and very dentate septa characteristic of exposed biotopes.

Figs. 94, 95 From Fantome Island, Palm Islands, collecting station 34.

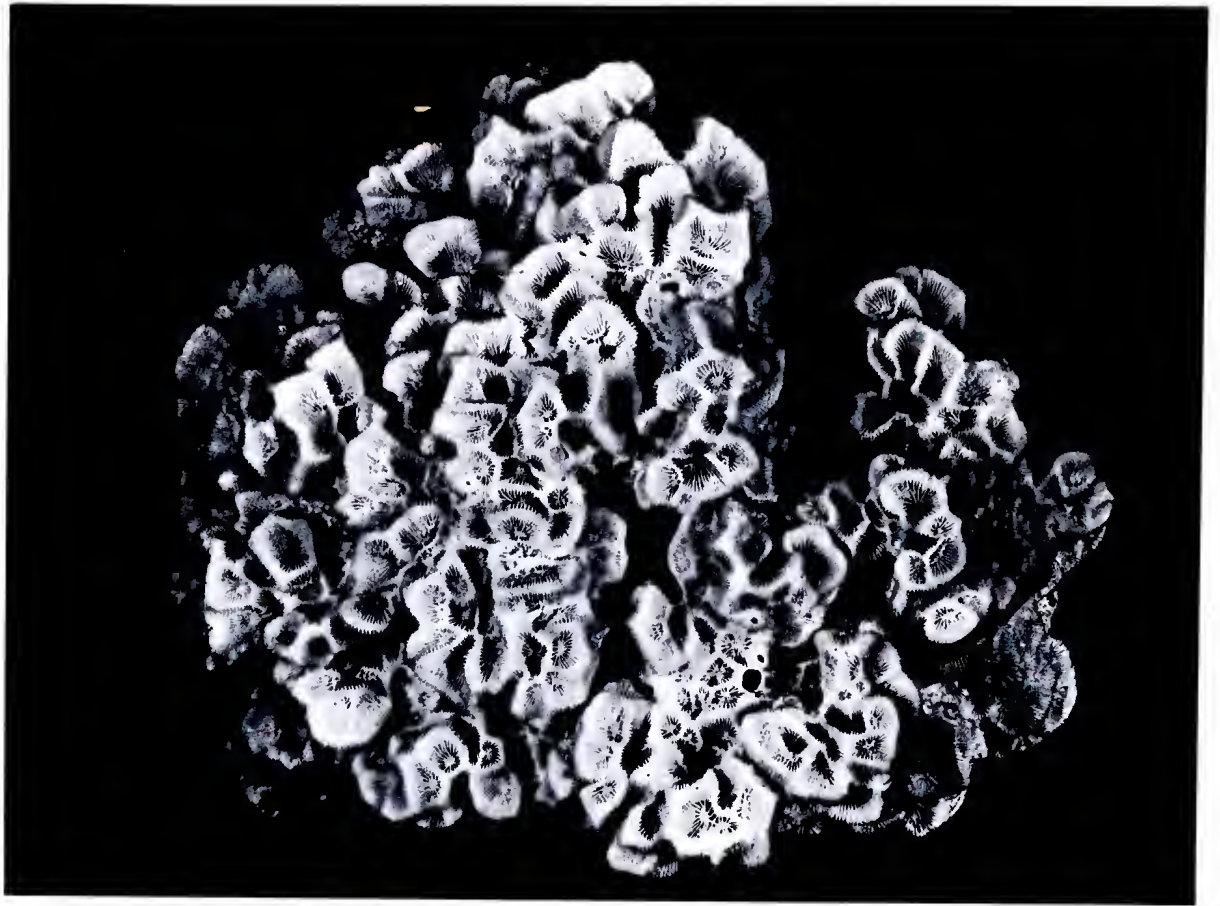
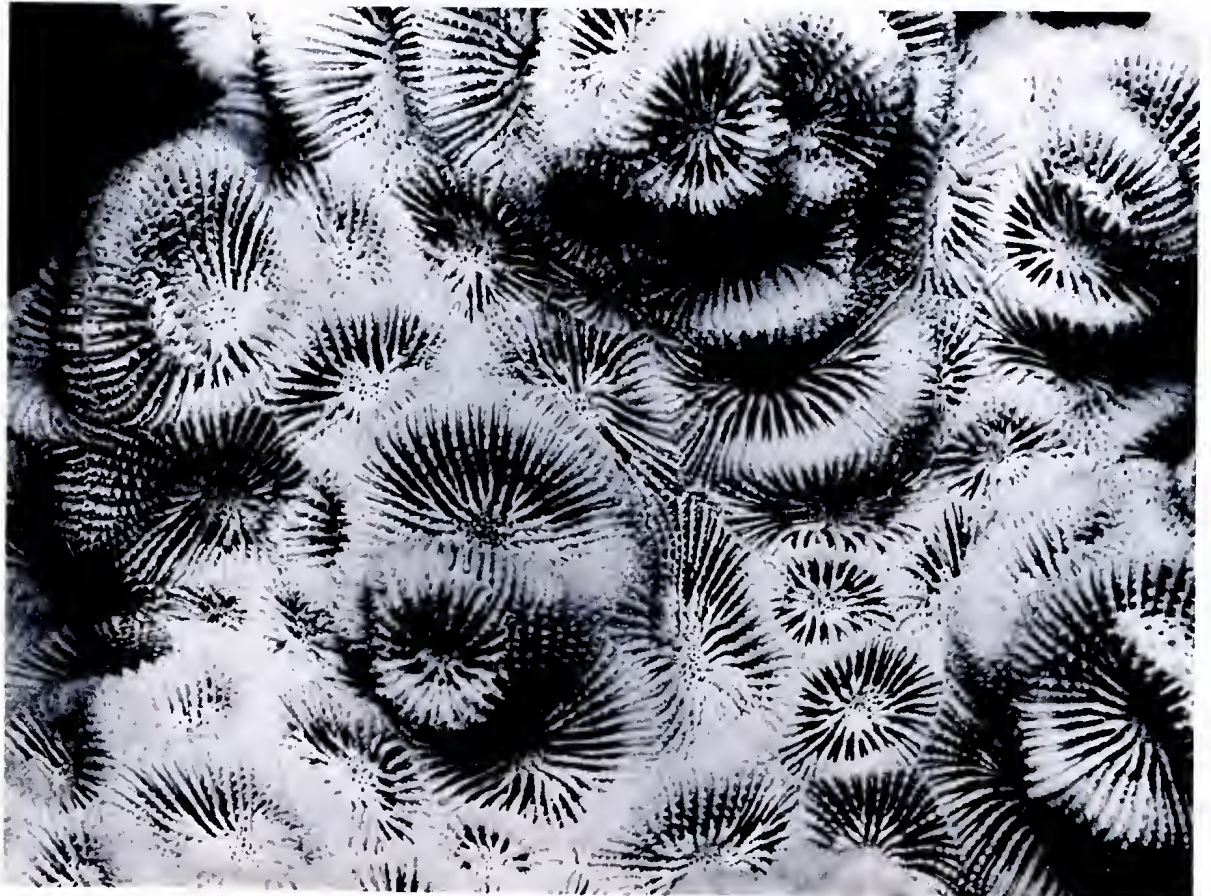


Fig. 96 The hillocky growth form of *Favites abdita*. Same corallum as illustrated in Fig. 95 ($\times 0.5$).

Fig. 97 *Favites halicora* from Thursday Island, collecting station 54, showing hillocky growth form ($\times 2.5$).



Favites abdita from deep or turbid water (Fig. 92).

Calices become increasingly shallow and less calcified as light availability decreases. Exothecal dissepiments become increasingly more apparent and the thecae broader. The septa are thin and have very elongated dentations; the columellae are reduced, frequently to a few twisted trabeculae.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to Samoa.

Favites halicora (Ehrenberg, 1834)

Synonymy

Astraea halicora Ehrenberg, 1834.

Goniastrea halicora (Ehrenberg); Klunzinger (1879).

?*Prionastrea halicora* (Ehrenberg); Ridley (1883).

Favia halicora (Ehrenberg); Gardiner (1904); Matthai (1914, 1923, 1924).

Favites halicora (Ehrenberg); Vaughan (1918); Hoffmeister (1925); Faustino (1927); Umbgrove (1940); Crossland (1948, 1952); Wells (1955b); Stephenson & Wells (1955); Ma (1959); Nemenzo (1959); Chevalier (1971); Rosen (1971); Scheer & Pillai (1974).

The type specimen of this species has been lost. Wijsman-Best (1972) referred this species to *F. chinensis* (now the senior synonym of *F. acuticollis*).

Material studied

Thursday Island, Great Detached Reef (4 specimens), **Tijou Reef** (2 specimens), **Houghton Island, Lizard Island** (2 specimens), **Three Isles, Hope Island** (4 specimens), **Low Isles** (4 specimens), **Palm Islands** (23 specimens), **Whitsunday Islands** (11 specimens).

These localities include collecting stations 1, 2, 5, 6, 34, 38, 40, 42, 43, 45, 54, 55, 57, 58, 60, 90, 91, 97.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918), Mayor (1918); **Low Isles**, Stephenson & Stephenson (1933), Crossland (1952), **Moreton Bay**, Wells (1955a); **Solitary Islands**, Veron *et al.* (1974); **Lord Howe Island**, Veron (1974).

Characters

Coralla have a similar range of growth forms to *F. abdita*. Most are encrusting or sub-massive but some are hillocky. They are cerioid with a tendency to become sub-plocoid in exposed biotopes. Calices are approximately 1cm in diameter. Septa are usually equal, although some corallites have a second and alternating cycle of reduced size. The septa are finely and regularly dentate except for their inner margins where the dentations become much larger and develop into one or more paliform lobes which may form a distinct paliform crown. Regular dentations usually extend down the innermost margin of the paliform lobes to the columella which is compact and spongy. The thecae are characteristically thick. Septa do not form ridges over the thecae. Budding is both intra- and extra-tentacular, the former clearly dominating in most coralla. Living colonies are usually a uniform pale yellow-brown (Fig. 434).

Skeletal variation

As previously noted, coralla from exposed biotopes tend to have calices which are sub-plocoid with thickened thecae. Those from very protected biotopes tend to have well developed, *Goniastrea*-like paliform lobes.



Fig 98A



Fig 99A



Fig 100A



Fig 101A

Affinities

This species is close to *F. abdita* but is distinguished from it by having more rounded corallites, thicker thecae and by the development of the paliform crown. It is not a synonym of *F. abdita* as suggested by Wijsman-Best (1972), who referred this species to *F. chinensis*.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to New Caledonia, the Loyalty Islands and Samoa.

Favites flexuosa (Dana, 1846)

Synonymy

Astraea flexuosa Dana, 1846.

Prionastraea vasta Klunzinger, 1879; Ortmann (1888, 1892).

Favites ellisiana Verrill, 1901.

Favia vasta (Klunzinger); Matthai (1914, 1924); Folkeson (1919).

Favites vasta (Klunzinger); (*pars*) Chevalier (1971).

Favites flexuosa (Dana); (*pars*) Chevalier (1971); Yabe, Sugiyama & Eguchi (1936).

Favites virens (Dana); Wijsman-Best (1972, 1976).

The type specimen of *F. flexuosa* (Fig. 102) clearly belongs to this distinct species, to which the names *F. virens* and *F. vasta* have been applied. The type of *F. virens* (Fig. 89) is probably a *F. abdita* (see p.55). The type of *F. vasta* is apparently lost; Klunzinger's (1879) figure of it (Vol. 3, Pl. IV, Fig. 12) is almost identical to Dana's *F. flexuosa*.

This synonymy does not include other numerous references to *F. virens* which may belong to *F. flexuosa*.

Material studied

Sue Island, Great Detached Reef (10 specimens), **Tijou Reef** (2 specimens), **Houghton Island, Jewell Reef** (2 specimens), **Yonge Reef, Lizard Island** (3 specimens), **Ribbon Reef, Three Isles** (4 specimens), **Hope Island** (2 specimens), **Low Isles** (2 specimens), **Bowl Reef, Palm Islands** (12 specimens), **Magnetic Island** (2 specimens), **Whitsunday Islands** (6 specimens), **One Tree Island, Solitary Islands**.

These localities include collecting stations 1, 2, 5, 9, 10, 17, 32, 34, 37, 40, 45, 55, 57, 60, 63, 85, 91, 97, 98, 99.

Previous records from Eastern Australia

Not previously recorded.

Figs. 98-101 *Favites halicora* ($\times 2.5$).

Fig. 98 From NE Fantome Island, Palm Islands, collecting station 34.

Fig. 99 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97, showing sub-plocoid calices.

Fig. 100 From Hope Island.

Fig. 101 From Juno Bay, Fantome Island, Palm Islands, collecting station 43, showing maximum development of paliform lobes.

Figs. 102-109 *Favites flexuosa* ($\times 2.5$).

Fig. 102 Holotype from Fiji Islands.

Figs. 103, 104 From Great Detached Reef (5m and 15m depth respectively), collecting station 1, showing calicular structures of coralla exposed to very strong wave action.

Fig. 105 From Bowl Reef, collecting station 10.

Fig. 106 From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.

Fig. 107 From the Palm Islands.

Fig. 108 From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.

Fig. 109 From Sue Island, collecting station 17.



Fig. 102A

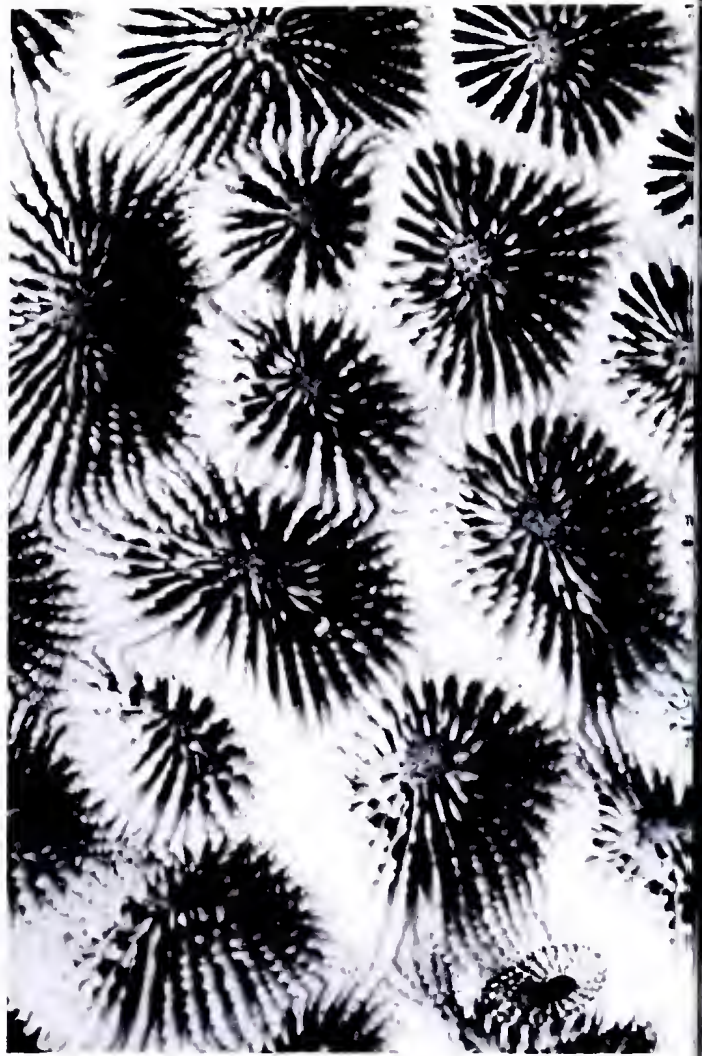


Fig. 103A

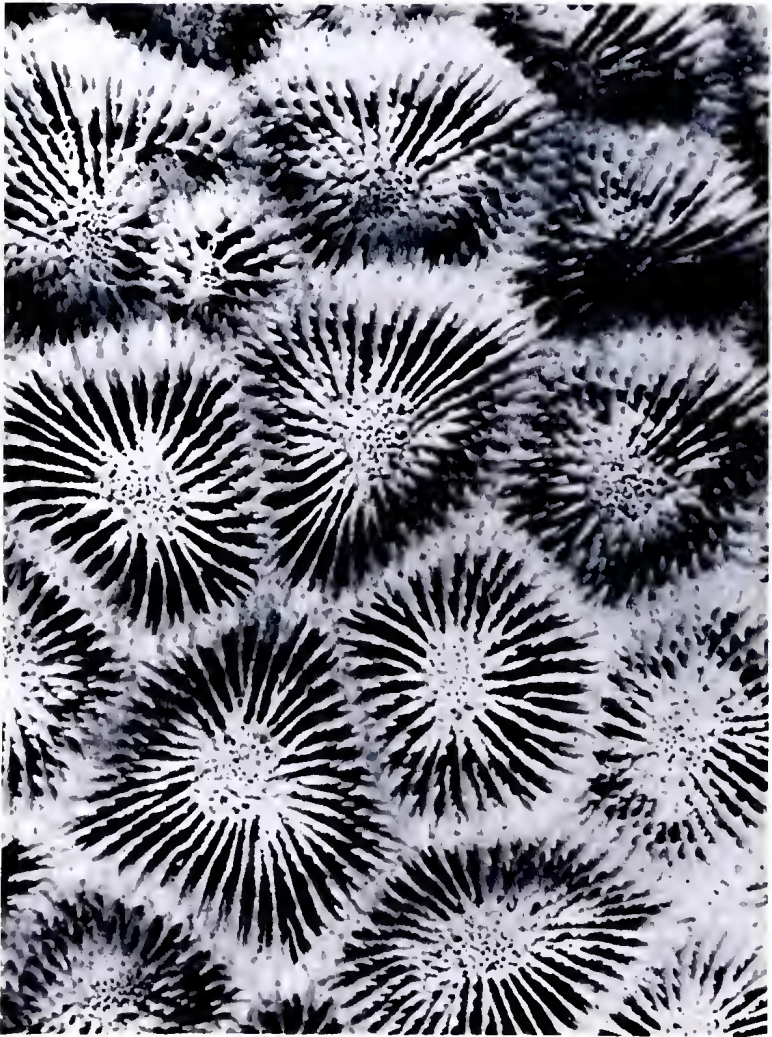


Fig. 104A

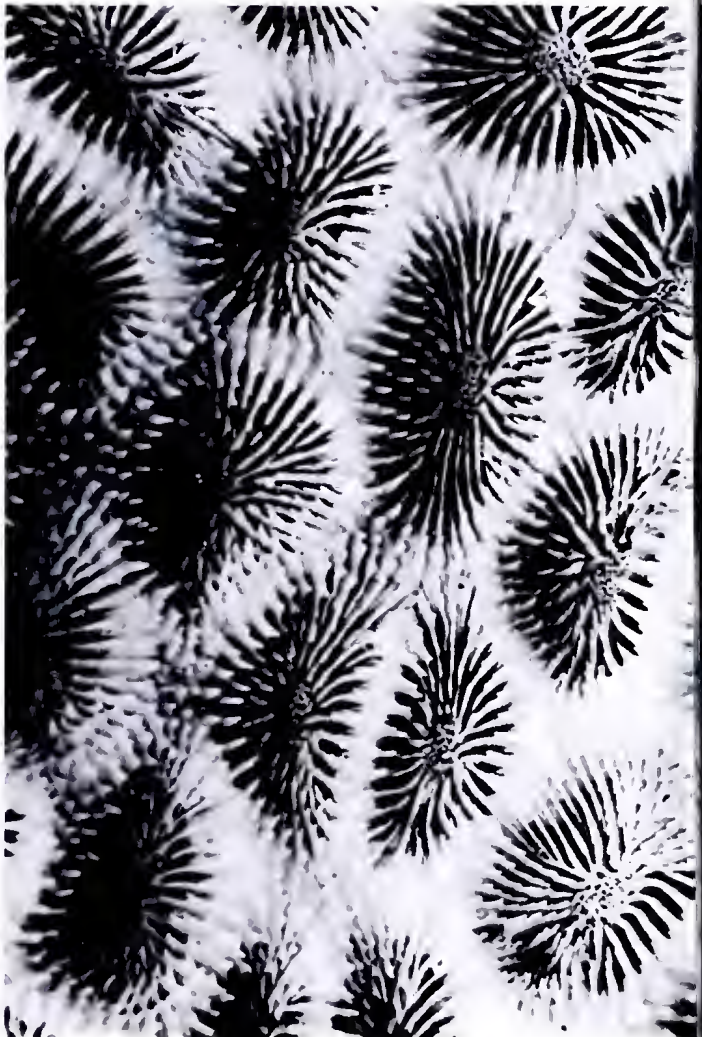
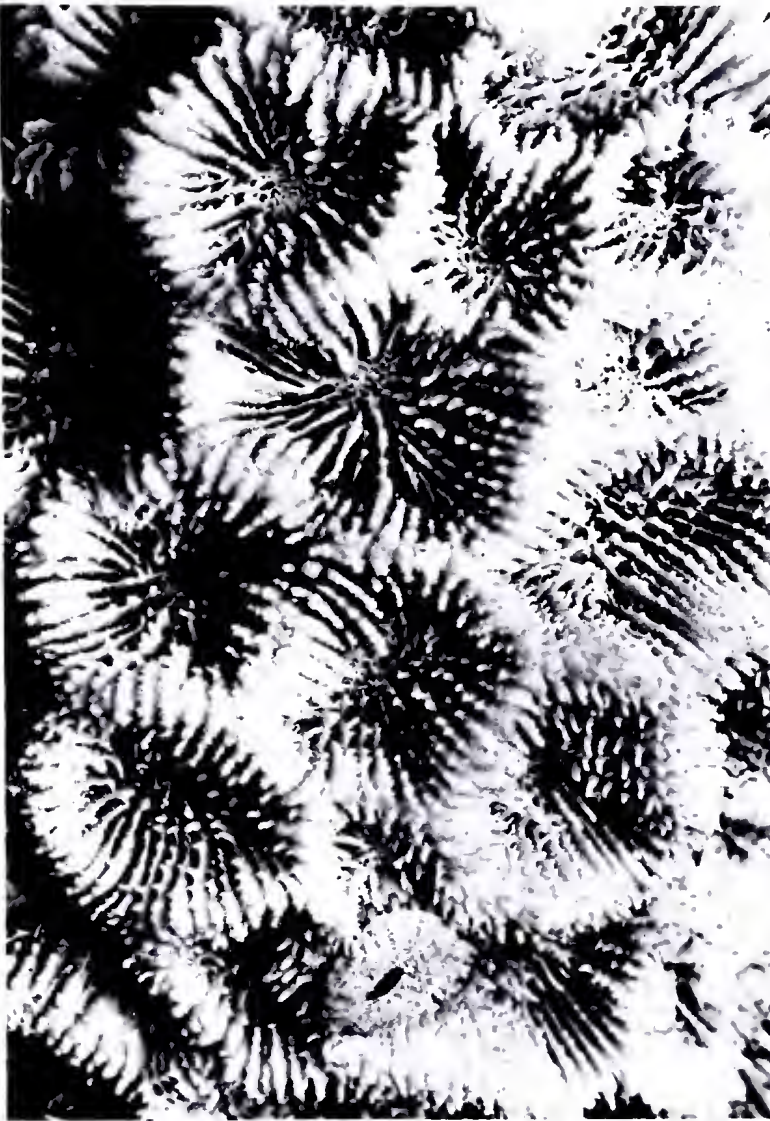


Fig. 105A

Fig. 109▲



108▲

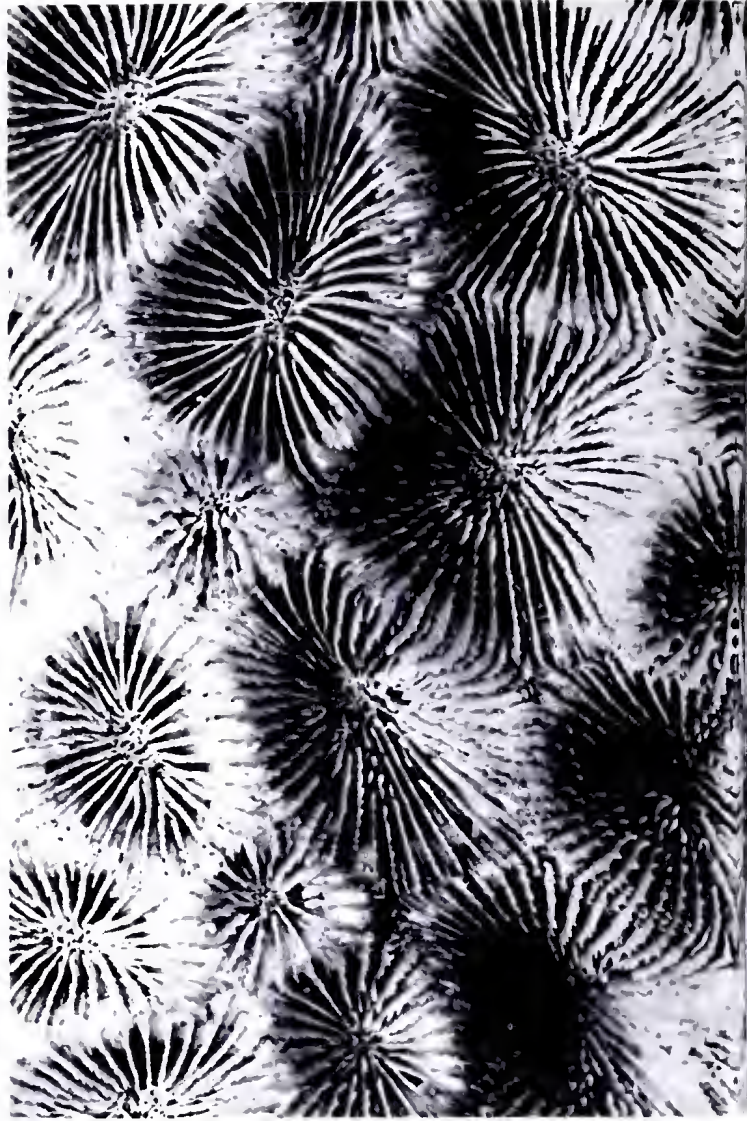
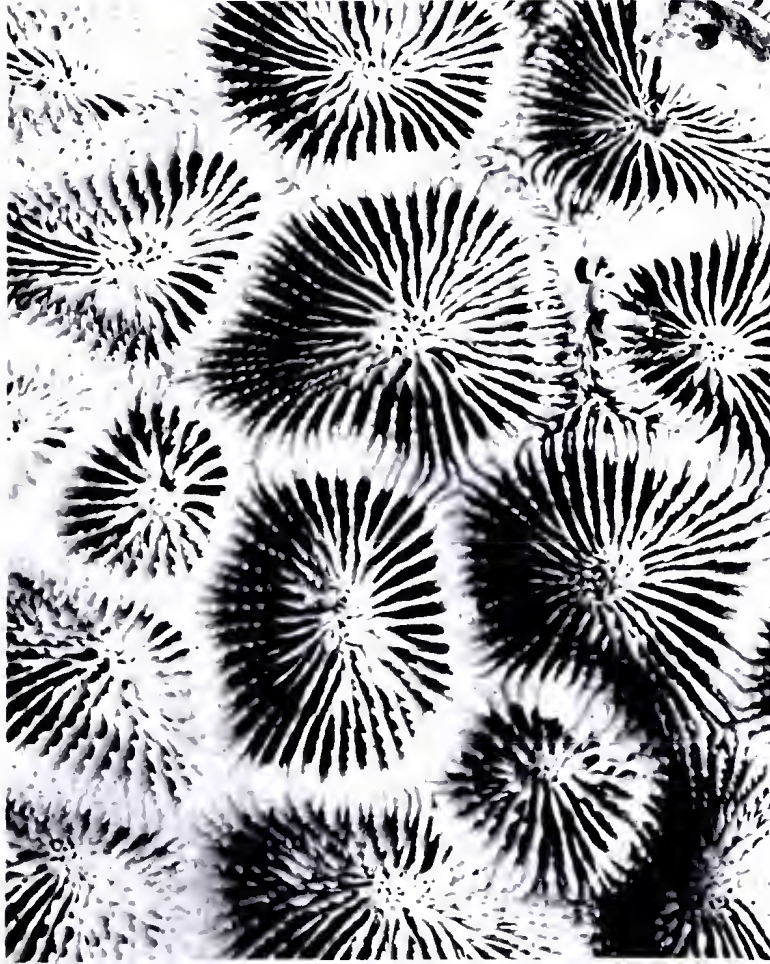
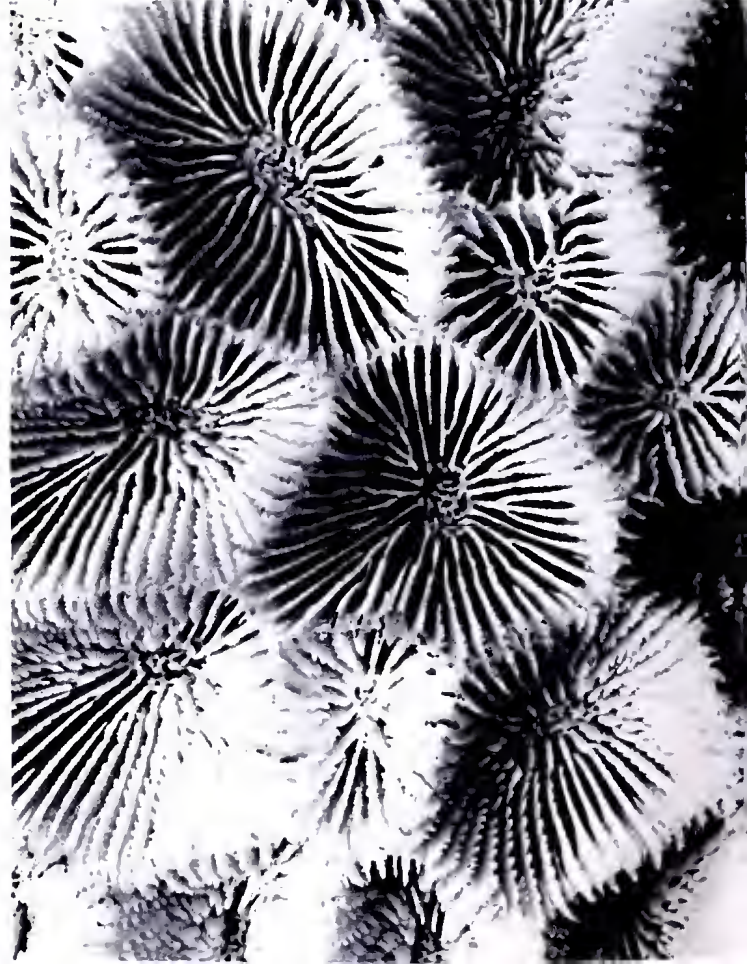


Fig. 107▲



106▲



Characters

Coralla are massive or encrusting, usually flat or spherical in shape, mostly with an even surface, not hillocky. Corallites are always completely cerioid, usually angular in outline, 1.5-2cm across. Septa are usually in two alternating orders, those of the first order being very strongly dentate, especially towards the centre where they usually form one or more irregular paliform lobes. Second order septa are usually much reduced, much thinner and usually slightly less exsert. All septa are usually regularly adjoined above the thecae. The columellae are small and compact. Budding is intratentacular in the manner characteristic of the genus.

Skeletal variations

Favites flexuosa from exposed biotopes (Fig. 103).

Coralla are heavily calcified with thick septa and wide columellae. Septa alternate strongly, the second order being reduced to narrow ridges.

Favites flexuosa from partly protected reef biotopes (figs. 104-108).

Coralla are always cerioid. The depth of the calices varies greatly (compare Figs. 106 and 108 from adjacent biotopes). Septa are fine, with elongated dentations.

Favites flexuosa from protected biotopes (Fig 109).

Coralla from turbid water have irregular calices with relatively exsert septa. Septal dentations are usually long, fine and mostly uneven. The columellae tend to become trabecular.

Distribution

Widely distributed throughout the Indo-Pacific.

Favites rotundata n.sp.

Material studied

Lizard Island (2 specimens), **MacGillivray Reef** (2 specimens), **Ribbon Reef, Palm Islands, Whitsunday Islands** (5 specimens), **Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex, Swain Reefs** (4 specimens).

These localities include collecting stations 65, 69, 74, 75, 79, 80, 97, 98, 100.

Previous records from Eastern Australia

Low Isles, (as *F. virens*) Crossland (1952).

Characters

Colonies are massive, either flat or dome shaped. Coralla are sub-plocoid, with circular, very large corallites (15-27mm across, with calices up to 20mm across) (Figs. 110-115). Budding is both intra- and extratentacular, monostomodaeal intratentacular budding being predominant. Septa are in three orders, although the first two are not always clearly differentiated. First order septa reach the columella and have a large paliform lobe. Second order septa are thinner and shorter but may also reach the columella and have a paliform lobe of reduced size. Third order septa are much reduced. All septa are dentate along their margins and have irregular granulations on their sides. The columellae are compact and spongy. The septo-costae are equally exsert except those of the third order which are reduced. Dentations are very regular, those of the septa and costae being similar. Septo-costae of adjacent corallites are usually regularly adjoined, although delineation between corallites is distinct. There is little or no ornamentation on the coenosteum.

Colours are usually dark greys, greens or browns and are uniform within individual colonies. Living polyps are distinctly fleshy and circular in outline (Figs. 116, 117). Living colonies are also illustrated in Figs. 436-438.

Skeletal variation

Variation within the present series is consistent with that of most *Favites* species. Coralla from most exposed biotopes have exsert thecae and well formed paliform lobes. They are usually dome-shaped or spherical and are very dense. Those from more protected biotopes are frequently flat, have much less calcified calicular structures and consequently coralla are much less dense.

Affinities

This species appears to have been called, or included in, *F. flexuosa* by some previous authors (discussed p.52). It is, however, a distinct species which does not closely resemble the holotype of *F. flexuosa*. It is always sub-plocoid, whereas *F. flexuosa* is cerioid and has larger, more rounded corallites.

Etymology

So named because of the distinctive circular appearance of the corallites and the retracted polyps.

Holotype

Dimensions: A dome shaped corallum 10.3cm high, 12cm maximum diameter.

Locality: SW Swain Reefs, collecting station 69.

Depth: 5m.

Collector: J. E. N. Veron and M. Pichon.

Holotype: British Museum (Natural History), 1977.1.1.6.

Paratypes

Fig. 111. Australian Institute of Marine Science

Fig. 112. Queensland Museum, Australia.

Fig. 114. Rijksmuseum van Natuurlijke Historie, Nederland, No. 10734.

Favites complanata (Ehrenberg, 1834)

Synonymy (partly after Chevalier, 1971)

Favia complanata Ehrenberg, 1834; Matthai (1914); Gravely (1927); Crossland (1931).

Astraea tesserifera Ehrenberg, 1834.

Prionastraea tesserifera (Ehrenberg); Edwards & Haime (1857); Klunzinger (1879).

Prionastraea spinosa Klunzinger, 1879.

Favites complanata (Ehrenberg); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Rossi (1954); Scheer (1967); Chevalier (1968, 1971).

The holotype of *F. complanata* (Fig. 118) is in the Museum für Naturkunde der Humboldt Universität (No. 695). This was apparently unknown to Chevalier (1971) who designated a neotype.

Material studied

Yorke Island, Nymph Island, Lizard Island (3 specimens), plug reef south of **Ribbon Reef, Three Isles, Hope Island** (4 specimens), **Lodestone Reef, Palm Islands** (5 specimens), **Whitsunday Islands** (3 specimens), **Bushy Island-Redbill Reef**.

These localities include collecting stations 13, 32, 43, 57, 64, 80, 86, 92, 97, 98, 99.

Previous records from Eastern Australia

Low Isles and Port Newry, Stephenson & Wells (1955).

Characters

Coralla are usually massive with an even surface. Corallites are approximately 12mm in diameter, cerioid or slightly sub-plocoid, and usually slightly angular in outline. Septa are

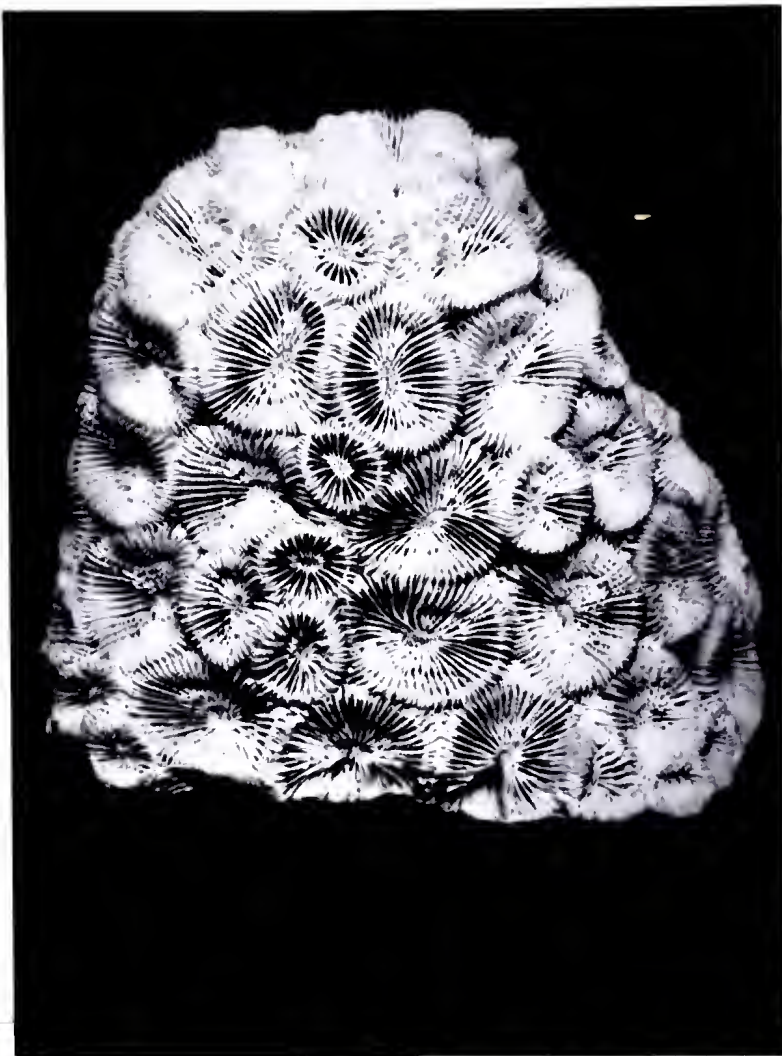


Fig. 110A

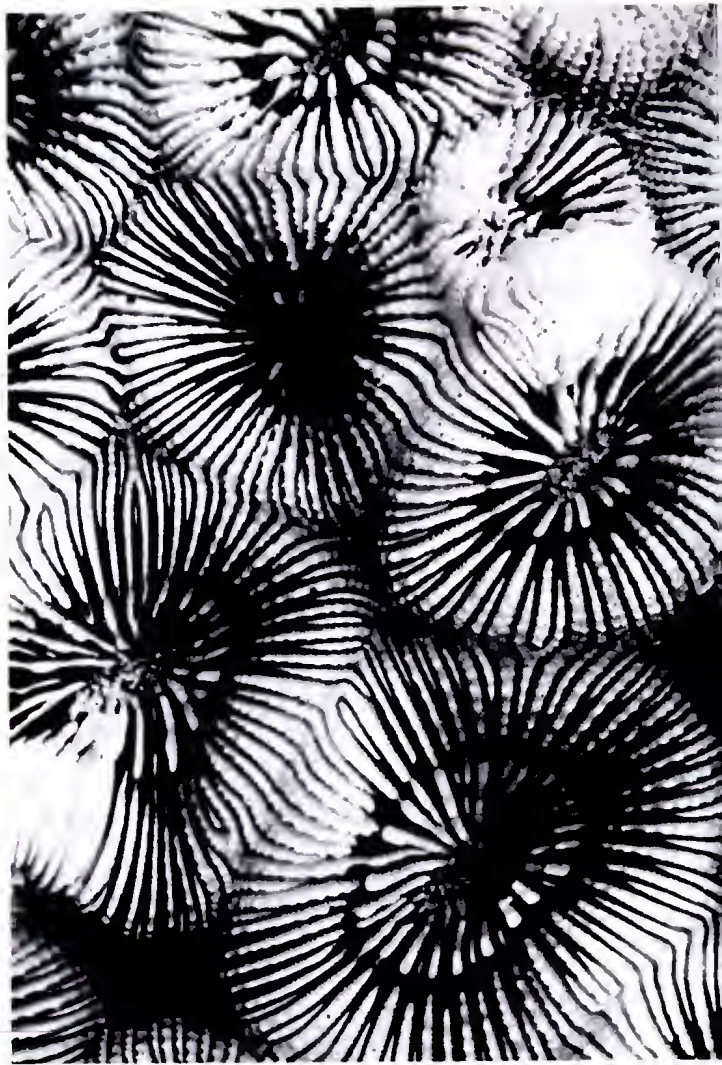


Fig. 111A

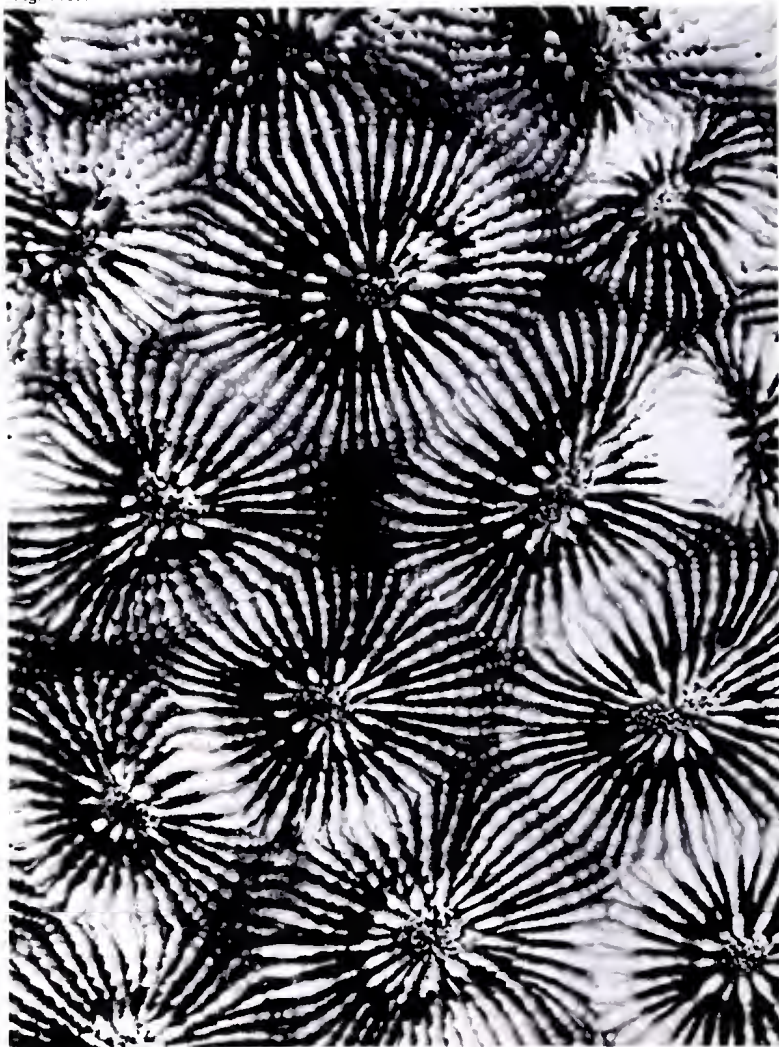


Fig. 112A



Fig. 113A

in two alternating cycles. Those of the primary cycle are thick, especially near the thecae, have 4 or 5 regular, very prominent dentations and a distinct paliform lobe. Secondary cycle septa are very reduced. Both cycles have fine granules on their sides. Septa of adjacent corallites are usually adjoined; sometimes an intercorallite groove is present. The columellae are usually large and compact. Costae, where present, are in two unequal cycles and are dentated in the same manner as the septa.

The only colour pattern recognised in living colonies (Fig. 439) is brown, sometimes with green centres.

Skeletal variation

Coralla from exposed biotopes tend to become sub-plocoid with circular corallites, having very shallow calices (Fig. 121). Septa are very thick and septal cycles very unequal. Those from protected biotopes (Figs. 119, 120) more closely resemble the type.

Affinities

Favites complanata is probably nearest to *F. bennettiae* at one extreme and *F. abdita* at the other, although, as can be seen by a comparison of the present figures, it does not closely resemble either of these species. Some specimens of *F. halicora* with thick thecae resemble *F. complanata*, especially in the ornamentation of the septa, but calices are smaller and usually more angular.

Figs. 110-115 *Favites rotundata* Figs. 111-115 ($\times 2.5$).

Fig. 110 Holotype from SW Swain Reefs, collecting Station 69 ($\times 0.8$)

Fig. 111 From Swain Reefs, collecting station 79, paratype.

Fig. 112 From Pompey Complex, collecting station 75, paratype.

Fig. 113 From SW Swain Reefs, collecting station 69, holotype (same specimen as Fig. 110).

Figs. 114, 115 From Bushy Island-Redbill Reef, collecting station 80, Fig. 114, paratype.

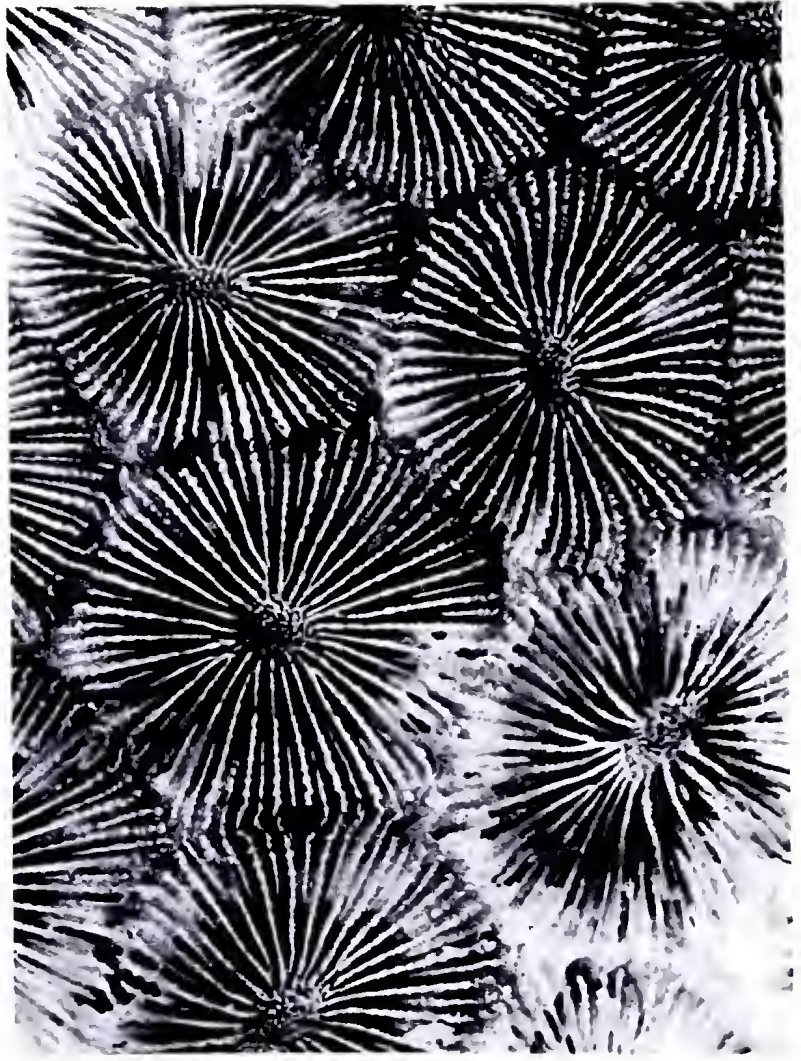
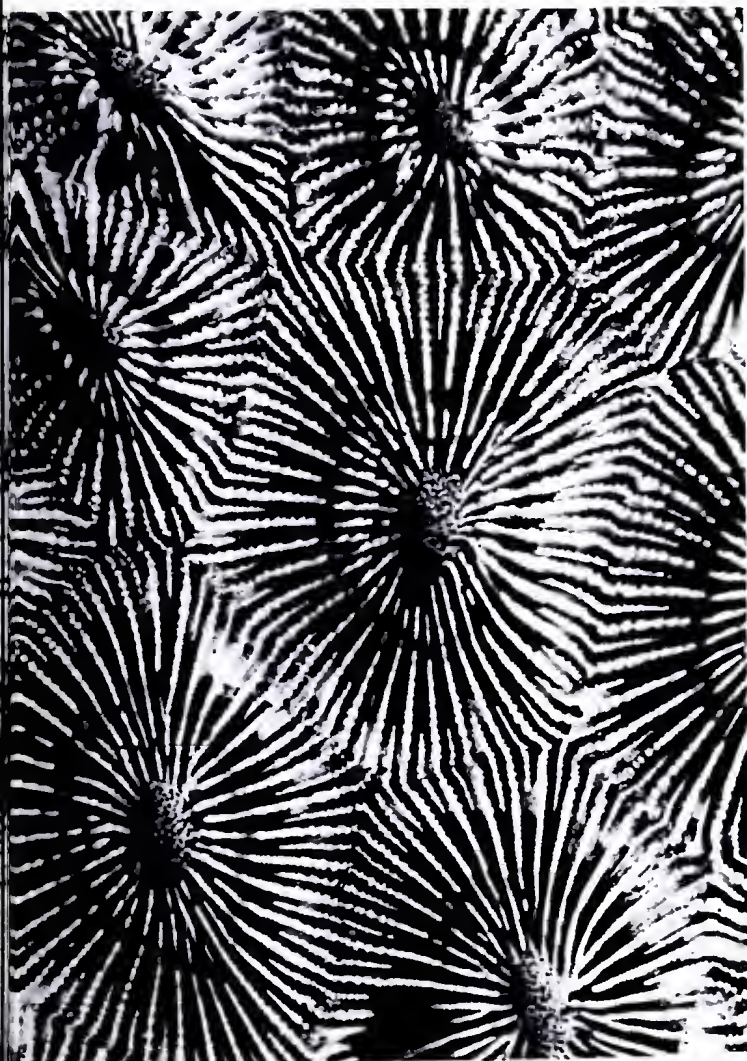


Fig. 115▲

Distribution

Widely distributed throughout the Indo-Pacific, from the Red Sea to Tahiti (Crossland, 1928, 1931) and the Tuamotu Archipelago (Newell, 1956).

Favites pentagona (Esper, 1794)

Synonymy (partly after Chevalier, 1971 and Wijsman-Best, 1972)

Madrepora pentagona Esper, 1794.

Astraea deformis Lamarck, 1816.

Aphrastraea deformis Edwards & Haime, 1848; Gardiner (1904).

Prionastraea gibbosissima Edwards & Haime, 1850.

Goniastrea rudis Edwards & Haime, 1850.

Plesiastrea haeckeli Bruggemann, 1878.

Favia adduensis Gardiner, 1904.

Stephanocoenia maldivensis Gardiner, 1904.

Favites pentagona (Esper); ?Matthai (1914); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Crossland (1948); Ma (1959); Utinomi (1971); Chevalier (1971); Wijsman-Best (1972).

Favites parvicella Nemenzo, 1959.

Favites gailei Chevalier, 1971.

Chevalier (1971) included Nemenzo's *F. parvicella* as a questionable synonym of *F. gailei* and separates these from *F. pentagona*. He recorded 5 and 2 coralla of these species respectively. The figured specimens of all three nominal species fall within the clearly defined range of the present series.

Figs. 116, 117 *Favites rotundata* from Swain Reefs, collecting station 69, *in situ*.



Fig. 116▲



Fig. 117▲

Material studied

Darnley Island, Yorke Island, Murray Islands (2 specimens), Sue Island, Thursday Island (3 specimens), Great Detached Reef (6 specimens), Tijou Reef (3 specimens), Jewell Reef, Yonge Reef, Nymph Island, Lizard Island (9 specimens), MacGillivray Reef, Low Isles (3 specimens), Lodestone Reef, Palm Islands (34 specimens), Magnetic Island, Whitsunday Islands (5 specimens).

These localities include collecting stations 1, 2, 5, 9, 12, 13, 17, 27, 29, 31, 32, 34, 35, 36, 37, 38, 41, 45, 46, 51, 55, 56, 57, 58, 60, 61, 74, 83, 85, 87, 90, 91, 97, 98.

Figs. 118-121 *Favites complanata* ($\times 2.5$).

Fig. 118 Holotype of *Favites complanata*.

Fig. 119 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.

Figs. 120, 121 From Lizard Island, collecting stations 32 and 100 respectively.

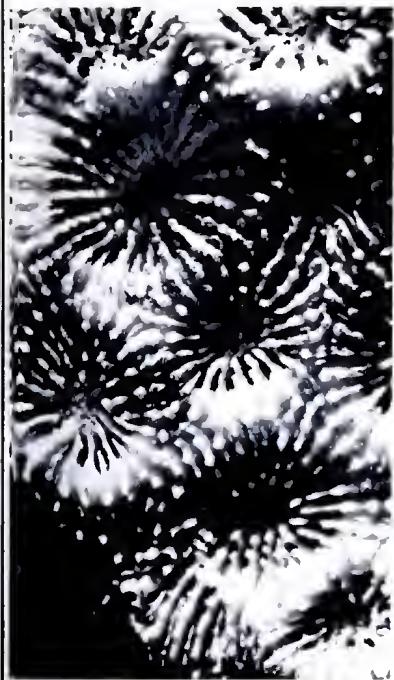


Fig. 118▲

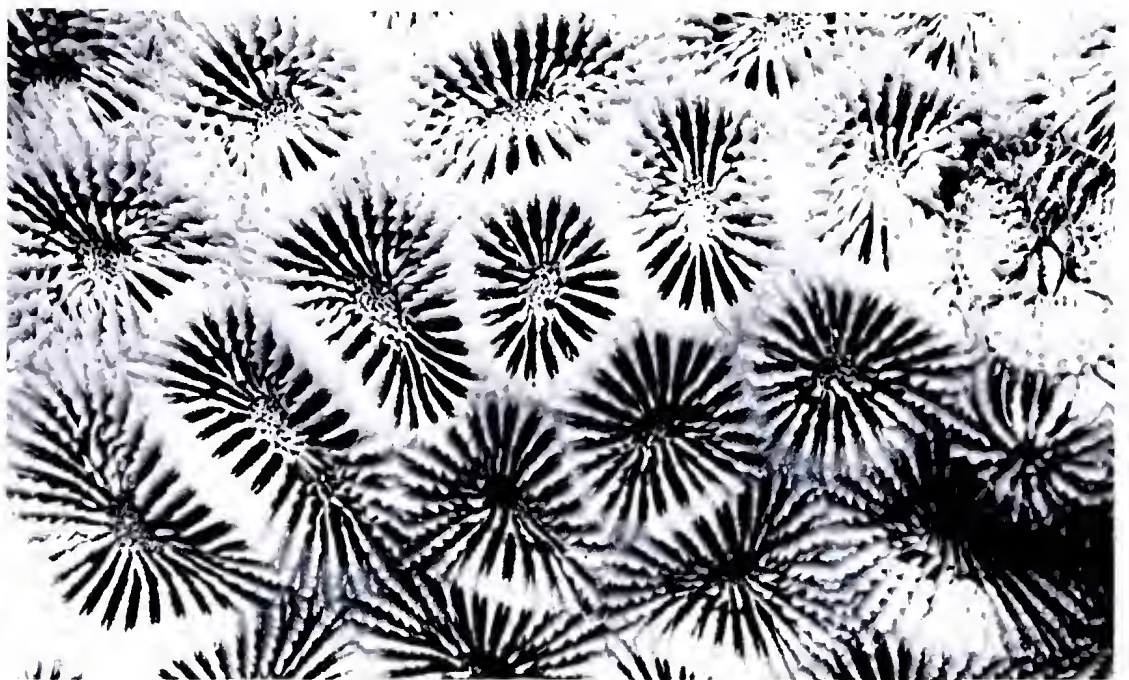


Fig. 119▲

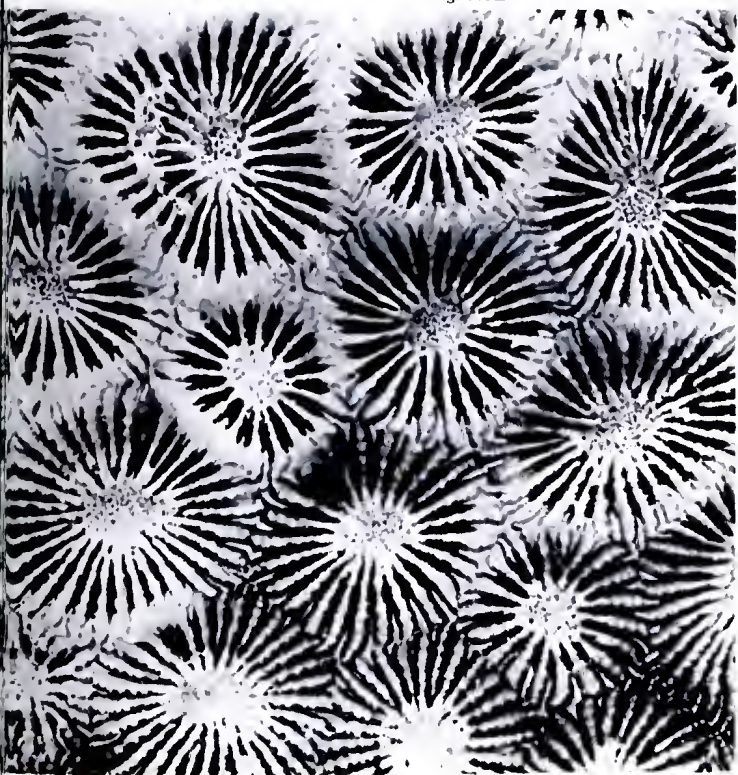


Fig. 120▲

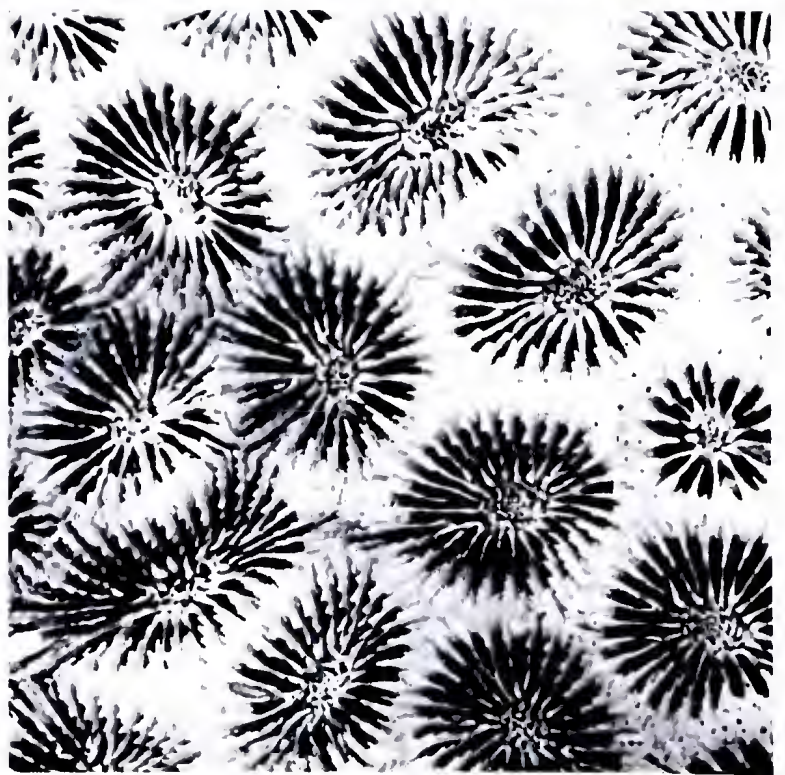


Fig. 121▲

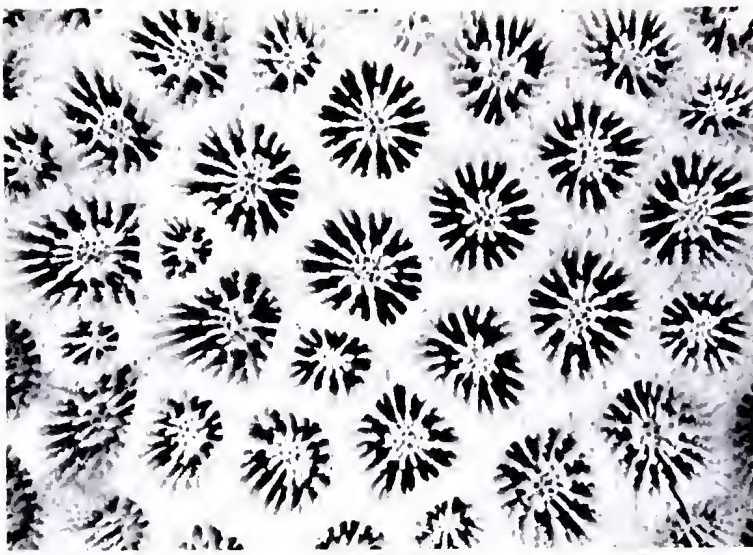


Fig. 122▲

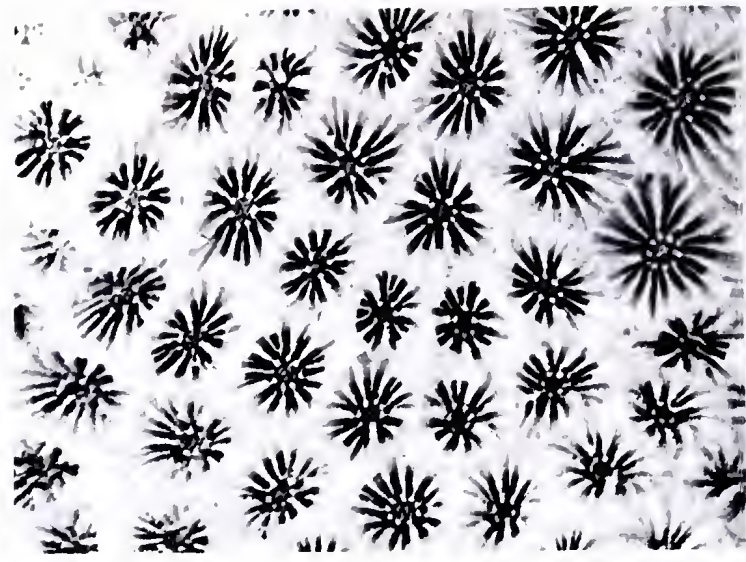


Fig. 123▲

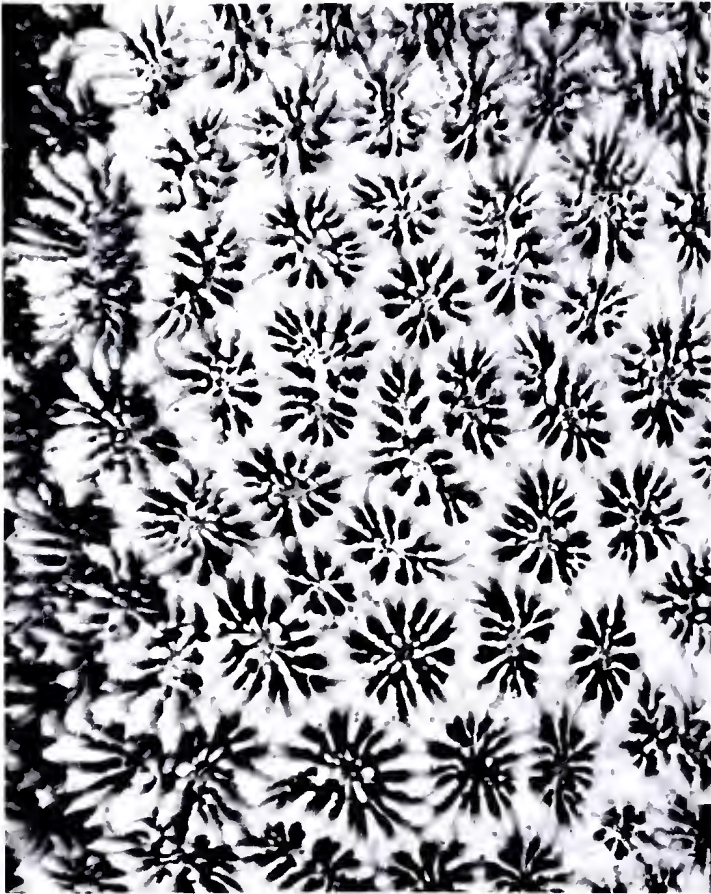


Fig. 124▲



Fig. 125▲



Fig. 126▲

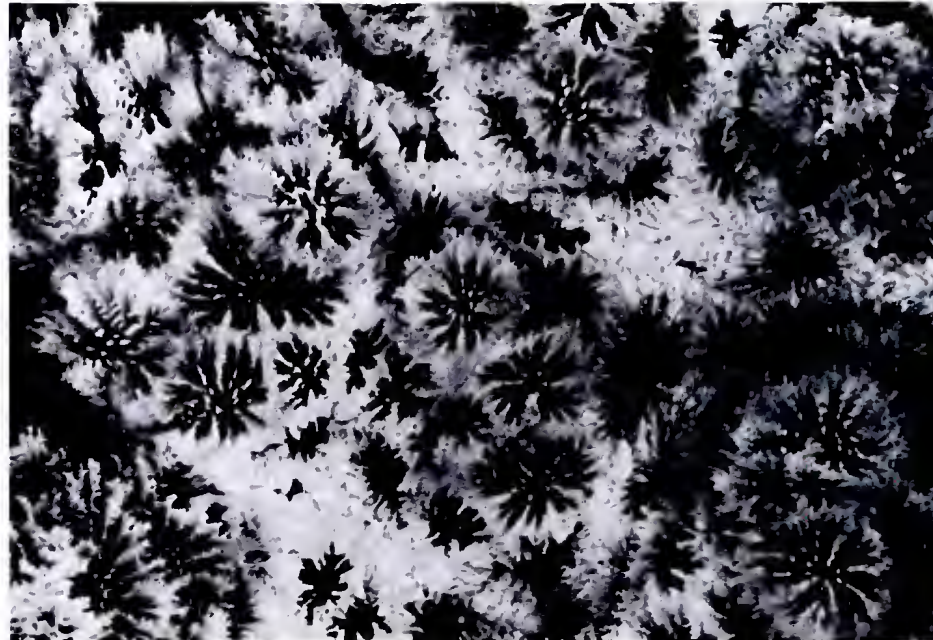


Fig. 127▲

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are encrusting, massive or sub-ramose. Corallites are cerioid, with diameters seldom exceeding 6mm. Usually two cycles of septa can be distinguished, although these have very variable lengths. Those septa reaching the columella have well developed paliform lobes which form a distinctive crown around the columella. The septa have dentations which become elongated and conspicuous in sub-ramose coralla. The columellae are usually loose and poorly developed. The septa are variably exsert over the thecae; those of adjacent corallites are frequently adjoined, with an intercalicular groove rarely being developed.

Budding is extremely marginal to extratentacular in all coralla in the present series (Fig. 126). This throws much doubt on the validity of including *F. pentagona* in *Favites*. It is retained in *Favites* here because it does not appear to be closely allied to any other genus and also because several other species of *Favites* and *Favia* may show some degree of extratentacular budding.

Colours are variable, most commonly brown with green oral discs. Some colonies, however, may be bright red, others a mixture of red and brown (see Figs. 440-442).

Figs. 122-127 *Favites pentagona* ($\times 2.5$).

- Fig. 122 From Great Detached Reef, collecting station 5.
- Fig. 123 From Iris Point, Orpheus Island, Palm Islands, collecting station 55.
- Fig. 124 From Dewar Island, Murray Islands, collecting station 29.
- Fig. 125 From Challenger Bay, Great Palm Island, collecting station 46, showing a wide range of corallite forms on an actively growing, sub-ramose colony.
- Fig. 126 From Fantome Island, Palm Islands, collecting station 34, showing predominance of extratentacular budding.
- Fig. 127 From Hazard Bay, Orpheus Island, Palm Islands, collecting station 45.
- Fig. 128 Retracted polyps of *Favites pentagona* from Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97 ($\times 4.0$).

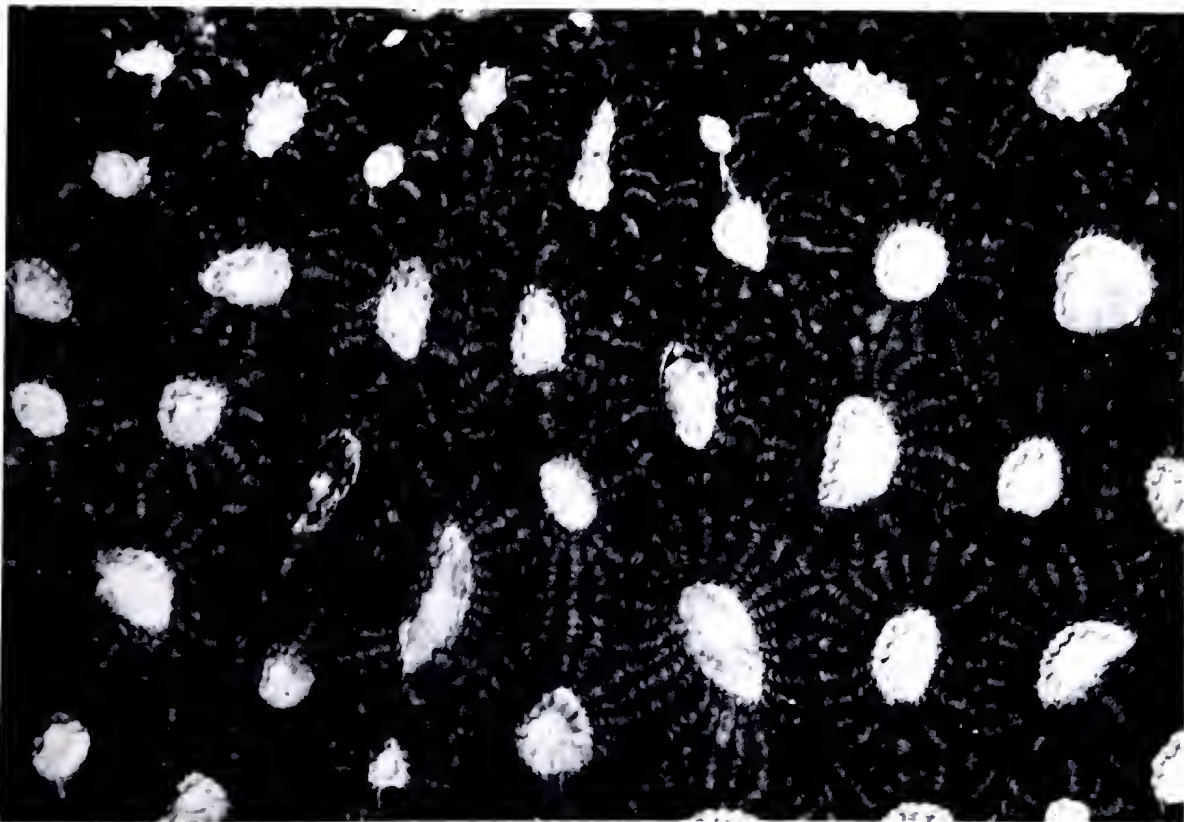


Fig. 128▲

Skeletal variation

The ecomorphs of this species illustrate a wide variation both in growth form and calice structure. Colonies may be encrusting (flat or irregular), massive (spherical or columnar) or sub-ramose. Large coralla of the present series frequently show more than one growth form.

Favites pentagona from exposed biotopes (Figs. 122-124).

Coralla are massive, frequently very dense and have a characteristically even surface. Corallites are relatively straight sided, with 4-6 angles. The paliform crown is conspicuously developed, the columella relatively well developed and compact. The septa are relatively even, only slightly exsert and heavily calcified. The thecae are also thick and dense.

Favites pentagona from protected biotopes (Figs. 125, 127).

Colonies are irregular in shape, encrusting, sub-massive or sub-ramose. Corallites show a correspondingly wide range of growth forms. On flattened surfaces, calicular structures correspond with the general description (above). One or more septa in each corallite are frequently very thickened and exsert. The septa become increasingly more exsert and dentate in sub-ramose coralla or parts of coralla. The thecae also become exsert, with the diameter of individual corallites being much greater at their outer surfaces than at their bases.

Distribution

Widely distributed from the Red Sea to New Caledonia and the Great Barrier Reef.

***Favites russelli* (Wells, 1954)**

Synonymy

Plesiastrea russelli Wells, 1954.

Favites rufa Wijsman-Best, 1972; Wijsman-Best (1976).

Material studied

Darnley Island, North West Reef, Thursday Island (2 specimens), **Great Detached Reef, Yonge Reef, Lizard Island** (5 specimens), **MacGillivray Reef** (2 specimens), **Palm Islands** (13 specimens), **Magnetic Island, Whitsunday Islands** (14 specimens), **Pompey Complex** (2 specimens), **Swain Reefs** (3 specimens).

These localities include collecting stations 3, 5, 14, 31, 32, 45, 54, 55, 57, 58, 59, 68, 70, 71, 74, 77, 81, 83, 85, 92, 97, 98, 102.

Previous records from Eastern Australia

Not previously recorded.

Characters

This little known species is common on the Great Barrier Reef where it occupies an extremely wide range of biotopes. Coralla are submassive or encrusting, cerioid or sub-plocoid, with corallites circular or irregular in outline. Three irregular orders of septa can sometimes be distinguished. Those of the first order are frequently highly exsert, and thicker than the others, becoming thinner towards the centre. Just within the thecae, the margins of all septa descend abruptly and deeply into the calice, those of the first and second orders terminating in a prominent, minutely granulated paliform lobe, which is separated from the septa by a deep notch. The thickened, exsert portions of the major septa are densely and irregularly granulated. Septa of higher orders are frequently adjoined to lower ones. The columellae are usually small and compact. Sub-plocoid forms have predominantly extratentacular budding, while intratentacular budding is usually dominant in cerioid coralla or parts of coralla.

Colonies are usually very brightly coloured (Figs. 443, 444), very often bright green or with the coenosarc and oral disc different colours.

Skeletal variation

Favites russelli ecomorph *russelli* (Figs. 130, 131).

This ecomorph occurs predominantly in partly protected biotopes where light availability is reduced. Colonies are plocoid with corallites well separated. Calices are circular with variable diameters up to 7mm. Septa are in three relatively distinct orders. First order septa are very thick and highly exsert. Second order septa are rarely thickened, scarcely exsert and mostly regularly dentate. Septa of higher orders are frequently adjoined to lower ones; some septo-costae are only present as costae. Costae are low and broad, flattened or rounded on top, with very narrow grooves between them and covered with minute granulations. The columellae are small and compact. Extratentacular budding may be dominant, the reverse of the norm.

The type specimen of this species is at an extreme of its growth form range.

Favites russelli ecomorph *rufa* (Figs. 132, 133).

This ecomorph occurs in most shallow water reef biotopes. Coralla are usually encrusting, sometimes submassive. Corallites are cerioid. Septa are more equal than in the *russelli* ecomorph, and those of adjacent corallites are seldom adjoined.

Favites russelli from *exposed biotopes* (Fig. 135).

Coralla tend to be massive and cerioid, with corallites very irregular in shape. They may have more than one centre. Septa are very irregularly exsert and very highly dentate. The paliform lobes are also very dentate and may be covered by masses of spinules.

Favites russelli from *turbid biotopes* (Figs. 136, 137).

As with other Faviidae from these biotopes, this species shows great reduction in the size of the calices and in the degree of calcification of all calicular structures. The coenosteum is a mass of vesicular blisters traversed by very fine costae.

Affinities

Some coralla from this species curiously resemble *Goniastrea palauensis* (compare Figs. 185 & 186), although these species are quite distinct underwater. Its generic position, however, is clear. Budding is primarily intratentacular and similar to that of other *Favites* species in being circumferential rather than subequal.

Distribution

Marshall Islands, New Caledonia, Indonesia and Great Barrier Reef.

Favites bennettiae n. sp.

Material studied

Yorke Island, Lizard Island (2 specimens), **Low Isles, Palm Islands** (22 specimens), **Magnetic Island** (2 specimens), **Whitsunday Islands** (6 specimens).

These localities include collecting stations 13, 33, 34, 38, 41, 44, 45, 55, 57, 59, 83, 85, 90, 91, 97.

Figs. 129-137 *Favites russelli* ($\times 2.5$).

Fig. 129 Holotype from Bikini Atoll, depth 22m.

Fig. 130 From outer slope, Yonge Reef, collecting station 3, depth 35m.

Fig. 131 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.

Fig. 132 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.

Fig. 133 From Thursday Island, collecting station 54.

Figs. 134, 135 (Same corallum) from Eclipse Island, Palm Islands, collecting station 59. Similar variation is found in many coralla of the present series.

Fig. 136 From Falcon Island, Palm Islands, collecting station 57.

Fig. 137 From Darnley Island, collecting station 31.

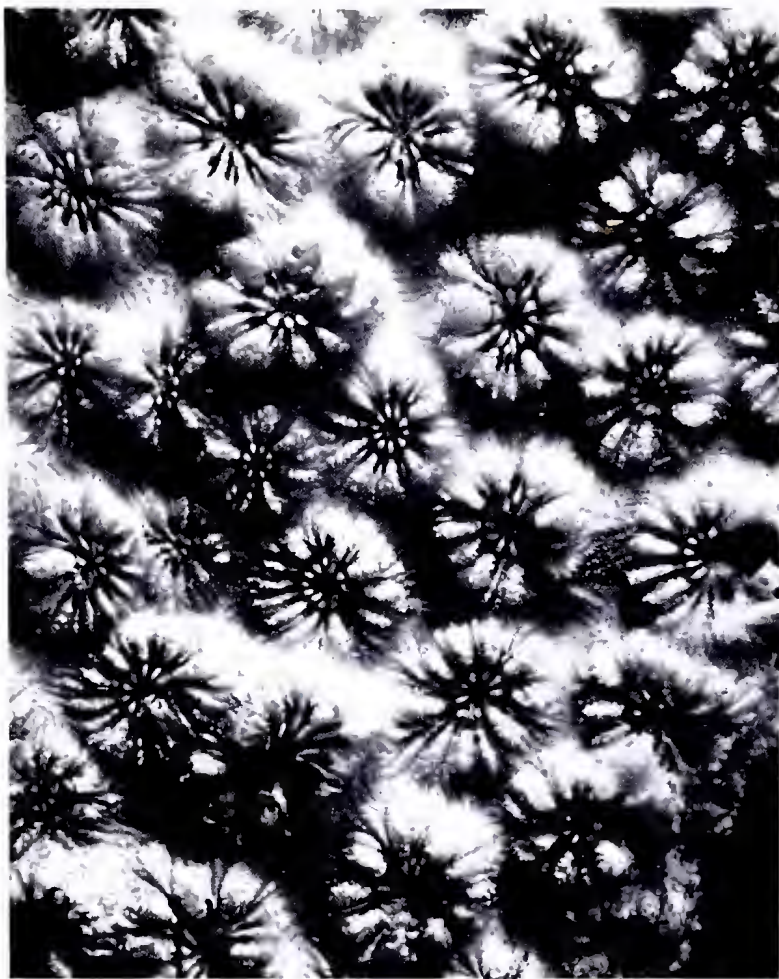


Fig. 129▲



Fig. 130▲

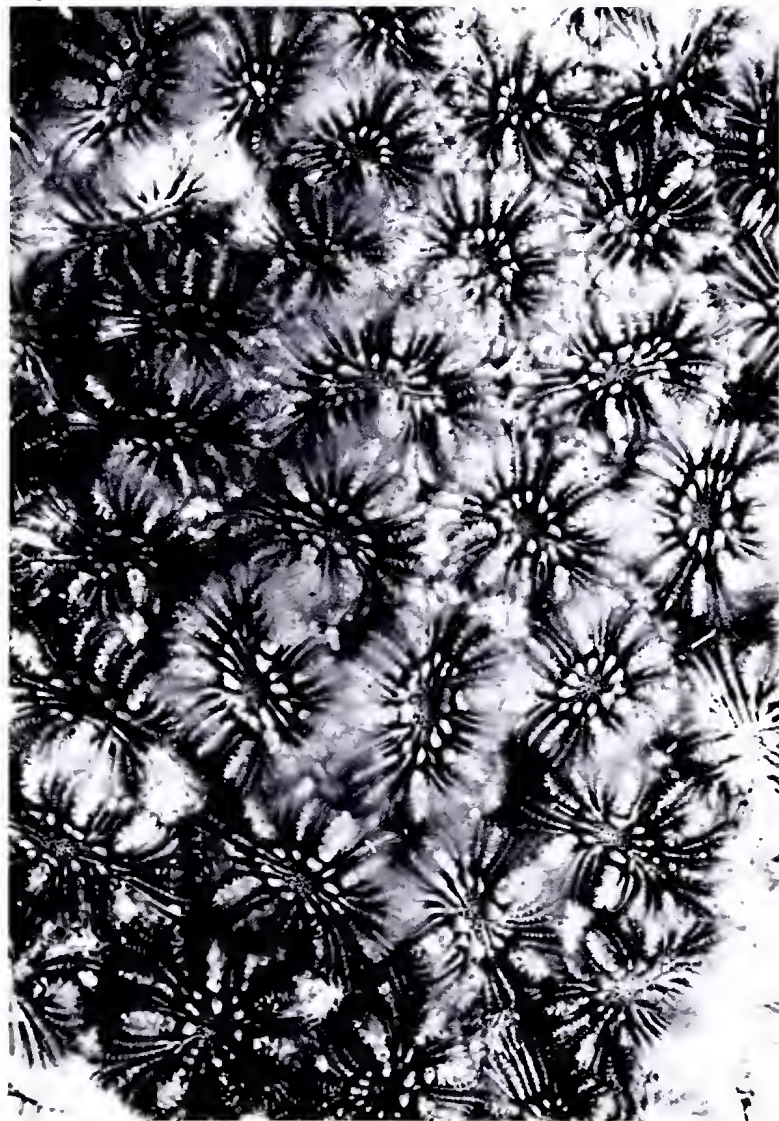


Fig. 131▲

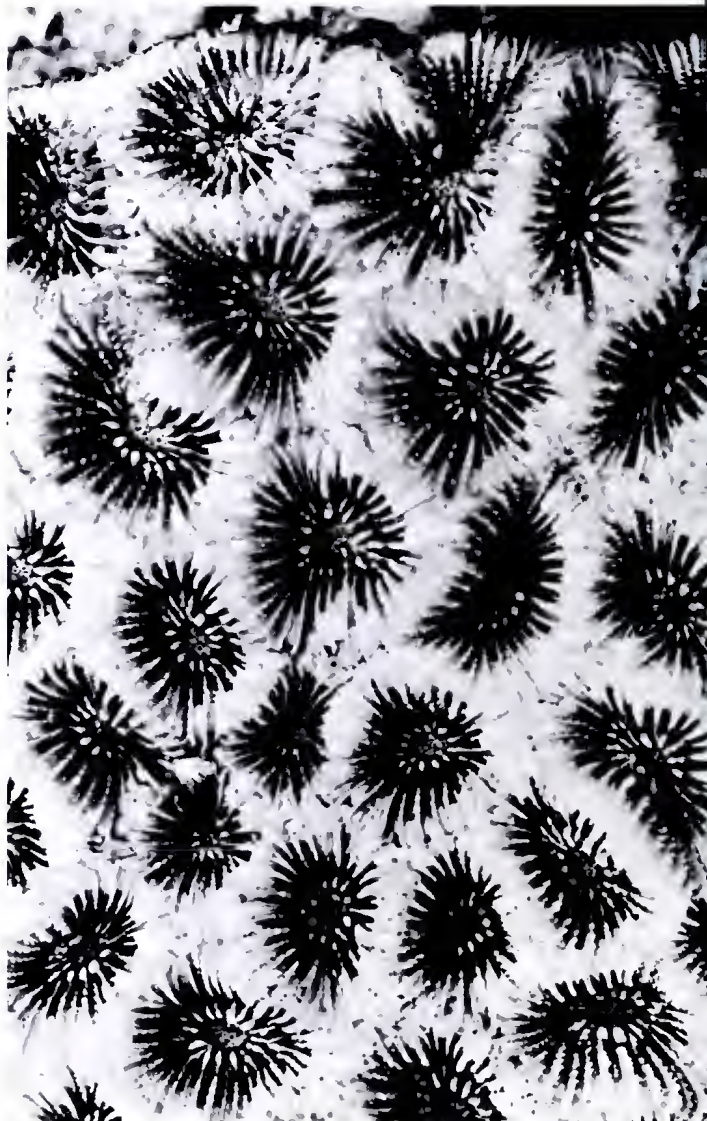


Fig. 132▲

Fig. 137

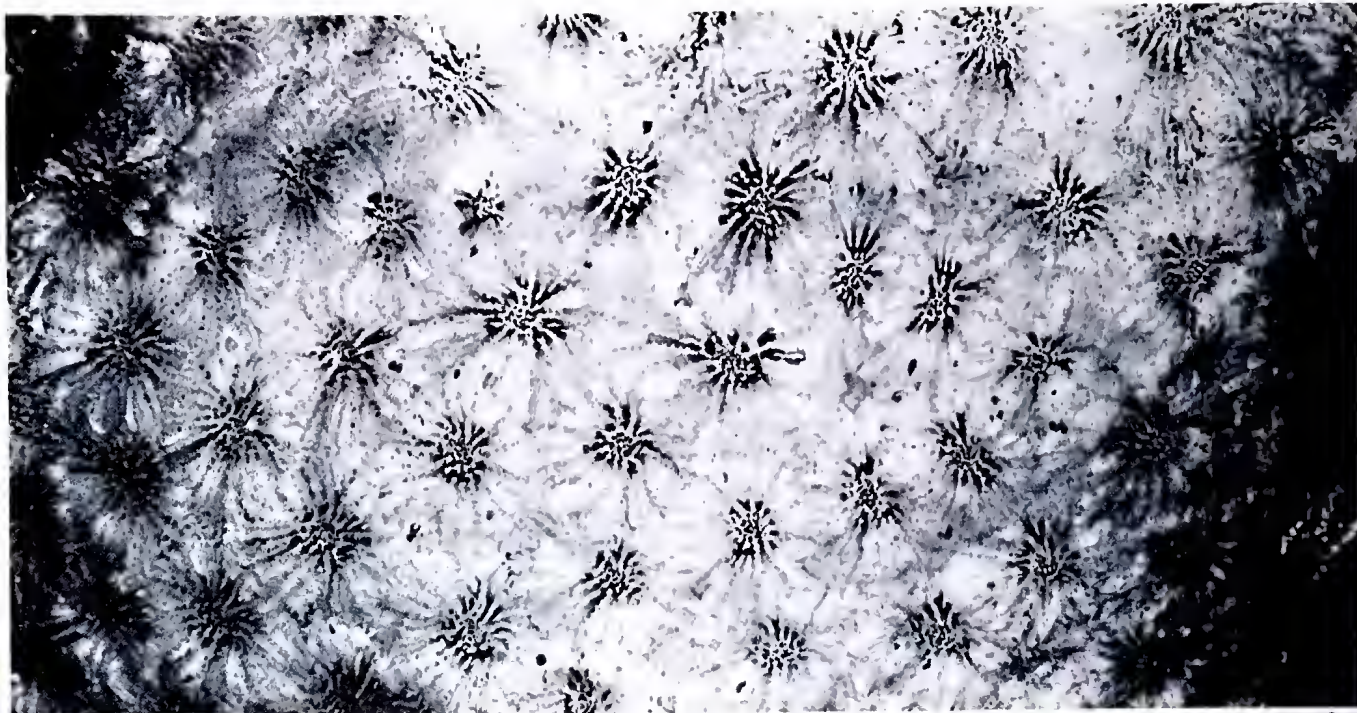


Fig. 135



Fig. 133

Fig. 136



Fig. 134

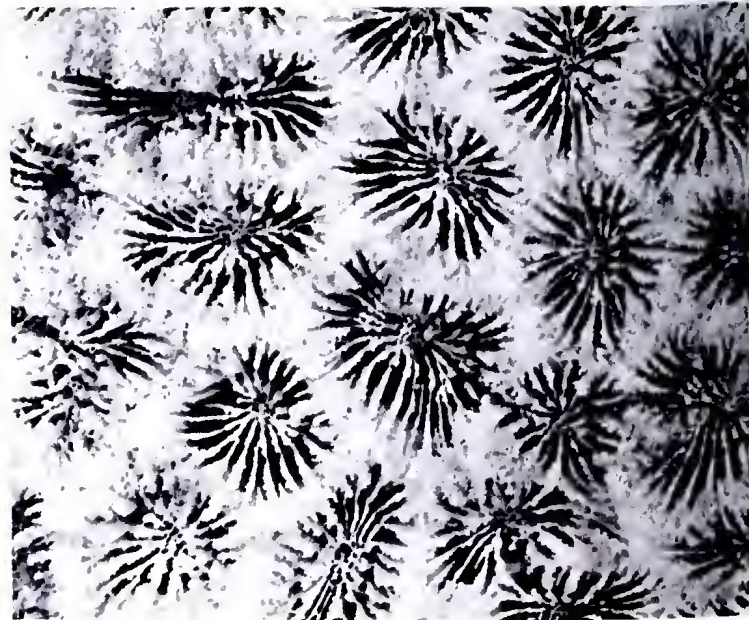




Fig. 138▲



Fig. 139▲

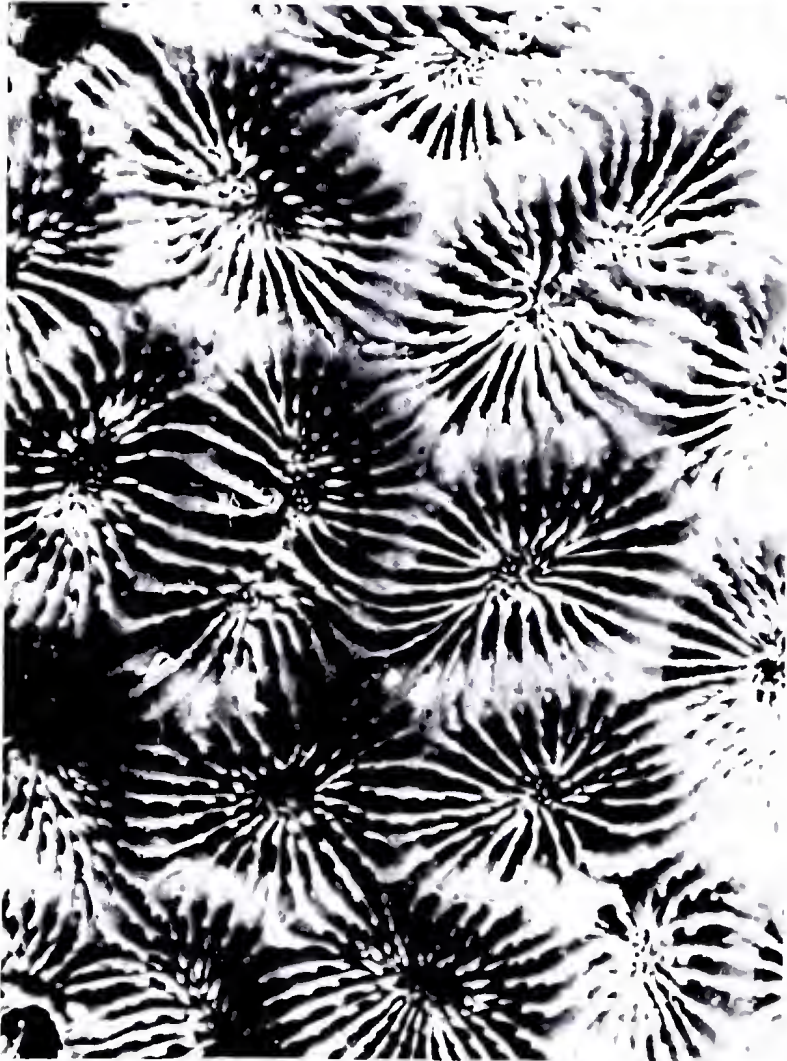


Fig. 140▲

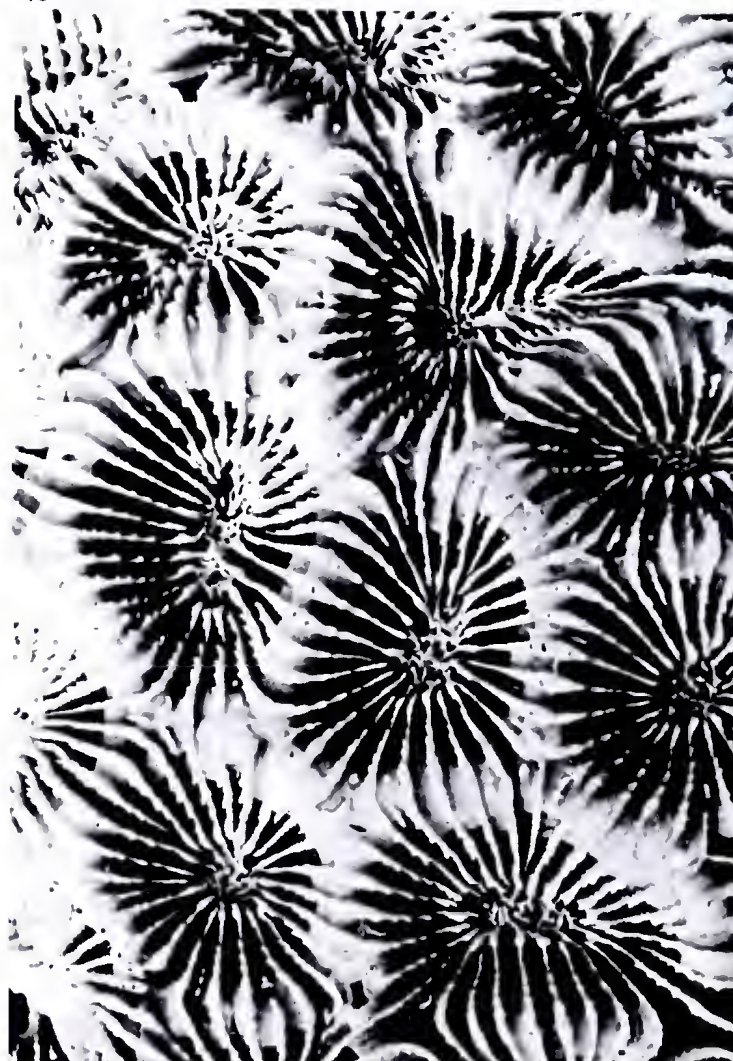


Fig. 141▲

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are massive or encrusting and cerioid, with mature calices averaging approximately 10mm in diameter. Elongated corallites occasionally have two or three centres. Septa are in two orders, although in some coralla the second order is not developed. First order septa are widely spaced and very prominent. They have well developed paliform lobes and are strongly dentate. Septa of adjacent corallites are adjoined and frequently very exsert. Second order septa are inconspicuous or absent. The columellae are compact and spongy. The thecae are usually thick.

Living colonies (Figs. 445-448) are mostly uniform in colour, usually with a grey coenosarc and grey-green oral disc.

Skeletal variation

This conspicuous, although usually uncommon, species has not been observed in biotopes exposed to strong wave action. The full range of variation within the present series is illustrated in Figs. 138-141. Colonies from protected biotopes or from turbid waters are usually flat and have very shallow calices which tend to be circular. Septa are usually thin with elongated dentations pointing inwards, and poorly developed paliform lobes. The columella tends to be trabecular and calicular structures are generally poorly calcified. Coralla from most reef biotopes (Figs. 140, 141) are usually dome shaped and have angular corallites, with the distinctive calicular structures described above.

Affinities

The generic status of this species is uncertain. Like *Oulophyllia crispera*, it may have polycentric corallites (Figs. 142, 143), although these are unusual in parts of colonies that are not actively dividing. The large size of the corallites and their coarse, lightly calcified septa resemble *O. crispera* from turbid biotopes. There is also a similarity to some *Favia rotumana* (e.g. Fig. 139) which also tends to have polycentric corallites. It is placed in *Favites* on the basis that corallites are usually monocentric, and that budding is intratentacular and similar to most other *Favites*. Within this genus, it is probably closest to *F. complanata* which also has large corallites with large, prominent septa.

Etymology

Named after Isobel Bennett, formerly of Sydney University.

Holotype

Dimensions: The maximum is 18.3cm, the minimum 6.0cm.

Locality: Falcon Island, Palm Islands, collecting station 57.

Depth: 5-10m.

Collector: J. E. N. Veron.

Holotype: British Museum (Natural History) 1977.1.1.3.

Paratypes

Australian Institute of Marine Science.

Queensland Museum, Australia.

Rijksmuseum van Natuurlijke Historie, Nederland, No. 10735.

Figs. 138-141 *Favites bennettae* ($\times 2.5$).

Fig. 138 Holotype from Falcon Island, Palm Islands, collecting station 57.

Fig. 139 From Yorke Island, collecting station 13.

Fig. 140 From Barber Island, Palm Islands, collecting station 83.

Fig. 141 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.



Fig. 142▲



Fig. 143▲



Fig. 144▲

GENUS *GONIASTREA* EDWARDS & HAIME, 1848

Generic synonymy

Goniastrea Edwards & Haime, 1848.

Type species *Astraea retiformis* Lamarck, 1816; subsequent designation Edwards & Haime, 1848.

Characters

Colonies are cerioid or sub-meandroid, very rarely sub-plocoid. Colony formation is by monostomodaal to polystomodaal budding. Paliform lobes are very prominent. Septal dentations are usually fine and regular.

Instability in the taxonomy of *Goniastrea* is partly a product of difficulties in defining boundaries between this genus and other related genera (see p.3 and 20) and partly a result of persistent taxonomic problems at the species level.

East Australian species can be divided into four groups:

- (1) Species with small, monocentric corallites – *G. retiformis* and *G. edwardsi*.
- (2) Species with usually larger corallites which are monocentric or sub-meandroid – *G. aspera* and *G. cf. favulus*.
- (3) Species with large corallites which are sub-meandroid – *G. pectinata* and *G. palauensis*.
- (4) Species with large meandroid valleys – *G. australensis*.

Of these seven species, only *G. retiformis* has had a stable taxonomic history. The names *G. edwardsi*, *G. aspera* and *G. favulus* apply to species mostly known by one or more other names which have recently been changed through questions of synonymy or priority. The name *G. pectinata* has been confused primarily with *G. benhami* (*G. australensis*) and its various synonyms. *Goniastrea palauensis* has previously been included in *Favia*, *Favites* or in ?*Goniastrea* (by Chevalier, 1971).

***Goniastrea retiformis* (Lamarck, 1816)**

Synonymy

Astraea retiformis Lamarck, 1816.

Astraea spongia Ehrenberg, 1834.

Astraea eximia Dana, 1846.

Goniastrea retiformis (Lamarck); Edwards & Haime (1846, 1857); Ortmann (1888, 1889, 1892); Klunzinger (1879); Bernard (1900); Gardiner (1904); Bedot (1907); von Marenzeller (1907); Gravier (1911); Matthai (1914, 1923, 1924); Vaughan (1918); Hoffmeister (1925); Faustino (1927); Gravely (1927); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1939); Crossland (1952); Stephenson & Wells (1955); Searle (1956); Nemenzo (1959); Pichon (1964); Scheer (1967, 1972); Chevalier (1968, 1971); Foidart (1970a, 1970b, 1972); Wijsman-Best (1972, 1976); Scheer & Pillai (1974); Pillai & Scheer (1974).

Goniastrea bournoni Edwards & Haime, 1849; Edwards & Haime (1857).

Material studied

Murray Islands, Great Detached Reef (4 specimens), **Tijou Reef** (3 specimens), **Houghton Island** (2 specimens), **Lizard Island, Eagle Reef** (2 specimens), **Three Isles** (5 specimens), **Hope Island** (7 specimens), **Low Isles** (3 specimens), **Palm Islands**

(4 specimens), **Wheeler Reef** (2 specimens), **Broadhurst Reef**, **Magnetic Island**, **Pompey Complex**.

These localities include collecting stations 1, 2, 5, 6, 19, 27, 34, 36, 40, 41, 84, 99, 105.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918); Mayor (1918), **Low Isles**, Crossland (1952), Stephenson & Wells (1955).

Characters

Colonies are usually massive, tending towards spherical or columnar growth forms which frequently exceed 1m in diameter. Common in intertidal zones, this species frequently forms microatolls. Both microatolls and columnar or spherical colonies are frequently composed of concentric layers of re-growth after death of part of the colony surface. Deeper water colonies may become encrusting.

Corallites are cerioid, with straight-sided walls having 4-6 angles which give a neat cellular appearance. Calices are mostly uniform in size, 3-5mm in diameter. There are three orders of septa, the first two often being indistinguishable. First order septa are usually slightly exsert. They plunge steeply within the calice to the level of the columella, then develop large paliform lobes which form a distinctive crown. They have irregular dentations on their inner margins. At the edge of the columella, dentations may turn at right angles to form a well defined pseudo-synapticular ring. Second order septa are either identical with those of the first order or are shorter, do not form paliform lobes and do not reach the columella. Third order septa are short, usually consisting of ridges or series of spines down the thecae. All septal structures are granulated. The columellae are small, trabecular and enclosed in pseudo-synapticular rings. Septa are not continuous over the thecae.

Living colonies usually have uniform colours, mostly pale brown (Fig. 449).

Distribution

Widely distributed throughout the Indo-Pacific, from the Red Sea to Samoa.

Goniastrea edwardsi Chevalier, 1971

Synonymy

Astraea parvistella Dana, 1846.

Goniastrea parvistella (Dana); *sensu* Vaughan (1918); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Nemenzo (1959); Foidart (1970a, 1970b, 1972); Wijsman-Best (1972).

Goniastrea solida (*pars*) Edwards & Haime, 1848; (*pars*) Edwards & Haime (1857); Gardiner (1899, 1904); Matthai (1914).

Goniastrea edwardsi Chevalier, 1971; Wijsman-Best (1976).

According to Vaughan (1918), Matthai's (1914) use of the name *solida* was invalid '... as it represents serial misidentification of Forskål's *Madrepora solida* which is a species of *Porites* according to von Marenzeller'. He then noted that 'Dana applied the name *Astraea parvistella* in 1846 to the same species' = *Goniastrea parvistella* (Dana) Verrill, 1872. This name has subsequently been used by many authors, some in reference to this species, others

Figs. 145-150 *Goniastrea retiformis*, Figs. 145-148 ($\times 5.0$), Figs. 149-150 ($\times 10.0$).

Figs. 145, 149 From Low Isles, collecting station 12.

Fig. 146 From Eyrie Reef, collecting station 19.

Fig. 147 From Great Detached Reef, collecting station 5.

Figs. 148, 150 From the Pompey Complex, collecting station 105.

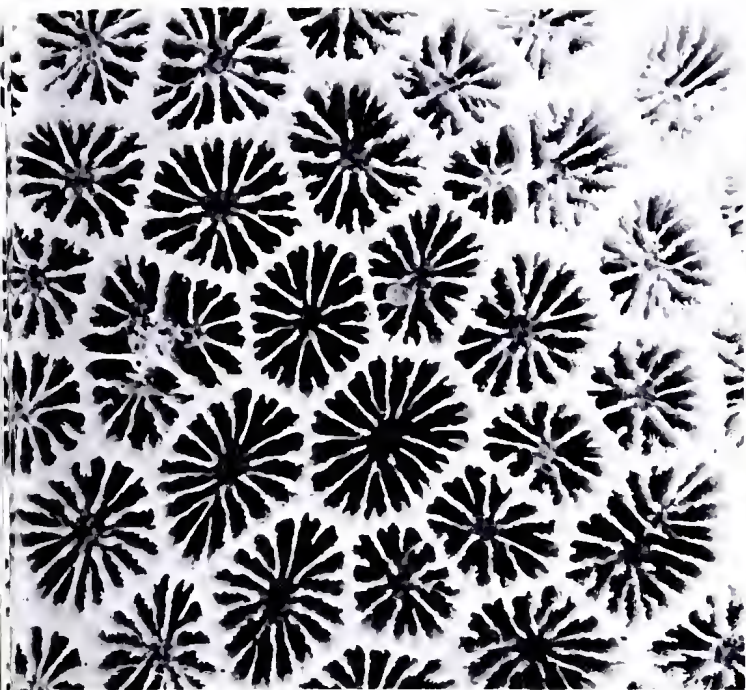


Fig. 145A

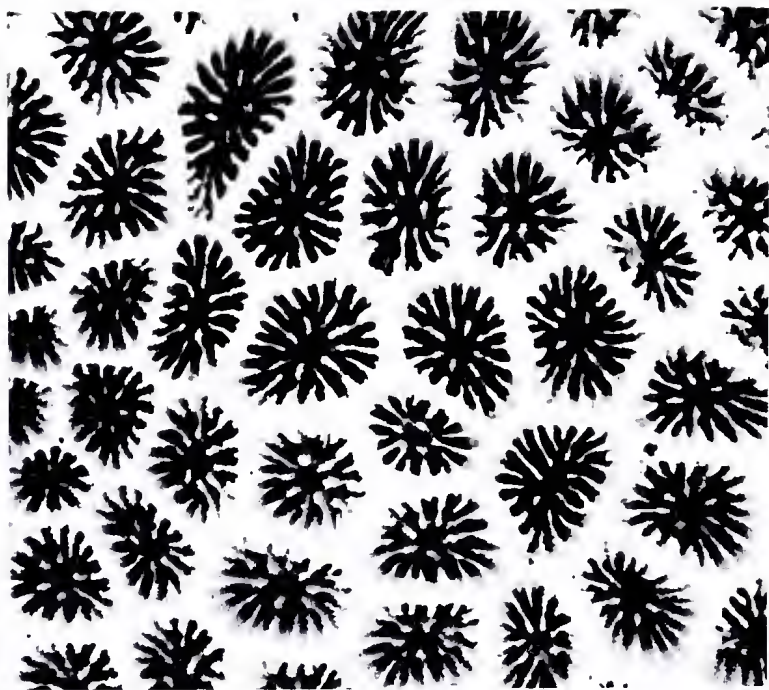


Fig. 146A

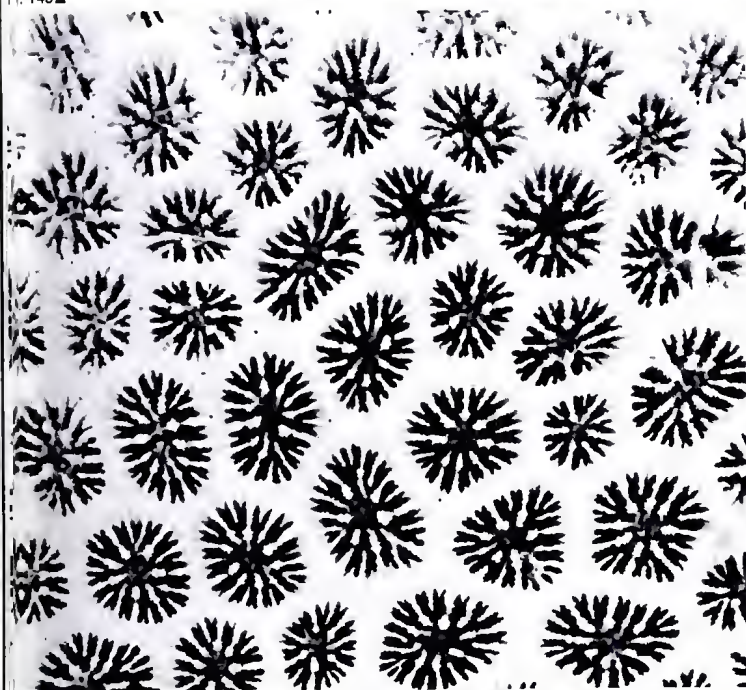


Fig. 147A

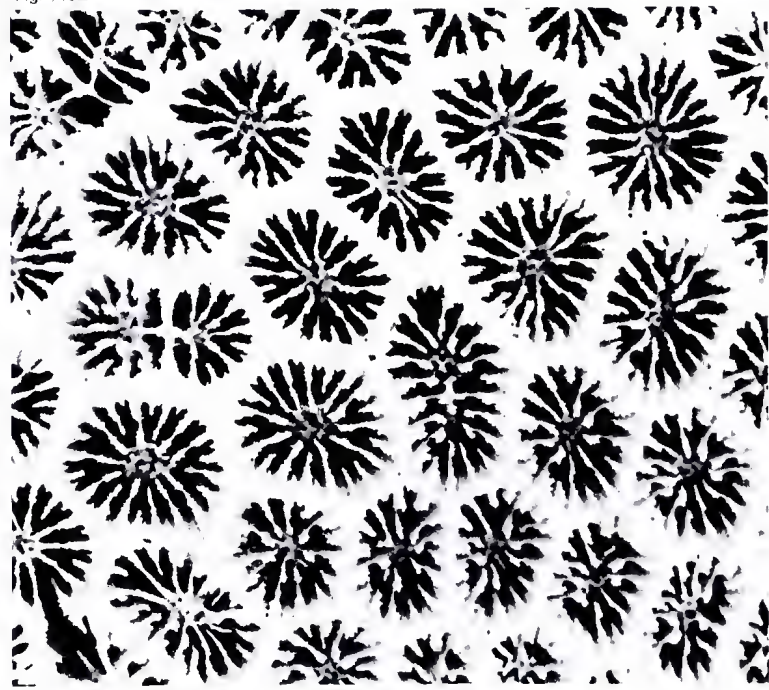


Fig. 148A



Fig. 149A



Fig. 150A

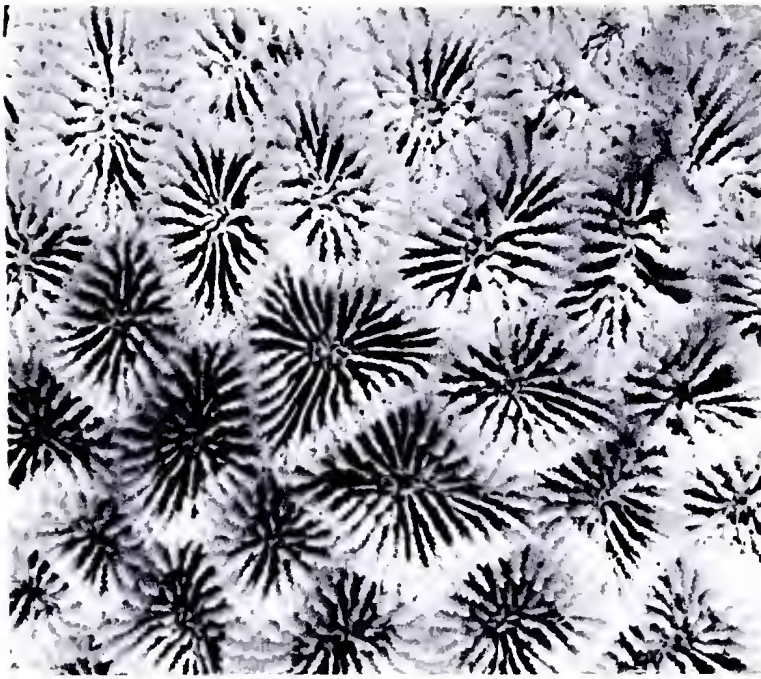


Fig. 151▲

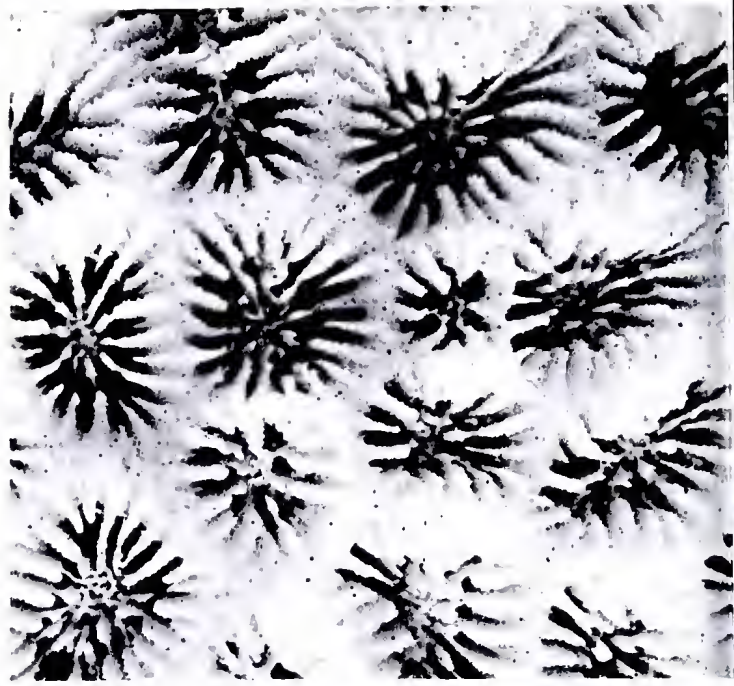


Fig. 152▲

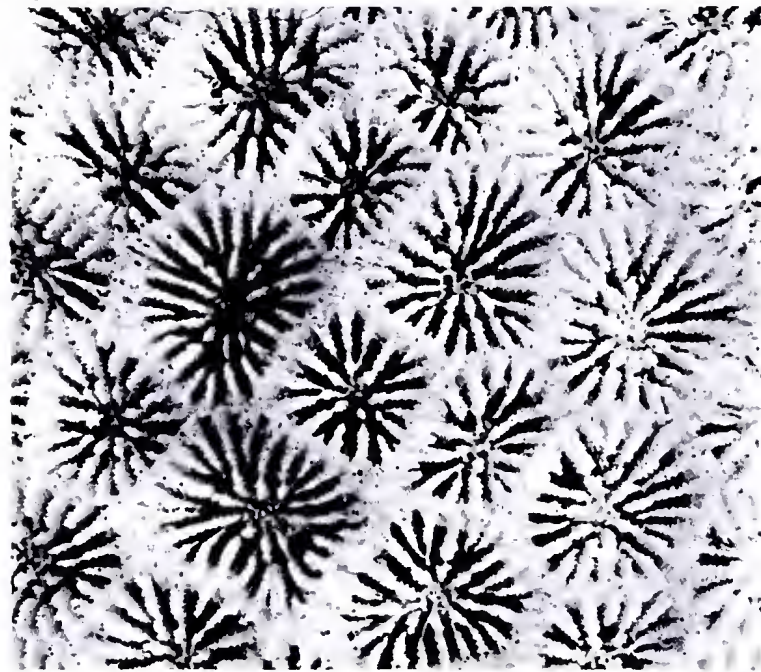


Fig. 153▲

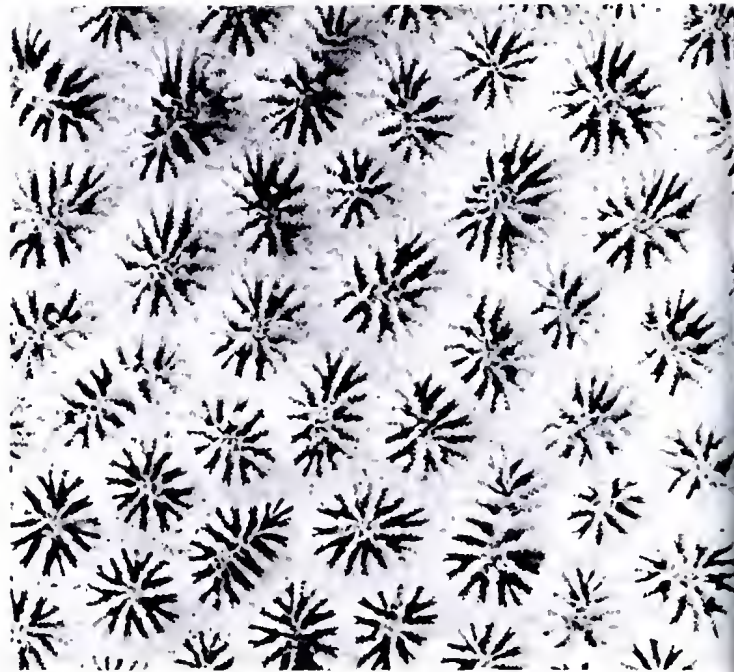


Fig. 154▲

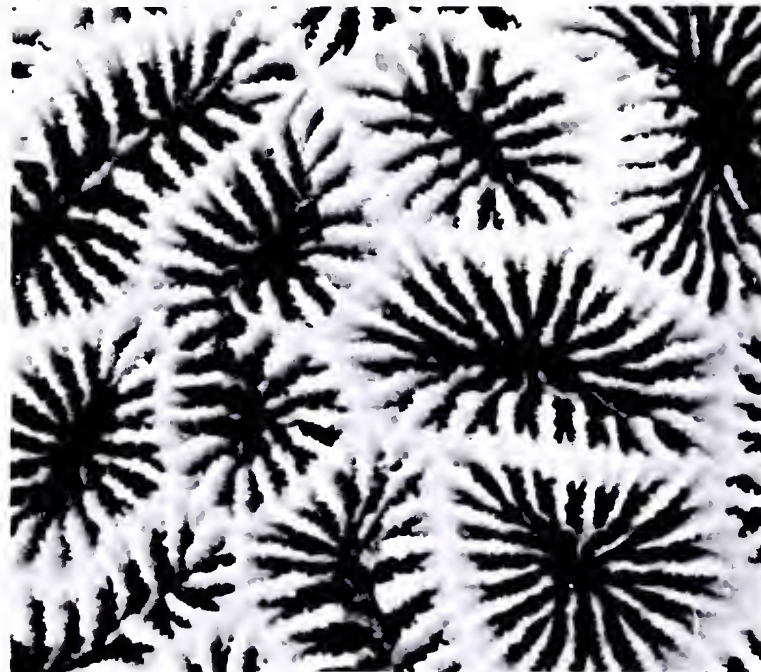


Fig. 155▲



Fig. 156▲

in reference to *G. retiformis*, with which this species has been confused. Chevalier (1971) designated one of the type series of *G. solida* as the type of *G. edwardsi* and listed its earlier synonyms. However, this name would appear to be redundant if *G. capitata* Studer (1881) belongs to the same species, as indicated by Chevalier (p. 245).

Material studied

Murray Islands, Sue Island, Great Detached Reef (13 specimens), **Tijou Reef** (3 specimens), **Bewick Island** (4 specimens), **Jewell Reef, Yonge Reef** (2 specimens), **Lizard Island** (2 specimens), **Hope Island, Low Isles, Lodestone Reef, Palm Islands** (15 specimens), **Rattlesnake Island, Broadhurst Reef** (4 specimens), **Whitsunday Islands, Pompey Complex.**

These localities include collecting stations 1, 2, 3, 5, 9, 17, 18, 27, 34, 41, 55, 57, 90, 91, 92, 97, 100, 105.

Previous records from Eastern Australia

Low Isles (as *G. solida*) Manton (1935); (as *G. parvistella*) Foidart (1970a).

Characters

Colony formation is the same as described for *G. retiformis*. Mature corallites are 2.5-7mm in diameter. Septa are usually in three distinct orders. First order septa are slightly exsert; they plunge vertically or near vertically inside the thecae, then project inwards to form a very large paliform lobe. The paliform lobe and the outer margin are usually thickened, granulated and have regular dentations, with corresponding trabecular ridges extending across the septa. Second order septa are most commonly about half the septal radius across. They have no paliform lobe and are not exsert. As with *G. retiformis*, the third order septa are much reduced, frequently consisting only of a ridge down the endothecae. The columellae are trabecular or spongy and very granulated. The theca is completely calcified and is without visible dissepiments. There are no costae. Septa of adjacent corallites are frequently separated by a thin ridge extending along the top of the relatively thick thecae.

Distribution

Recorded from the Indian Ocean, as far west as the Seychelles Islands, to the Pacific Ocean, as far east as the Loyalty Islands.

***Goniastrea aspera* Verrill, 1865**

Synonymy

Goniastrea aspera Verrill, 1865; Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938).

Prionastrea spectabilis Verrill, 1872 = *Astraea (Fissicella) magnifica* Dana, 1846.

Goniastrea spectabilis (Verrill); Wijsman-Best (1972).

Goniastrea incrustans Duncan, 1889; Matthai (1924); Foidart (1971); Chevalier (1971).

Goniastrea mantonae Crossland, 1952; Stephenson & Wells (1955); Nemenzo (1959); Foidart (1971).

Goniastrea equisepta Nemenzo, 1959.

The name *G. aspera*, used by the Japanese, is the senior synonym of the common species for which Crossland proposed the new name, *G. mantonae* and Chevalier (1971) and Wijsman-Best (1972) the older names *G. incrustans* and *G. spectabilis* respectively. Nemenzo's (1959)

Figs. 151-156 *Goniastrea edwardsi*, Figs. 151-154 ($\times 5.0$), Figs. 155-156 ($\times 10.0$).

Figs. 151, 155 From Low Isles, collecting station 12.

Fig. 152 From Maer Island, Murray Islands, collecting station 27.

Fig. 153 From Great Detached Reef, collecting station 5.

Figs. 154, 156 From the Pompey Complex, collecting station 105.

G. equisepta appears almost identical to his *G. mantonae* and he made no mention of any difference between them. Although the types of *G. aspera* and *G. spectabilis* (Figs. 157, 158) are very different, there is little doubt that they are different ecomorphs of the same species.

Material studied

Three Isles (3 specimens), **Hope Island** (2 specimens), **Low Isles** (2 specimens), **Palm Islands** (12 specimens), **Wheeler Reef** (2 specimens), **Rattlesnake Island** (3 specimens), **Magnetic Island** (7 specimens).

These localities include collecting stations 37, 43, 55, 84, 85.

Previous records from Eastern Australia

Low Isles, (as *Favia (Goniastrea) pectinata*) Stephenson & Stephenson (1933), Marshall & Stephenson (1933), (as *Goniastrea*) Manton (1935), (as *Goniastrea mantonae*) Crossland (1952); **Magnetic Island**, (as *Goniastrea* sp.) Foidart (1971).

Characters

Coralla are rounded, either massive or encrusting. Corallites are cerioid with straight sided walls, 7-10mm in diameter. The thecae are usually thin and the corallites deep and cellular in appearance. Septa are very evenly spaced and only slightly exsert. They are either of the same order or are regularly arranged in two alternating orders which descend abruptly. The paliform crowns are usually very conspicuous, with the paliform lobes regularly spaced and very broad. The inner margins of the paliform lobes descend vertically to the columellae, which are usually small and very compact. The margins of the septa and paliform lobes are finely dentate. Budding is usually monostomodaecal but may be tristomodaecal in areas of rapid division.

Colonies are usually uniform pale brown in colour.

Skeletal variation

It is to be noted that most coralla in the present series come from similar biotopes, characterised by shallow, turbid water. It is very common in protected bays of Magnetic Island, less so in protected bays of the Palm Islands which are further from the coast. Variations in calice structures are correspondingly small, being mostly restricted to degree of development of the paliform lobes (Figs. 159-162). Chevalier (1971) and Wijisman-Best (1972) also recorded little variation in *G. aspera* of New Caledonia, where this species also appears to be restricted to shallow water inside the barrier reefs. The type specimen has reduced paliform lobes and relatively irregular septal dentations characteristic of coralla from more exposed biotopes. The type of *G. spectabilis* is clearly from a protected environment.

Colonies of *G. aspera* are frequently formed from more than one original planula. In such cases, the delineation of the true component colonies is clearly marked by a zone of abnormal growth produced by equal or near equal competitive interaction. As with other species, such formations are most commonly found on soft substrates where sites for planula settlement are very limited.

Affinities

This species is similar to *G. favulus* which occupies similar biotopes but is readily distinguished from it, even underwater, by the nature of the paliform lobes which are more elongated and rounded. Figs. 159, 161, 162, 165 & 166 show these two species collected from the same biotope.

Distribution

Palau, Mergui Archipelago, Indonesia, Philippines, New Caledonia, Great Barrier Reef.

Figs. 157-162 *Goniastrea aspera* ($\times 5.0$).

Fig. 157 Holotype of *Goniastrea aspera*.

Fig. 158 Holotype of *Goniastrea spectabilis*.

Fig. 159 From Maude Bay, Magnetic Island, collecting station 84.

Fig. 160 From Iris Point, Orpheus Island, collecting station 55.

Figs. 161, 162 From Florence Bay, Magnetic Island, collecting station 85.

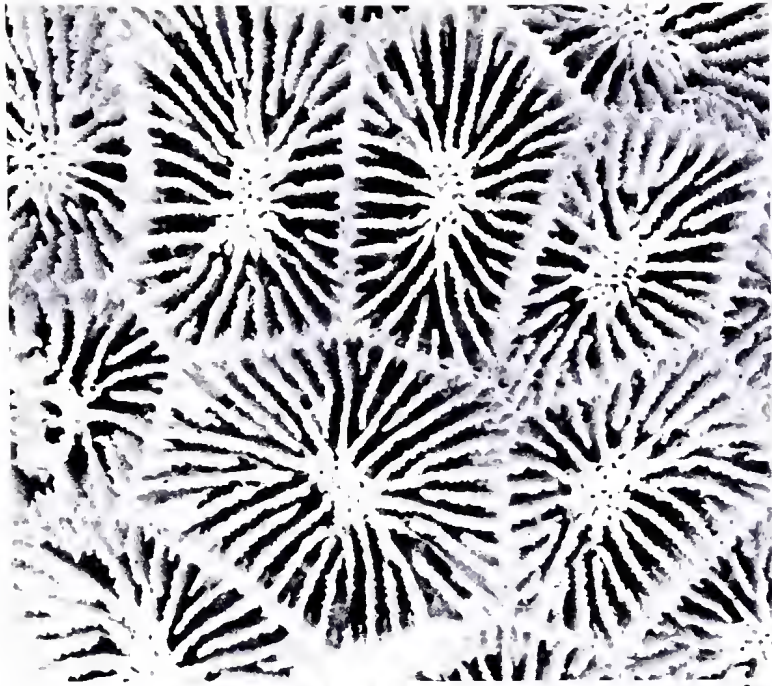


Fig. 162A

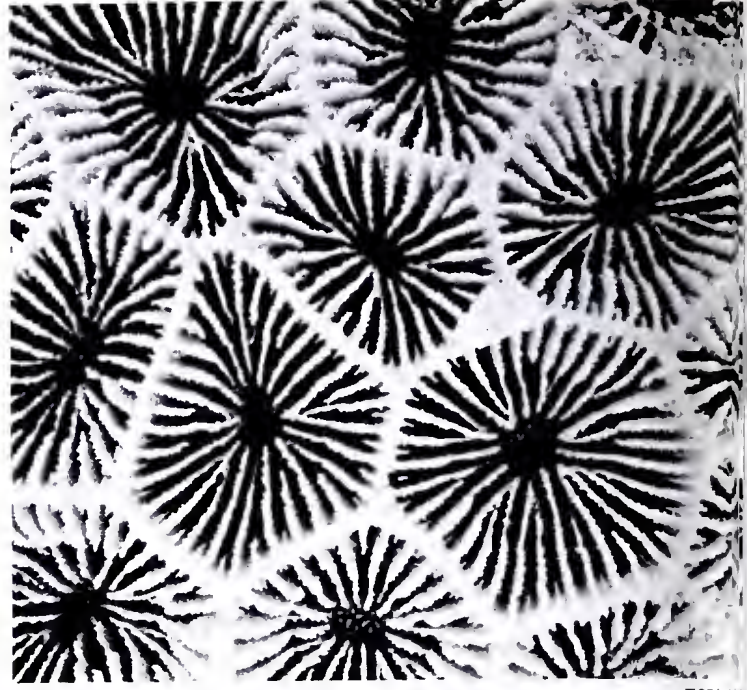


Fig. 161A

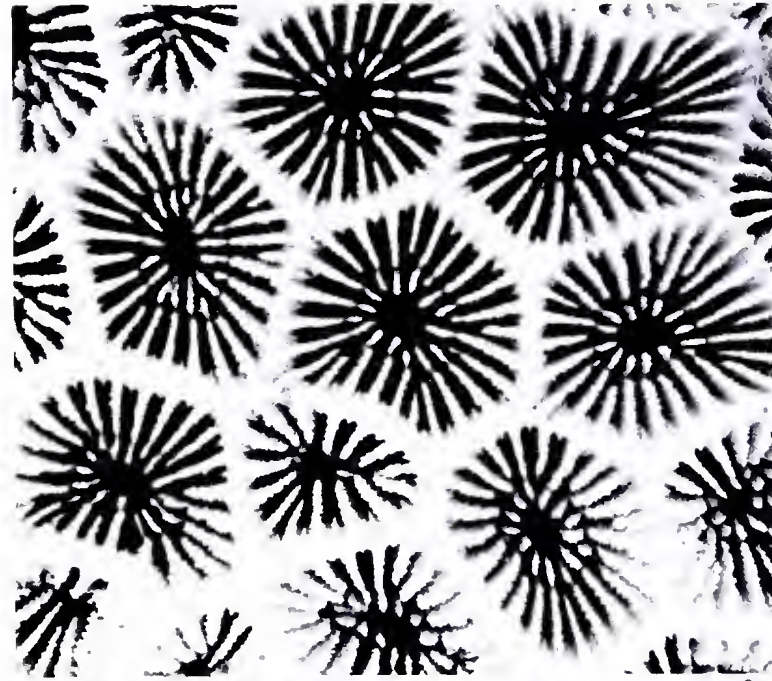


Fig. 160A

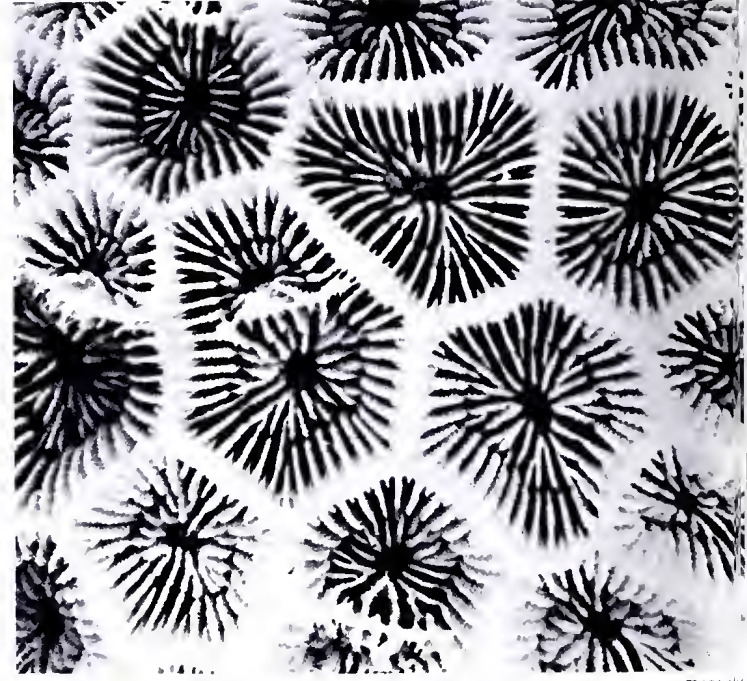


Fig. 159A

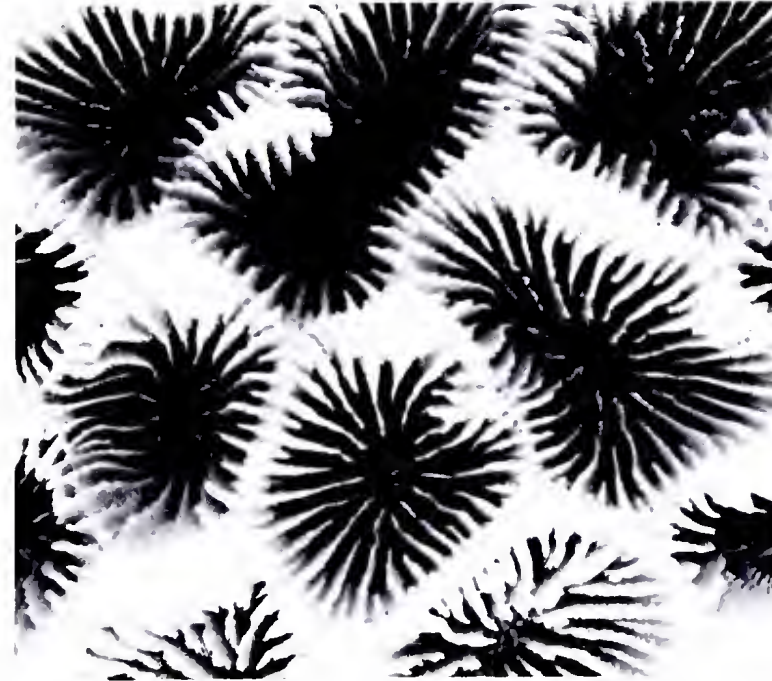


Fig. 158A

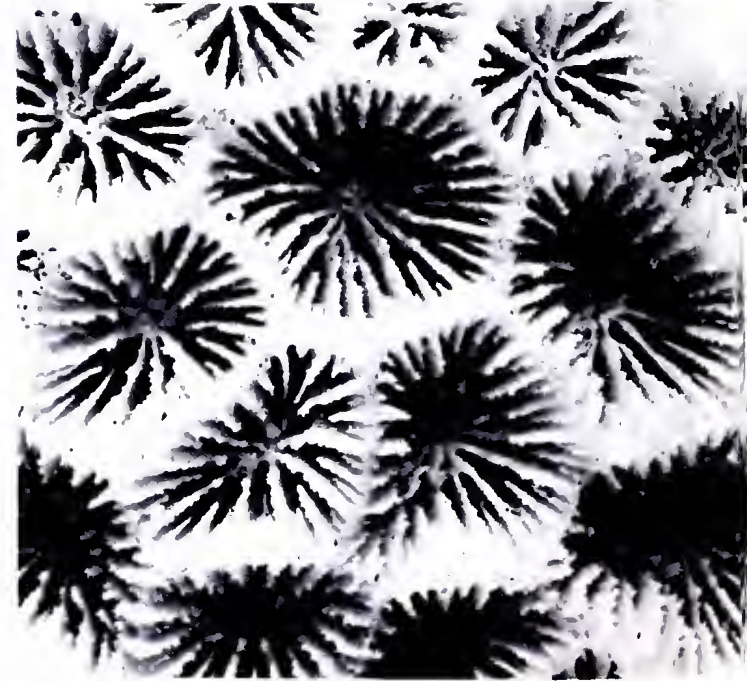


Fig. 157A

Goniastrea cf. favulus (Dana, 1846)

Synonymy

Astraea (Fissicella) favulus Dana, 1846.

Goniastrea favulus (Dana); Wijsman-Best (1972, 1976).

It should be noted that there are no specimens in the present series which are clearly the same species as Dana's type (Fig. 164). However, the present series is in close agreement with the series of Wijsman-Best (1972) from New Caledonia, which includes specimens closer to the type.

Material studied

North West Reef (2 specimens), **Great Detached Reef** (2 specimens), **Houghton Island** (3 specimens), **Three Isles** (11 specimens), **Hope Island**, **Low Isles** (4 specimens), **Lodestone Reef**, **Palm Islands** (9 specimens), **Wheeler Reef** (5 specimens), **Rattlesnake Island**, **Magnetic Island** (4 specimens), **Lord Howe Island** and vicinity.

These localities include collecting stations 5, 14, 40, 41, 84, 85.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are massive or submassive, rarely encrusting. Corallites are monocentric or polycentric and sub-meandroid. Septa are in two orders. First order septa have large, prominent paliform lobes which form a well defined crown around the columella. They may also have several secondary paliform lobes or dentations of smaller size which may terminate in minute horizontal fans. The septal margins and the inner margins of the paliform lobes are finely dentate. First order septa are usually slightly exsert; second order septa are not exsert and seldom extend inwards more than half the calice radius. All septa are granulated. The columellae are compact and spongy. Polycentric valleys have conspicuous centres linked by

Fig. 163 *Goniastrea aspera* at Picnic Bay, Magnetic Island, at low tide (photo: J. Lucas)



continuous, spongy, rather than trabecular, columellae. The thecae are thin, except in coralla from very exposed biotopes. The septa of adjacent corallites are usually not adjoined. Living colonies are usually dull green and brown in colour.

Affinities

Although this is a well defined species, its taxonomic position is far from clear. As previously noted, the type of *G. favulus* is not in close agreement with the present series and Wijsman-Best (1972) concluded that *G. aspera* was a synonym of *G. favulus*. The conclusions of the present study result from a comparison of the holotypes of *G. spectabilis*, *G. aspera* and *G. favulus* with the present collections. However, this genus needs revision on a broader geographic basis, including the type localities, before its taxonomy can become completely stabilised.

Distribution

Wijsman-Best (1972) recorded this species from the Laccadive Islands, Indonesia, Hong Kong, Philippines, Great Barrier Reef, Torres Strait, New Caledonia and Fiji (type locality).

Goniastrea pectinata (Ehrenberg, 1834)

Synonymy (partly after Chevalier, 1971 and Wijsman-Best, 1972)

Astraea pectinata Ehrenberg, 1834.

Astraea favistella Dana, 1846.

Astraea sinuosa Dana, 1846.

Astraea cerium Dana, 1846; Quelch (1886).

Goniastrea planulata Edwards & Haime, 1849; Edwards & Haime (1857); Matthai (1914); Vaughan (1918); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Nemenzo (1959); Ma (1959).

Goniastrea quoyi Edwards & Haime, 1849; Edwards & Haime (1857); Brüggemann (1879b); Quelch (1886); Bedot (1907).

Goniastrea grayi Edwards & Haime, 1849; Edwards & Haime (1857); Quelch (1886); Ma (1959).

Goniastrea pectinata (Ehrenberg); Klunzinger (1879); Gardiner (1904); von Marenzeller (1907); Gravier (1911); Matthai (1914, 1923); Vaughan (1918); Hoffmeister (1925); Faustino (1927); Thiel (1932); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1940); Crossland (1952); Rossi (1954); Stephenson & Wells (1955); Searle (1956); Nemenzo (1959); Ma (1959); Pichon (1964); Utinomi (1965); Scheer (1967); Chevalier (1968, 1971); Rosen (1971); Wijsman-Best (1972, 1976); Pillai, Vine & Scheer (1973); Scheer & Pillai (1974); Pillai & Scheer (1974).

Goniastrea favistella (Dana); Quelch (1886).

Goniastrea coronalis Quelch, 1886.

Goniastrea columella Crossland, 1948; Pillai, Vine & Scheer (1973).

?*Goniastrea regularis* Chevalier, 1971.

The synonymy of *G. planulata* with *G. pectinata* has been discussed in some detail by Crossland (1952). The holotype of *G. columella* has short, irregular, mostly monocentric valleys with strongly dentate septa. It closely resembles Fig. 170. Several specimens of the present series are close to *G. regularis* (e.g. Fig. 171) but these do not appear to be a distinct species.

Material studied

Yorke Island, Murray Islands (3 specimens), east of barrier reef, east of **Murray Island** (41-48m), **Sue Island, Thursday Island, Great Detached Reef** (8 specimens), **Tijou Reef, Bewick Island, Houghton Island, Lizard Island** (4 specimens), **Eagle**

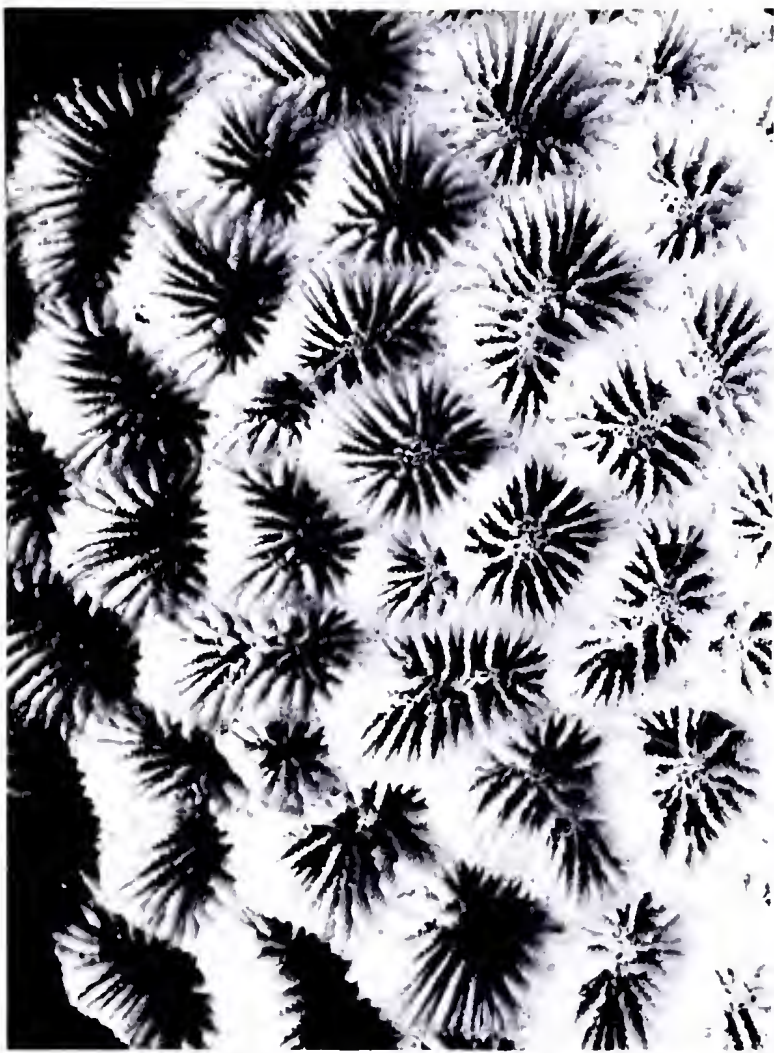


Fig 164A

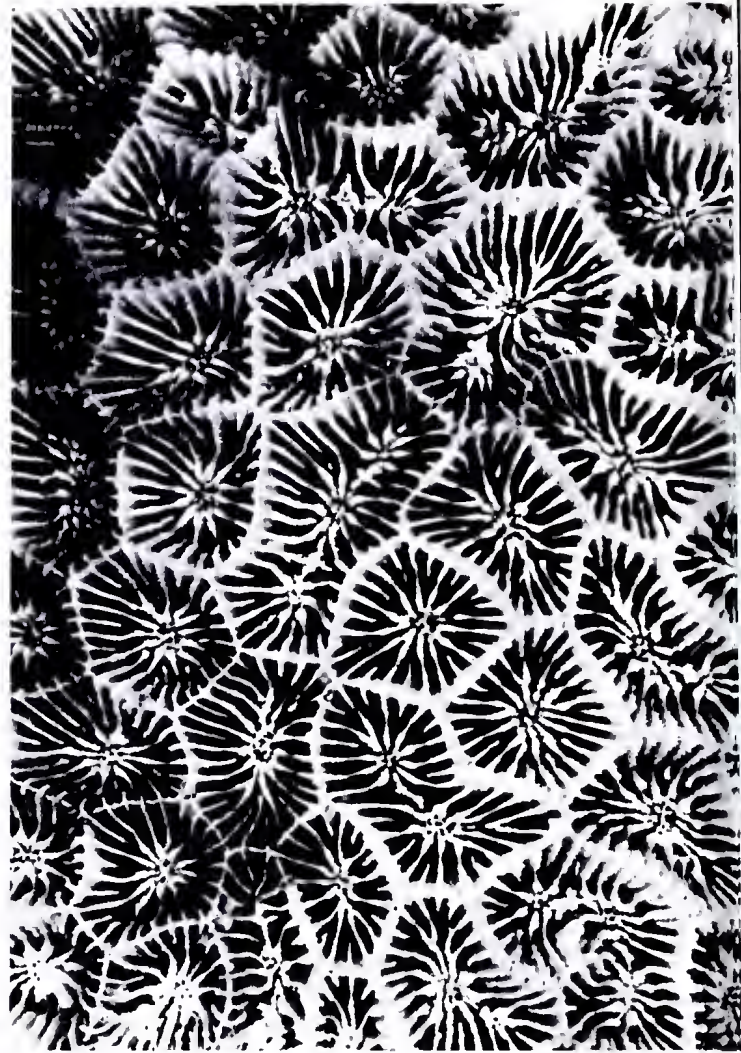


Fig 165A

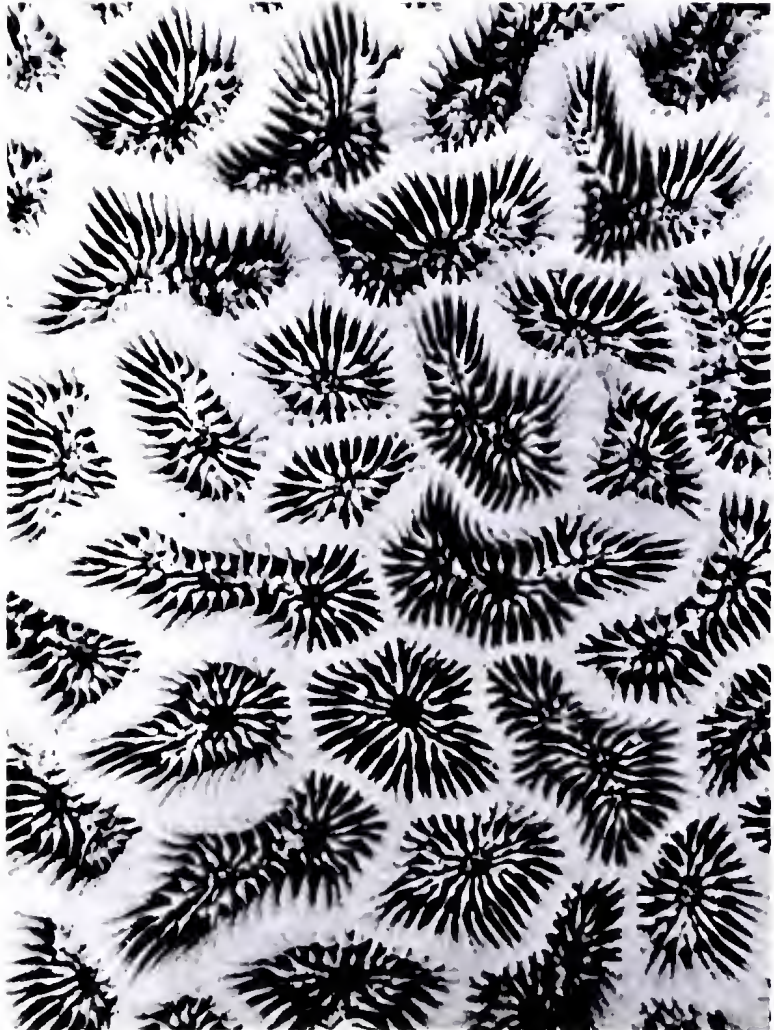


Fig 166A



Fig 167A

Reef (2 specimens), **Three Isles** (2 specimens), **Hope Island** (6 specimens), **Low Isles** (7 specimens), **Palm Islands** (35 specimens), **Broadhurst Reef** (4 specimens), **Rattlesnake Island**, **Magnetic Island** (4 specimens), **Whitsunday Islands** (27 specimens), **Bushy Island-Redbill Reef** (4 specimens), **Pompey Complex** (6 specimens), **Swain Reefs** (8 specimens), **Lord Howe Island**.

These localities include collecting stations 1, 5, 6, 7, 13, 17, 18, 19, 28, 32, 34, 35, 36, 37, 38, 40, 42, 54, 55, 57, 58, 60, 67, 69, 71, 75, 77, 79, 85, 86, 90, 91, 94, 97, 98, 103, 104, 105.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918), Mayor (1918); **Low Isles**, Crossland (1952), Stephenson & Wells (1955); **North West Islet**, Hedley (1927); **Heron Island**, **Solitary Islands**, Veron *et al.* (1974); **Lord Howe Island**, Veron (1974).

Characters

Colonies are mostly submassive or encrusting. Corallites are monocentric or sub-meandroid, seldom with more than three centres. Two orders of septa can be distinguished in most colonies, although in some the second order may be extremely reduced or absent, while in others it may be confused with the first order. First order septa have well developed paliform lobes or series of paliform lobes in the form of large dentations and are usually slightly exsert. The septa are finely dentate along their upper margins and have fine granules on their sides. The thecae are of variable thickness but do not show the extremes of variation found in *G. australensis*.

Colonies are usually a uniform pale brown colour (Fig. 450), but may be darker where light availability is reduced. Colonies exposed to strong sunlight may be pale violet or pink.

Skeletal variation

Much of the growth form variation attributed to this species (e.g. by Vaughan, 1918 and Chevalier, 1971) results from confusion with other species. Although this species occupies a wide range of biotopes, only two intergrading ecomorphs can be distinguished.

Goniastrea pectinata from exposed biotopes (Figs. 169, 172).

Colonies are massive or submassive. Corallites are monocentric or valleys are short. Calices average approximately 5mm in diameter and are thus conspicuously larger than those of *G. edwardsi*, which resembles this species in these biotopes (compare Figs. 172, 173). The theca is thick and the first order septa are thickened above the thecae. Paliform lobes are well developed and form a conspicuous crown around the columella. The latter varies from a few twisted trabeculae in some coralla to a compact spongy structure in others. Monocentric coralla frequently have an intercalicular groove.

Goniastrea pectinata from semi-protected biotopes (Figs. 168, 170).

Coralla from the majority of reef biotopes that are protected from very strong wave action but exposed to strong illumination are usually partly polycentric, submassive or encrusting (Fig. 450 is characteristic). They are usually conspicuously less dense than those from protected biotopes and the width of the thecae is more variable (Fig. 175). The inner margins of the septa are frequently twisted to run lengthwise along the valleys, forming trabecular linkages.

Figs. 164-167 *Goniastrea* cf. *favulus* ($\times 5.0$).

Fig. 164 Holotype of *Goniastrea favulus*.

Fig. 165 From Florence Bay, Magnetic Island, collecting station 85, same biotope as the *G. edwardsi* illustrated in Figs. 154 & 155.

Fig. 166 From Maude Bay, Magnetic Island, collecting station 84, same biotope as the *G. edwardsi* illustrated in Fig. 152.

Fig. 167 From Houghton Island, collecting station 40.

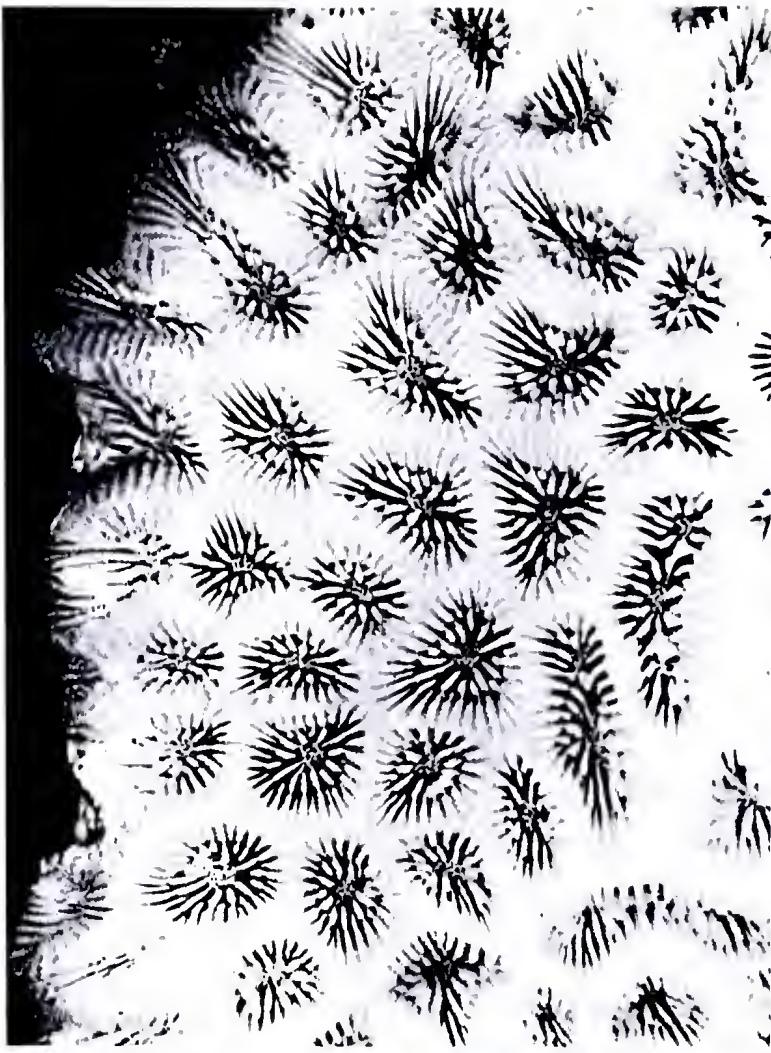


Fig. 168A

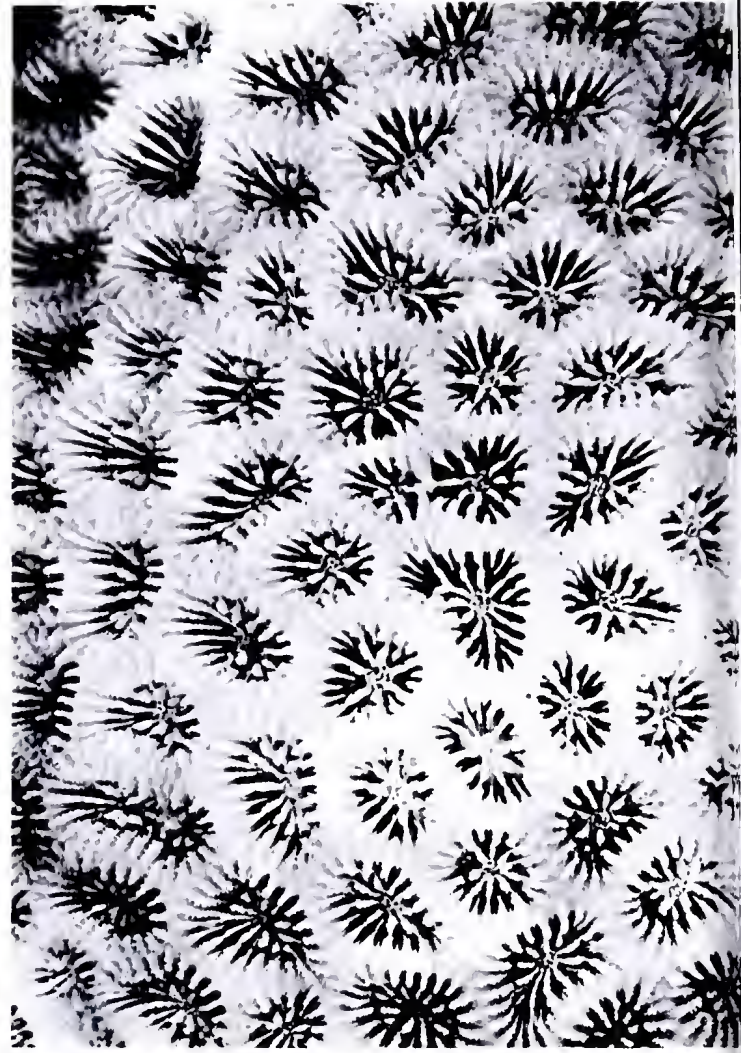


Fig. 169A

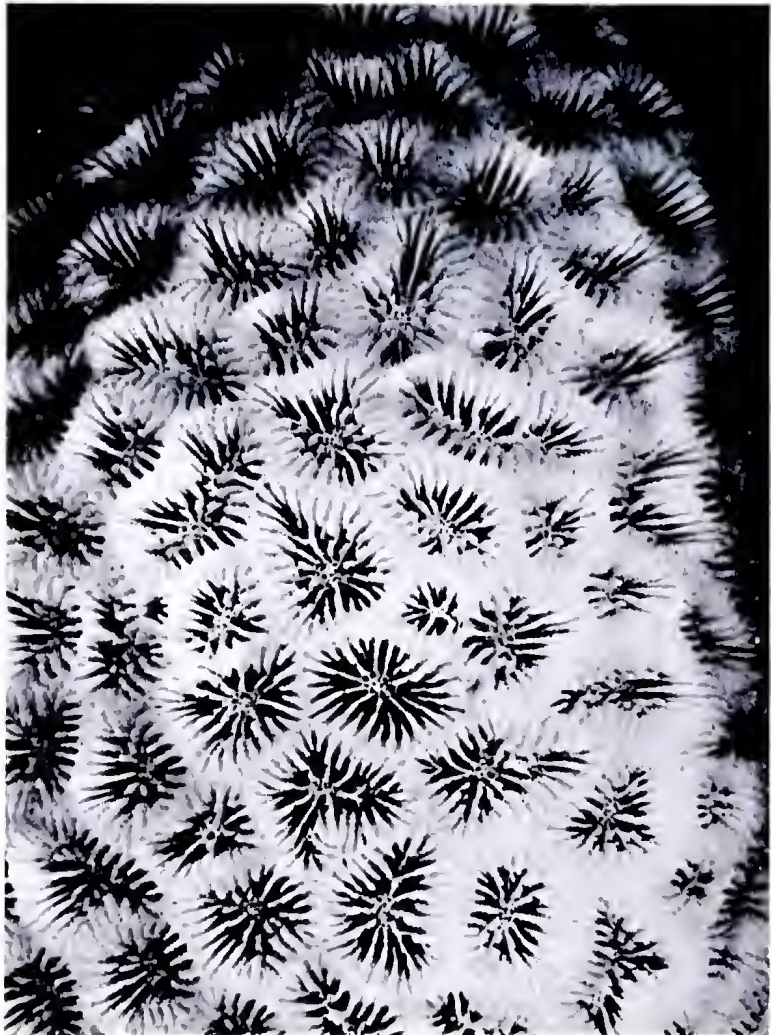


Fig. 170A

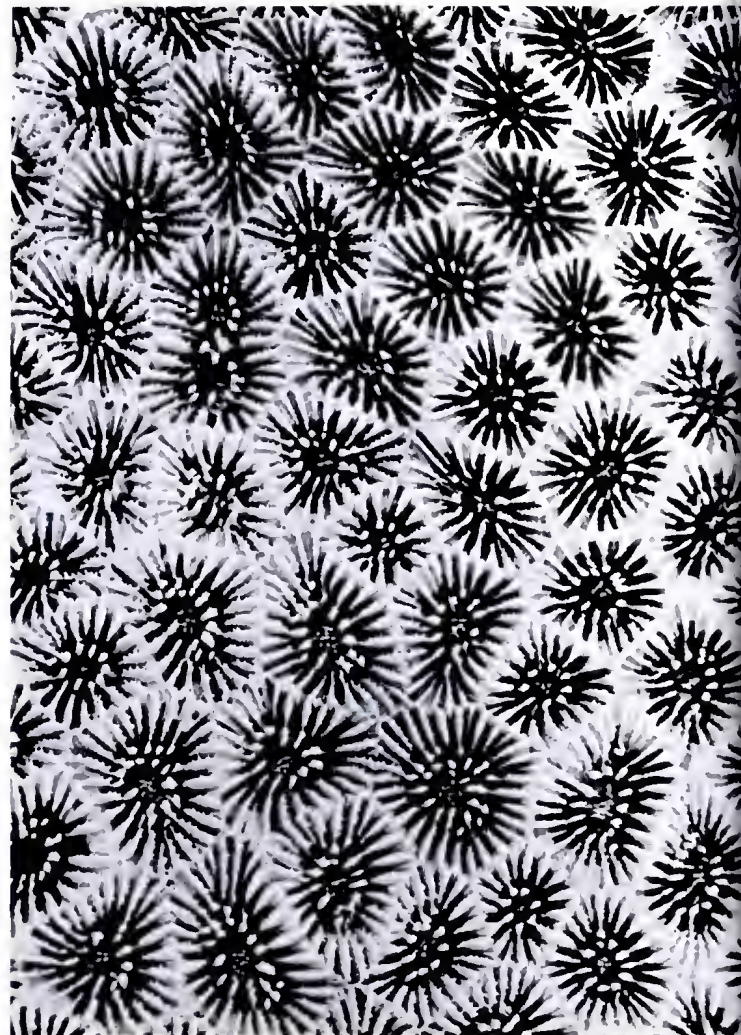


Fig. 171A

Affinities

Ecomorphs from exposed biotopes are closest to *G. edwardsi* and *G. retiformis*; those from more protected biotopes, which have a tendency to meander, are closest to *G. australensis*. The former two species, as collected from the one uniform biotope, are compared with *G. pectinata* in Figs. 172-174. Differences between *G. pectinata* and *G. australensis* are discussed below (p. 94).

Distribution

Widely distributed throughout the Indo-Pacific.

Figs. 168-171 *Goniastrea pectinata* ($\times 2.5$).

Figs. 168, 169 From Great Detached Reef, collecting station 5.

Fig. 170 From Bewick Island, collecting station 18.

Fig. 171 From Bullumbooroo Bay, Great Palm island, collecting station 35.

Figs. 172-174 *Goniastrea pectinata*, *Goniastrea edwardsi* and *Goniastrea retiformis* (respectively) from the same biotope, Broadhurst Reef ($\times 5.0$).



Fig. 173▲



Fig. 174▲

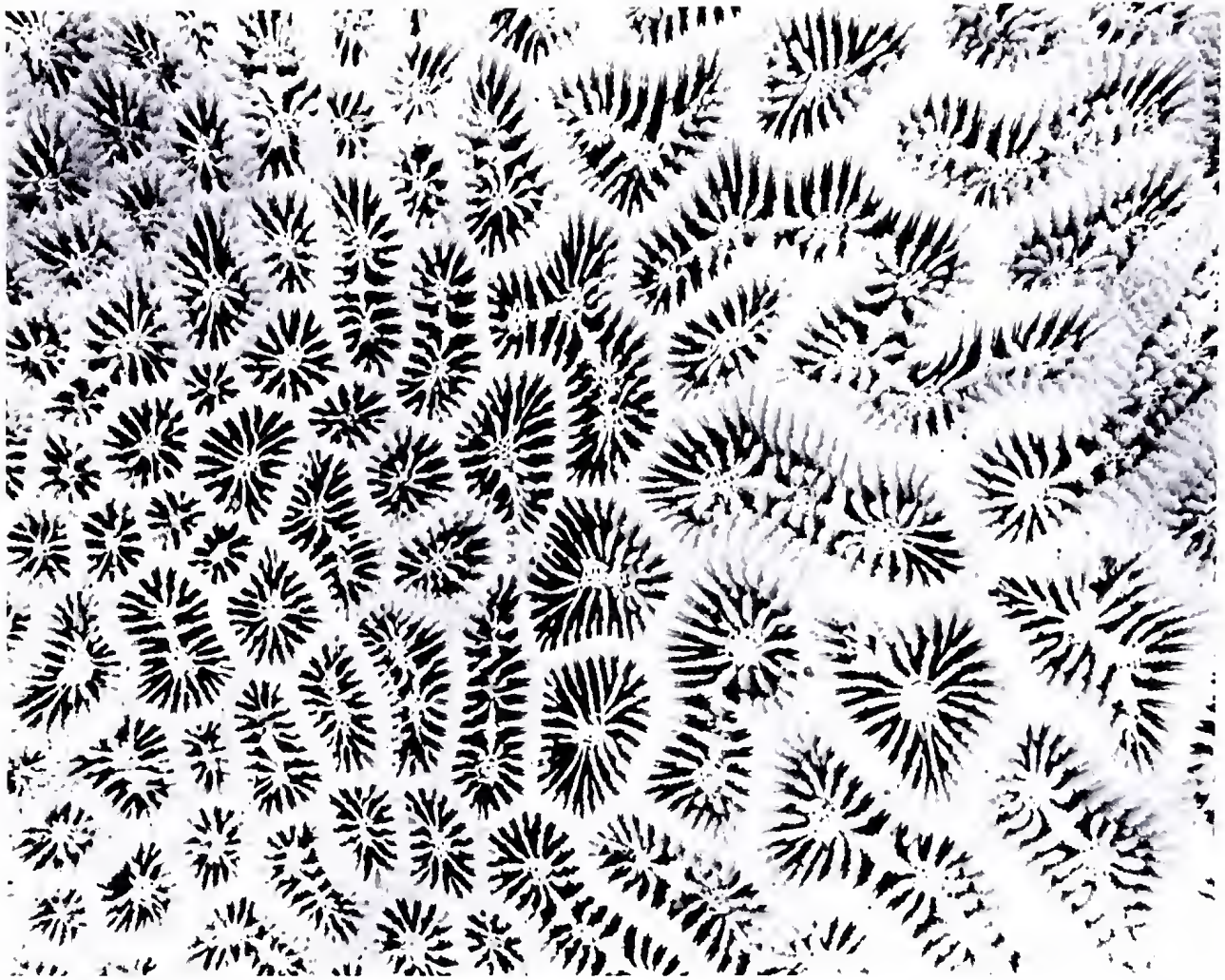


Fig. 175 Skeletal variation in a small area of one colony of *Goniastrea pectinata* from Fantome Island, Palm Islands, collecting station 34 ($\times 2.5$).

***Goniastrea australensis* (Edwards & Haime, 1857)**

Synonymy

Prionastraea australensis Edwards & Haime, 1857.

Coeloria australensis (Edwards & Haime); Rehberg (1892).

Goniastrea benhami Vaughan, 1917; Vaughan (1918); Crossland (1952); Stephenson & Wells (1955); Searle (1956); Ma (1959); Pillai, Vine & Scheer (1973).

Goniastrea australensis (Edwards & Haime); Wijsman-Best (1972).

Goniastrea pectinata (Ehrenberg), (*pars*) Chevalier (1971).

Material studied

Yorke Island, Murray Islands, Thursday Island (3 specimens), **Lizard Island** (2 specimens), **Palm Islands** (31 specimens), **Magnetic Island** (4 specimens), **Whitsunday Islands** (36 specimens), **Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex** (8 specimens), **Swain Reefs** (12 specimens), **Solitary Islands** (8 specimens), **Lord Howe Island** (2 specimens).

Figs. 176-181 *Goniastrea australensis* ($\times 2.5$).

Fig. 176 From Rabbit Island, near Lord Howe Island.

Fig. 177 From Esk Island, Palm Islands, collecting station 42.

Fig. 178 From Swain Reefs, collecting station 77.

Fig. 179 From Bullumbooroo Bay, Great Palm Island, collecting station 35.

Fig. 180 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.

Fig. 181 From Swain Reefs, collecting station 79.

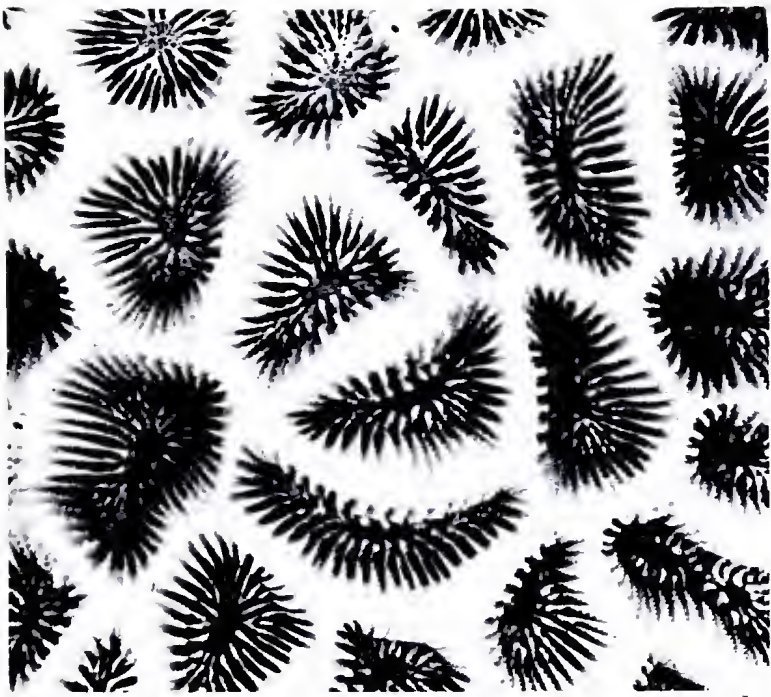


Fig 181A

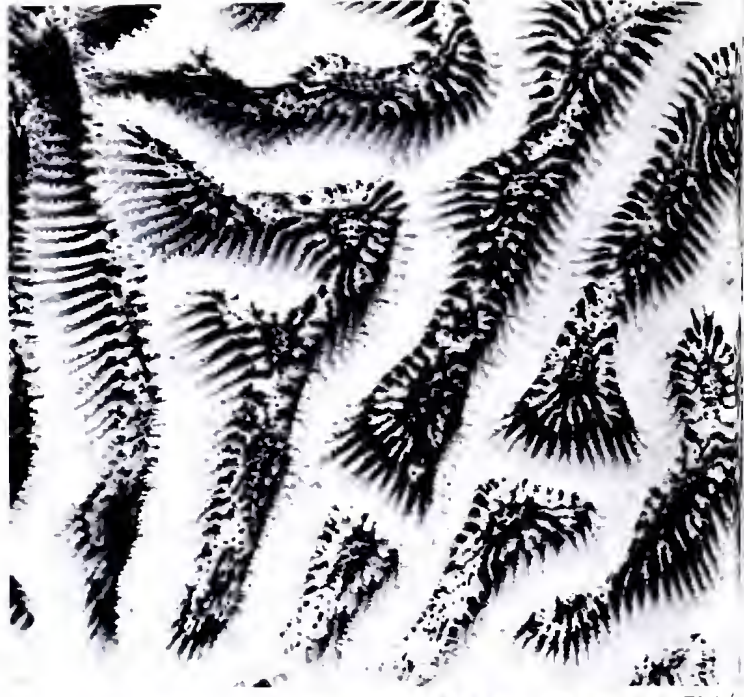


Fig 180A



Fig 179A



Fig 178A

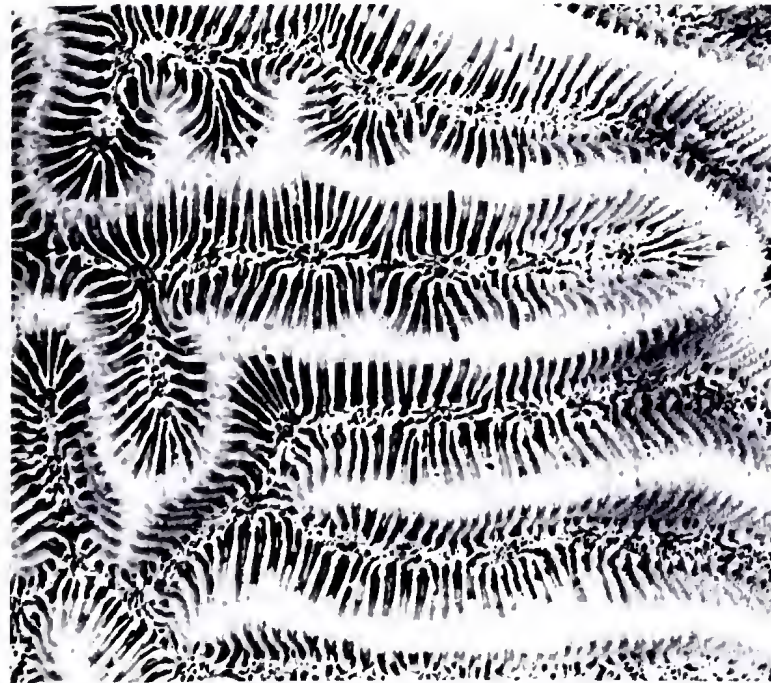


Fig 177A

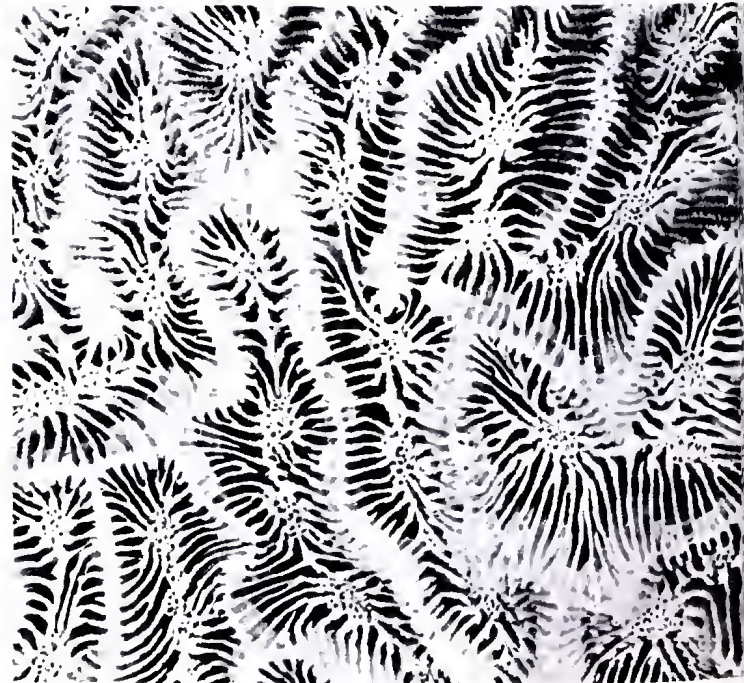


Fig 176A

These localities include collecting stations 13, 28, 32, 34, 35, 36, 37, 38, 42, 43, 54, 55, 56, 57, 60, 67, 68, 69, 70, 71, 75, 77, 79, 80, 85, 93, 97, 98, 103, 104, 105.

Previous records from Eastern Australia

Murray Islands, (as *G. benhami*) Vaughan (1918); **Low Isles**, (as *G. benhami*) Crossland (1952), Stephenson & Wells (1955); **Heron Island**, (as *G. benhami*) Salter (1954); **Solitary Islands**, Veron *et al.* (1974); **Lord Howe Island**, Veron (1974).

Characters

Colonies are massive, submassive or encrusting. They may be meandroid with valleys of indefinite length or sub-meandroid with valleys of 1, 2 or 3 centres, or combinations of both. Centres are usually very distinct with large, conspicuous columellae linked by trabecular-like septal processes. Valleys of most colonies are deep and steep sided. The septa are regularly spaced, are usually equal and usually have paliform lobes. The latter frequently have many fine dentations along their margins and spines over their sides which may develop into trabecular linkages integrated with the columella. Septal margins are finely dentate. Septa are usually evenly exsert, with those of adjacent valleys adjoined over the thecae. The thecae may show great variation in thickness; coralla with very wide thecae may be separated by a groove and may become sub-plocoid.

Skeletal variation

There is usually little variation in this species within the one biotope. Coralla from different biotopes, however, may be divided into very distinctive ecomorphs.

Goniastrea australensis ecomorph *benhami* (Fig. 176).

Coralla from temperate localities (including the type locality of *G. benhami*, the Kermadec Islands), are very meandroid with relatively irregular valleys. There is usually a high degree of fusion between septa so that a small proportion form paliform lobes.

Goniastrea australensis from *protected biotopes* (Fig. 177).

Coralla from deep or turbid water usually have reduced columellae, with centres often indistinguishable. The septa are fine, have reduced paliform lobes, and are usually very regularly spaced. Thecae are usually wide with very vesicular exothecal dissepiments.

Goniastrea australensis from *fringing reefs* (Figs. 178-180).

Coralla from partly protected, shallow biotopes, such as are usually associated with fringing reefs or the back reef margin of patch reefs, usually have valleys of reduced length. The columellae are well developed with well defined centres. Septa are usually regular and evenly spaced. Coralla of some biotopes may consistently have only 1, 2 or 3 centres.

Goniastrea australensis from *exposed reef biotopes* (Fig. 181).

Coralla exposed to strong sunlight in shallow reef waters may become very heavily calcified, with wide thick thecae and greatly thickened calicular structures. Valley lengths show unlimited variation; even within one corallum, valleys may be monocentric on concave surfaces and of indefinite length on convex ones.

Affinities

This is the only fully meandroid *Goniastrea* and thus is usually readily distinguishable from other species of the genus. Underwater, meandroid ecomorphs may resemble *Platygyra lamellina* but are usually distinguishable by their paliform lobes. Ecomorphs from semi-protected biotopes (e.g. fringing reefs) which tend to be sub-meandroid or monocentric, are close to *G. pectinata* but are readily distinguished underwater by having valleys of more regular width and more regularly spaced septa (compare Figs. 171 & 179 from the same biotope). These two species may be difficult to separate in heterogeneous collections. They are confused by Vaughan (1918), who included part of his *G. benhami (australensis)* in *G. pectinata* and consequently found the variation in the latter 'simply bewildering' (p. 115); they are incorrectly synonymised by Chevalier (1971).

Distribution

Kermadec Islands, Great Barrier Reef, New Caledonia, Formosa, Philippines, Japan.

Goniastrea palauensis (Yabe, Sugiyama & Eguchi, 1936)

Synonymy

Favia palauensis Yabe, Sugiyama & Eguchi, 1936; Ma (1937); Eguchi (1938).

Goniastrea cf. *palauensis* (Yabe, Sugiyama & Eguchi); Chevalier (1971).

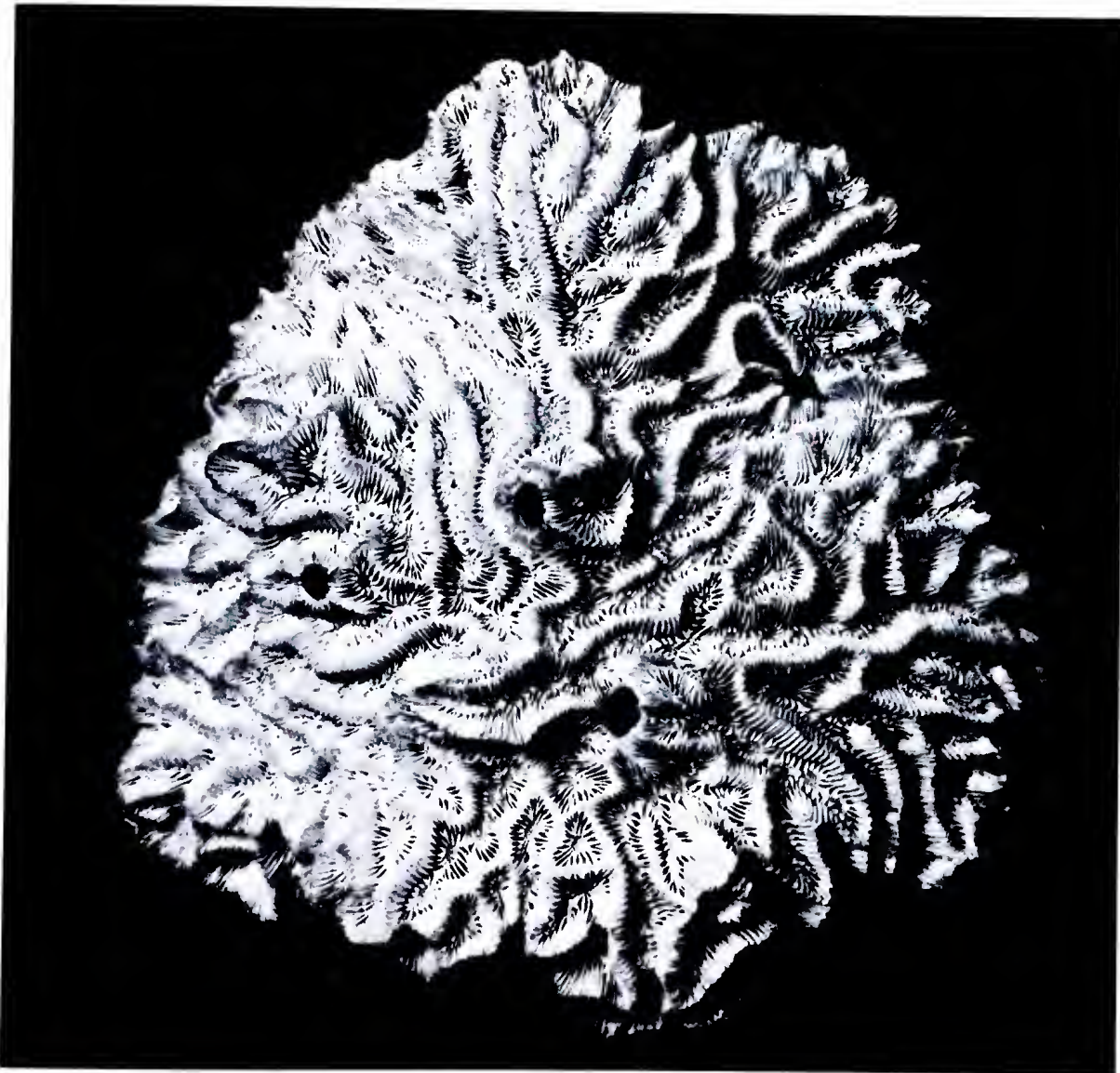
Favites palauensis (Yabe, Sugiyama & Eguchi); Wijsman-Best (1972).

This well defined species is placed in *Goniastrea* because variation in growth form (especially tendency to meander) is similar to other species of the genus, especially *G. pectinata*, and because the septa and paliform lobes are *Goniastrea*-like.

Material studied

Murray Islands (2 specimens), **North West Reef** (2 specimens), **Thursday Island** (3 specimens), **Lizard Island**, **Hope Island** (4 specimens), **Low Isles**, **Palm Islands** (34 specimens), **Keeper Reef**, **Magnetic Island**, **Whitsunday Islands** (7 specimens), **Bushy Island-Redbill Reef** (3 specimens).

Fig. 182 *Goniastrea australensis* from the Solitary Islands ($\times 1.0$).



These localities include collecting stations 14, 21, 29, 34, 35, 37, 38, 42, 43, 45, 53, 54, 55, 56, 60, 80, 85, 90, 93, 97, 98, 100.

Previous records from Eastern Australia

Vaughan's (1918) Plate 43, Figs. 5 and 5a, of *G. pectinata* from **Murray Island** appear to be this species.

Characters

Colonies are massive or encrusting, usually flattened or hillocky. Corallites are monocentric and usually straight-sided with 3 to 6 angles; colonies are cerioid or (rarely) sub-plocoid. The mean diameter of mature calices varies from 6 to 15mm, depending mostly on the thickness of the thecae. Two orders of septa can usually be distinguished, although their lengths vary greatly. This species is characterised by an extremely prominent paliform crown, the paliform lobes always having vertical inner margins descending to the compact, deep seated columella. They are usually thicker than the septa and, as with the septa, have fine dentations. Septa of adjacent corallites are frequently adjoined over the theca. The thickness of the thecae is the most variable character of the species, varying from 2 to 8mm in cerioid colonies. Sub-cerioid colonies have weakly developed costae.

Colonies are usually pale brown or dull green (Fig. 452), although those from deeper water are usually dark brown.

Skeletal variation

The above description applies to the majority of specimens of the present series, most of which come from very protected biotopes. However, as pointed out by Wijsman-Best (1972), this readily recognisable species does not appear to occupy exposed biotopes, or if it does, the corresponding ecomorph has not been recognised.

Goniastrea palauensis from partly exposed biotopes (Figs. 185, 186).

Coralla from areas subject to some wave action or moderate currents have irregularly shaped corallites with thecae of irregular heights. Septa are irregularly exsert, frequently with one or two being much thicker and more exsert than the others. The septal dentations are very prominent. Such colonies are usually irregular in shape.

Goniastrea palauensis from protected biotopes (Fig. 184).

Most coralla from turbid water, or from clear water protected from wave action or currents, have angular, cerioid calices with evenly exsert septa and very prominent paliform lobes. Colonies are usually dome shaped, with those from turbid water seldom attaining a diameter of more than 20cm.

Affinities

The generic designation of this species is commented on above and is discussed by Chevalier (1971). Curiously, the first of the above ecomorphs may be difficult to distinguish from *Favites russelli* ecomorph *rufa* in large collections. Otherwise this species does not closely resemble any other.

Distribution

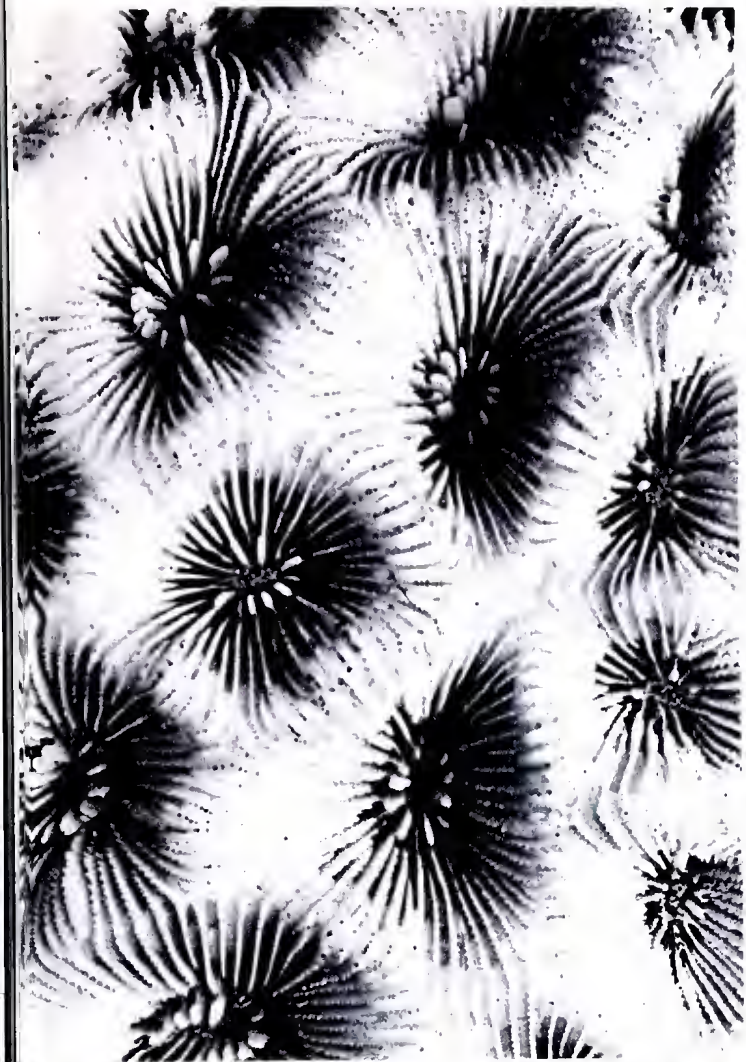
Previously recorded only from Palau and New Caledonia.

Figs. 183-186 *Goniastrea palauensis* ($\times 2.5$).

Fig. 183 From SE Cape, Great Palm Island, collecting station 38.

Fig. 184 From NW Reef, collecting station 14.

Figs. 185, 186 From Fantome Island, Palm Islands, collecting station 34.



183A

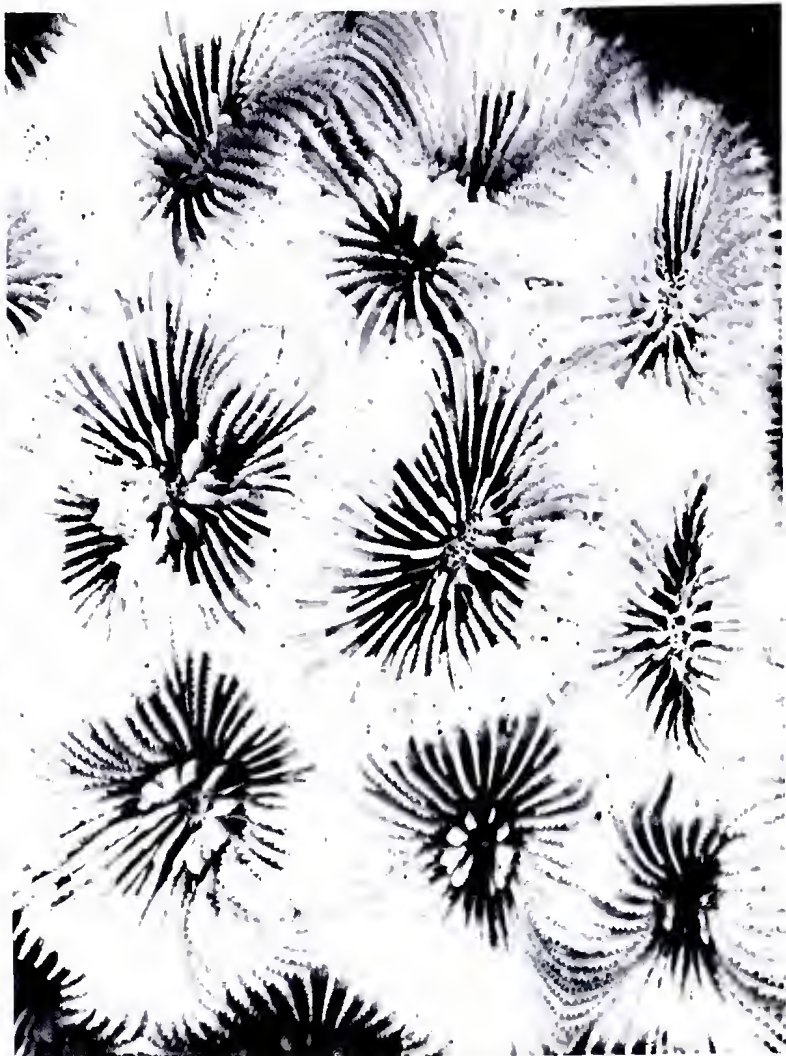


Fig. 184A



185A



Fig. 186A

Generic synonymy

Platygyra Ehrenberg, 1834; Vaughan & Wells (1943); Wells (1956).

Astroria Edwards & Haime, 1848.

Coeloria Edwards & Haime, 1848; Matthai (1928); Crossland (1952); Alloiteau (1957).

Type species *Platygyra labyrinthica* Ehrenberg, 1834 (*non Madrepora labyrinthica* Ellis & Solander (1786)? = *Madrepora daedalea* Ellis & Solander (1786) *non Madrepora daedalea* Forskål (1775)).

The taxonomy of this genus has been, and in some cases still is, made unnecessarily complex by excessive adherence to antiquated hierarchies of nomenclature on the one hand and apparent lack of appreciation of natural variability on the other. As late as 1975, Chevalier described, figured and named ten 'varieties' of *P. daedalea*, four 'varieties' of *P. sinensis* and split his newly described *P. pini* into two named 'varieties'. Thus his account of *Platygyra* covers sixteen 'varieties', which are artificially created units, with no clear biological significance. The logical extension of this process for larger collections would be to create more and more 'varieties' until a situation is reached where species units are given endless nomenclatorial complexity. At each of two extremes, Nemenzo (1959) has described a new species (*P. exigua*) from a single specimen, and Stephenson & Wells (1955) commented that 'within the genus there seem no firm points for separating any of the species'.

Clearly, the genus *Platygyra* is composed of a relatively small number of species, most of which display wide genotypic and phenotypic variations. The large collections of the present study indicate that all discernible skeletal variants are continuous within a given species but are only loosely correlated with each other.

Five species of *Platygyra* are recognised from eastern Australia. Of these, four have massive growth forms, two of which (*P. sinensis* and *P. pini*) usually have very short or monocentric valleys, while the other two (*P. daedalea* and *P. lamellina*) usually have long valleys (Fig. 187). These two groups are themselves divided on the basis of substantial differences in skeletal structure. Thus, these species are normally readily distinguishable within a given biotope. However, specific differences may become obscure in large collections from a wide variety of biotopes, where the skeletal characters of one species overlap with those of another from a different biotope. This problem, inherent in several genera of Scleractinia, is minimised by broad descriptions of *Platygyra* species that accommodate extremes of variability, and which at the same time exclude overlap with other species.

The following account is applicable to the vast majority of the specimens in the present collection. The remainder represent extremes of variation and are not identifiable without reference to other species of the genus from the same biotope. The latter possibly involves at least one rare species which is not included in the present publication.

***Platygyra daedalea* (Ellis & Solander, 1786)**

Synonymy

Madrepora daedalea Ellis & Solander, 1786.

?*Platygyra labyrinthica* Ehrenberg, 1834.

Maeandrina daedalea (Ellis & Solander); Dana (1846).

Maeandrina rustica Dana, 1846.

Astroria daedalea (Ellis & Solander); Edwards & Haime (1849).

Astroria astraiformis Edwards & Haime, 1849.

Astroria esperi Edwards & Haime, 1849.

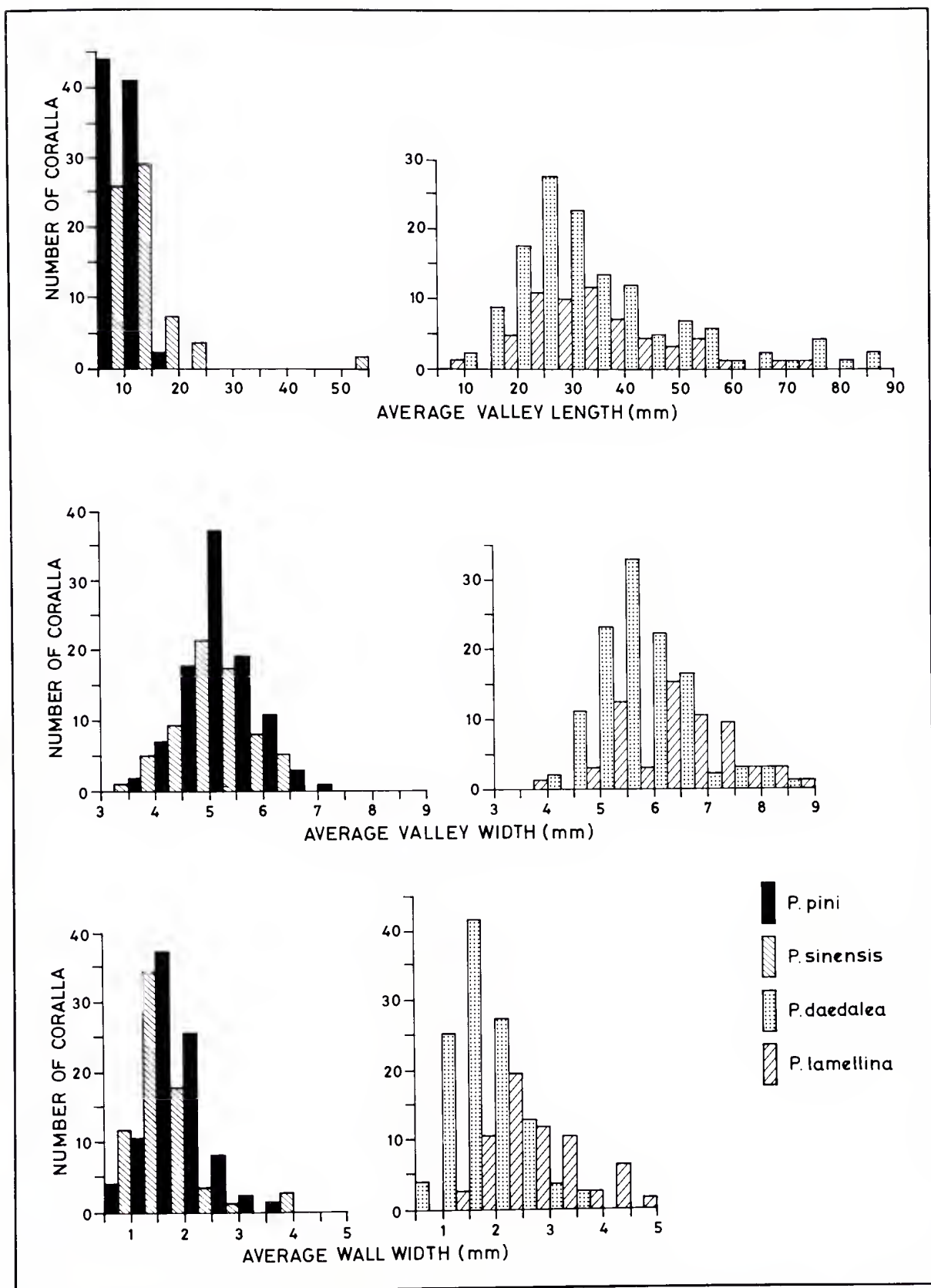


Fig. 187 Comparison of the mean valley length per corallum of the *Platygyra* species indicated.

Fig. 188 Comparison of the mean valley width per corallum of the *Platygyra* species indicated.

Fig. 189 Comparison of the mean wall width per corallum of the *Platygyra* species indicated.

Coeloria daedalea (Ellis & Solander); Verrill (1864); Brüggemann (1879b); Studer (1881); Gardiner (1899, 1904); Bedot (1907); Matthai (1923, 1924, 1928); Gravely (1927); Crossland (1952).

Coeloria astraiformis (Edwards & Haime); Edwards & Haime (1857); Klunzinger (1879); Gardiner (1899, 1904); Matthai (1923, 1924); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1940); Crossland (1952).

Coeloria esperi (Edwards & Haime); Edwards & Haime (1857); Klunzinger (1879); Quelch (1886); Whitelegge (1898); Gardiner (1899).

Maeandra daedalea (Ellis & Solander); Vaughan (1918); Faustino (1927).

Maeandra astraiformis (Edwards & Haime); Vaughan (1918).

Coeloria rustica (Dana); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1940).

Platygyra rustica (Dana); Wells (1954, 1955b); Stephenson & Wells (1955); Ma (1959); Scheer (1967, 1972); Eguchi (1968); Utinomi (1971).

Platygyra daedalea (Ellis & Solander); Nemenzo (1959); Ma (1959); Pichon (1964); Chevalier (1968, 1975); Wijsman-Best (1972).

Platygyra astraiformis (Edwards & Haime); Ma (1959); Wells (1955b); Scheer (1972).

Platygyra esperi (Edwards & Haime); Ma (1959).

Wells (1936) notes that *Madrepora daedalea* Ellis & Solander is preoccupied by *M. daedalea* Forskål, a species of *Alveopora*, and that this may be raised as an objection to the use of the name *Platygyra daedalea*.

It is probable that the synonymy of this widespread species may be further extended to include several nominal fossil species, as well as many species names of recent corals that have mostly fallen into disuse or have been used for restricted geographic areas only.

Material studied

Yorke Island, Murray Islands (2 specimens), **Sue Island, North West Reef, Great Detached Reef** (16 specimens), **Tijou Reef** (10 specimens), **Bewick Island** (2 specimens), **Houghton Island** (2 specimens), **Yonge Reef, Lizard Island** (3 specimens), **Eagle Reef** (2 specimens), **Three Isles** (4 specimens), **Hope Island** (3 specimens), **Low Isles** (5 specimens), **Palm Islands** (61 specimens), **Lodestone Reef, Wheeler Reef** (5 specimens), **Rattlesnake Island, Magnetic Island** (2 specimens), **Whitsunday Islands** (13 specimens), **Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex** (4 specimens), **Swain Reefs** (7 specimens), **Solitary Islands**.

These localities include collecting stations 1, 2, 5, 6, 9, 13, 14, 17, 18, 19, 28, 34, 35, 36, 37, 40, 41, 42, 45, 55, 56, 57, 60, 71, 76, 77, 78, 79, 80, 81, 85, 90, 93, 97, 98, 100, 103, 105.

Previous records from Eastern Australia

Murray Islands, (as *Maeandra daedalea* and *Maeandra astraiformis*) Vaughan (1918); **Low Isles**, (as *Coeloria astraiformis*) Crossland (1952); **Heron Island**, Salter (1954).

Characters

Colonies are usually massive, either rounded or flattened; sometimes they are encrusting. Valleys are usually long, although some colonies have short valleys and some have mixtures

Figs. 190-195 *Platygyra daedalea* ($\times 2.5$).

Fig. 190 From Bullumbooroo Bay, Great Palm Island, collecting station 35.

Figs. 191, 193-195 From different biotopes at Iris Point, Orpheus Island, Palm Islands, collecting station 55.

Fig. 192 From Great Detached Reef, collecting station 5, showing thickening of skeletal elements.

Fig. 194 From Fantome Island, Palm Islands, collecting station 34.



130A

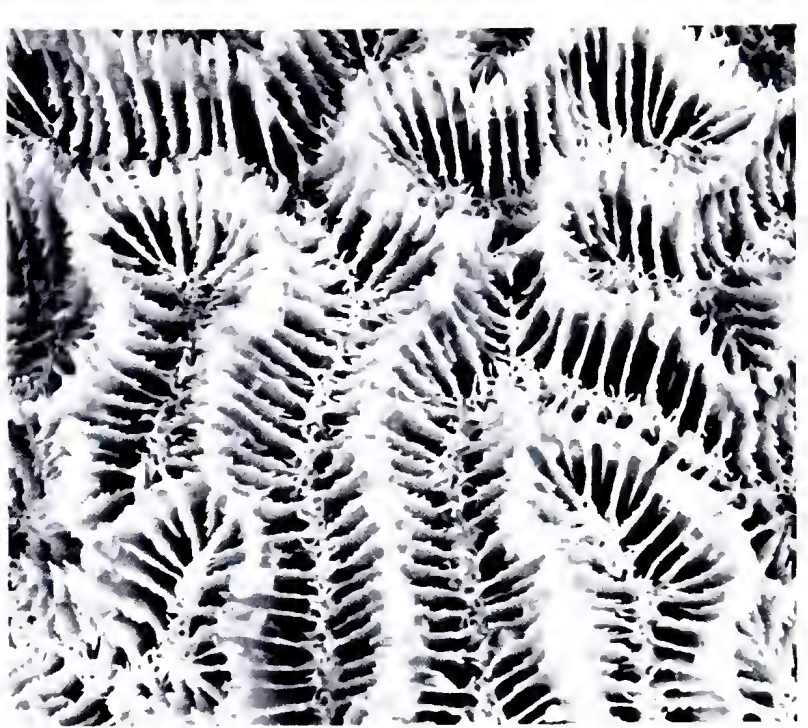
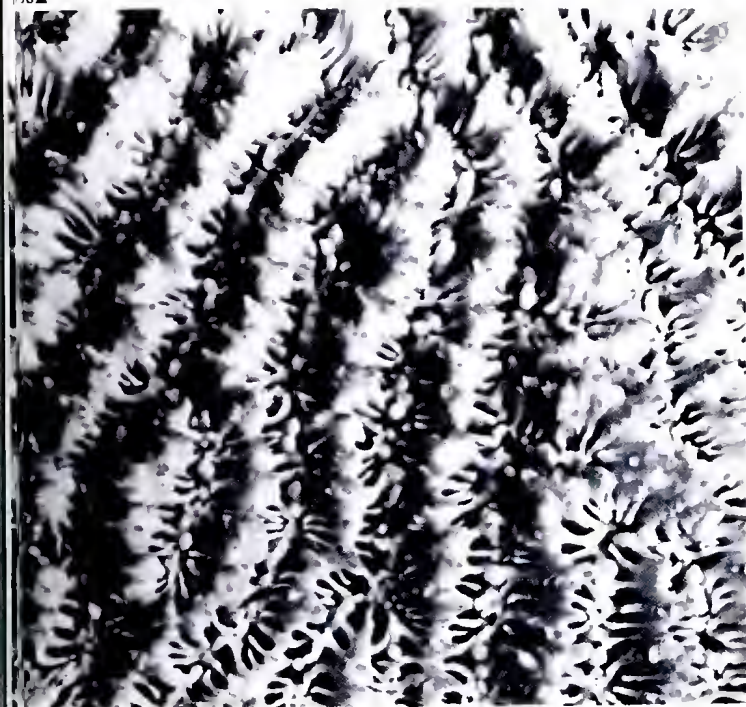


Fig. 191A



132A

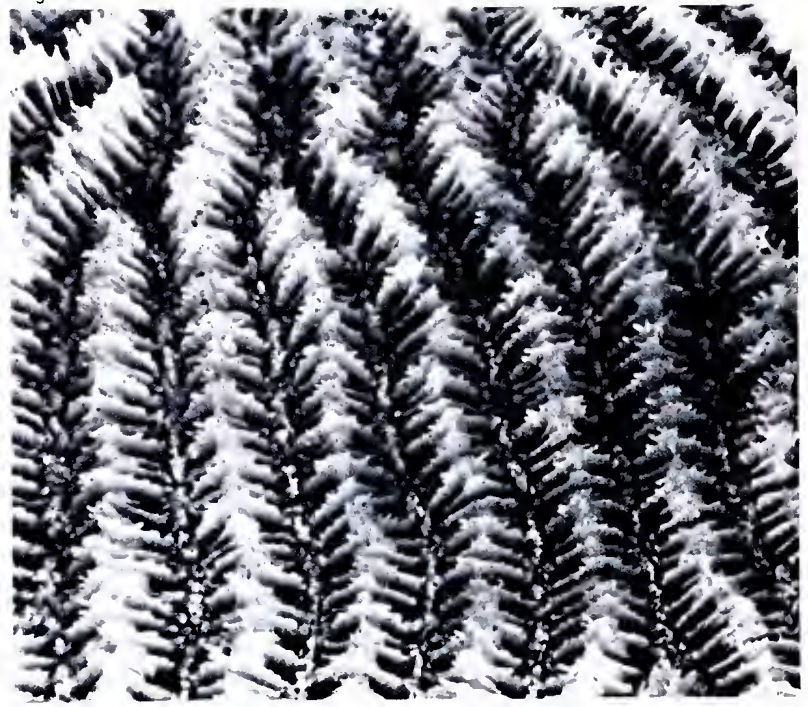


Fig. 193A



134A

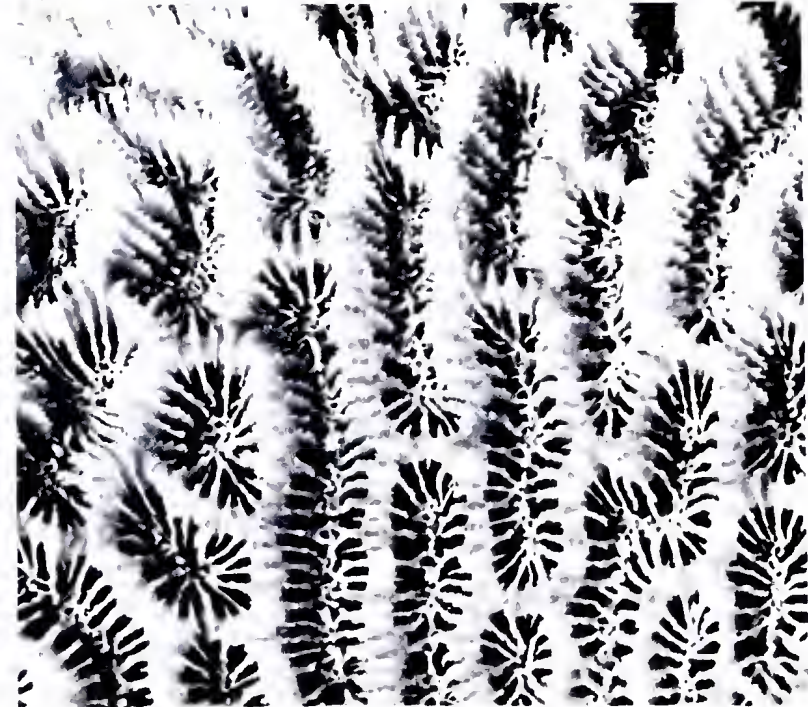


Fig. 195A

of both (Fig. 195). The walls are usually narrow and often perforated. Septa are very exsert, usually having pointed or ragged tips, and are frequently adjoined by fine trabecular linkages above the wall (Fig. 191). Septa of the first two orders, if recognisable, are usually equal. They have large dentations, especially on their lower edges where they are frequently twisted to form fine horizontal plates, as described for *P. pini*. They descend abruptly down into the valleys. As with other *Platygyra*, fine granulations are present on the sides of the septa. Paliform lobes are usually found only in short, broad valleys and even then are poorly developed. The spongy, trabecular columellae are of variable widths but are usually conspicuous. Centres are not usually formed or form only where valleys join.

Colonies are often brightly coloured (Figs. 453, 454), frequently with brown walls and green valleys. However, colours are variable, both among colonies and within the same colony, with darker colours occurring on the shaded sides.

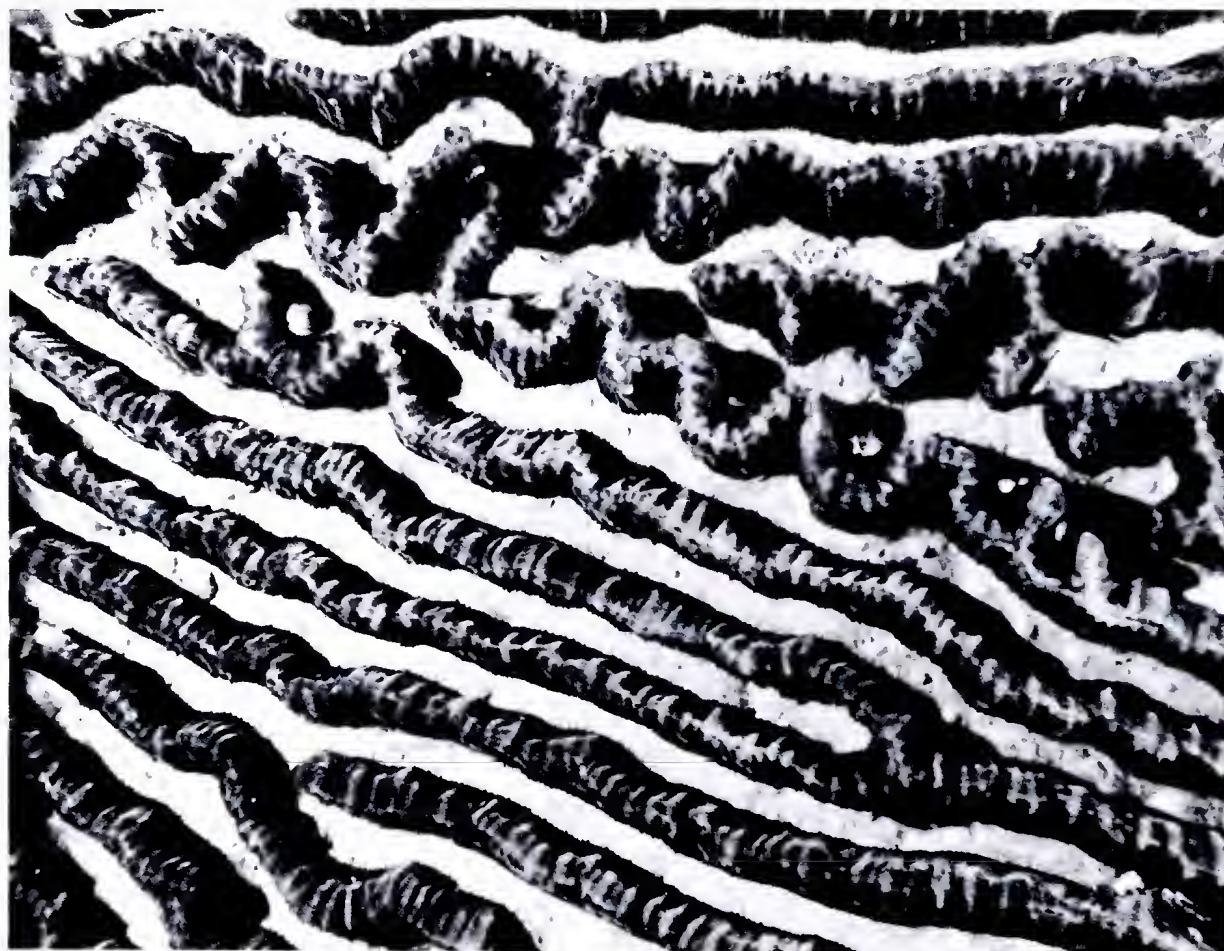
Skeletal variation

This study supports Chevalier's (1975) assertion that many nominal species of *Platygyra* result from the growth form variations of this one polymorphic species. The lack of conservative skeletal characters makes *P. daedalea* particularly difficult to define in large collections, although it is readily recognisable underwater and in large collections from single biotopes.

A large component of the long series of varieties described by Chevalier appears to be genetic in origin; thus, colonies with widely differing skeletal characteristics are frequently found together within the one biotope. Environmentally induced variations, which are uniform throughout much of the Faviidae, are superimposed on genotypic ones and thus changes in growth form from one biotope to another can be readily determined.

There are three principal ecomorphs which are broadly associated with the main biotopes this species occupies.

Fig. 196 *Platygyra daedalea*, *in situ*, from the Palm Islands ($\times 2.0$).



Platygyra daedalea from exposed biotopes.

This form occurs in most reef situations which are exposed to wave action and are well illuminated. Colonies tend towards a spherical condition. Calicular characters are as described above for the species in general. Valleys are mostly long and meandroid (Fig. 190) but may be short, even monocentric. Valley length is relatively constant within given coralla and appears to be largely genetically determined. In colonies exposed to strong currents, all skeletal elements may be markedly thickened (Fig. 192).

Platygyra daedalea from biotopes with relatively poor illumination.

This form is common in turbid water, deep water, and on the sides of steeply sloping fringing reefs. Colonies tend to be rather flat. Valleys are usually long and straight and are perpendicular to the growing edge of the colony. The septa have very long dentations, especially at their crests. The columellae are usually very loose and narrow, often consisting only of a single row of trabecular linkages. The walls are usually narrow (Fig. 194 is typical).

This association between modified calicular characters and the flattened growth forms of the colonies is not universal and growth forms more characteristic of one ecomorph are sometimes associated with calicular characters more often associated with the other. However, these colonies are almost always associated with biotopes which are themselves of an intermediate nature.

Platygyra daedalea microatolls.

This species commonly forms microatolls in very shallow ponded water. As with all microatoll-forming species, colonies form flat discs, with active growth occurring only at the circumference of the disc. Such colonies are always well illuminated and exposed to some wave action and hence have the calicular character of the first ecomorph.

Distribution

Widely distributed throughout the Indo-Pacific.

Platygyra lamellina (Ehrenberg, 1834)

Synonymy (synonymy of Edwards & Haime, 1849, 1857 after Wijsman-Best, 1972)

Maeandra lamellina Ehrenberg, 1834; Edwards & Haime (1857); von Marenzeller (1907); Gravier (1907, 1911); Vaughan (1918); Hoffmeister (1925); Faustino (1927); Yabe & Sugiyama (1935).

Platygyra lamellina (Ehrenberg); Wells (1936, 1955b); Stephenson & Wells (1955); Searle (1956); Nemenzo (1959); Ma (1959); Utinomi (1965, 1971); Scheer (1967, 1972); Chevalier (1968); Rosen (1971); Pillai, Vine & Scheer (1973); Pillai & Scheer (1974); Scheer & Pillai (1974).

Coeloria lamellina (Ehrenberg); Matthai (1924, 1928); Yabe, Sugiyama & Eguchi (1936); Crossland (1938, 1941, 1952); Umbgrove (1940); Rossi (1954).

Coeloria bottai Edwards & Haime, 1849; Edwards & Haime (1857); Ridley (1883); Matthai (1924).

Coeloria laticollis Edwards & Haime, 1849; Edwards & Haime (1857).

Coeloria subdentata Edwards & Haime, 1849.

Coeloria forskaliana Edwards & Haime, 1849; Matthai (1924).

Coeloria leptoticha Klunzinger, 1879; Quelch (1886); Rehberg (1892); Ortmann (1892).

Coeloria arabica Klunzinger, 1879; Rehberg (1892); Bedot (1907); Matthai (1923).

It is probable that the synonymy of *P. lamellina* includes several other nominal species. However, these names are not in general use and their taxonomic status has not been studied.

This species was placed in synonymy with *P. daedalea* by Stephenson & Wells (1955) from their Low Isles collection; it was reinstated by Wijsman-Best (1972) from studies at New Caledonia, and re-synonymised by Chevalier (1975) also from a New Caledonia collection.

Chevalier commented that he was unable to use the criteria accepted by Wijsman-Best and others for separating these species in his collection.

Material studied

Yorke Island, Barrier Reef NE of Murray Islands, Sue Island, Thursday Island (2 specimens), **Great Detached Reef** (2 specimens) **Tijou Reef, Houghton Island,**

Figs. 197-200 *Platygyra lamellina* ($\times 2.5$).

Fig. 197 From Barber Island, Palm Islands, collecting station 83.

Fig. 198 From Thursday Island, collecting station 54.

Fig. 199 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91.

Fig. 200 From Curaçoa Island, Palm Islands, collecting station 56.

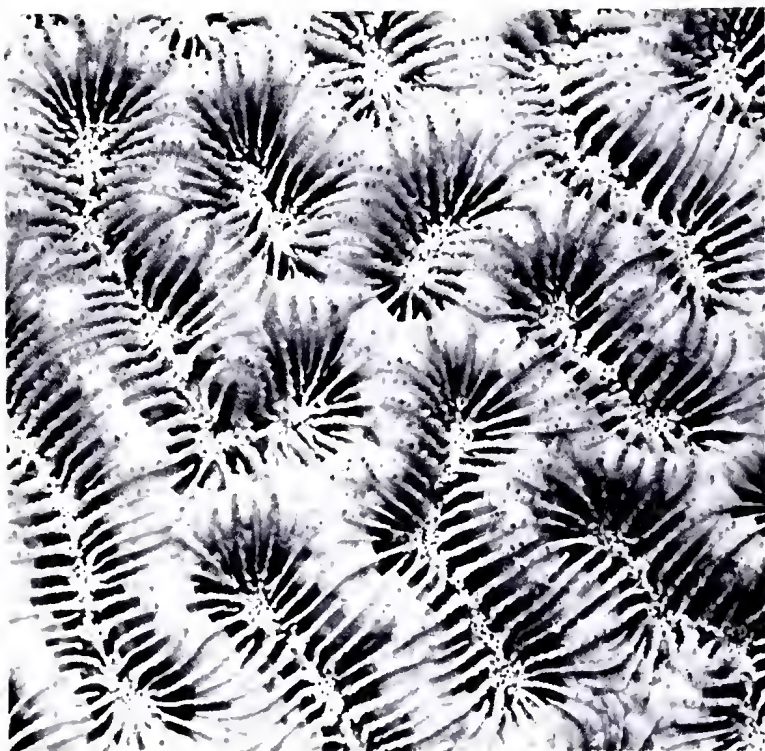


Fig. 197▲



Fig. 198▲

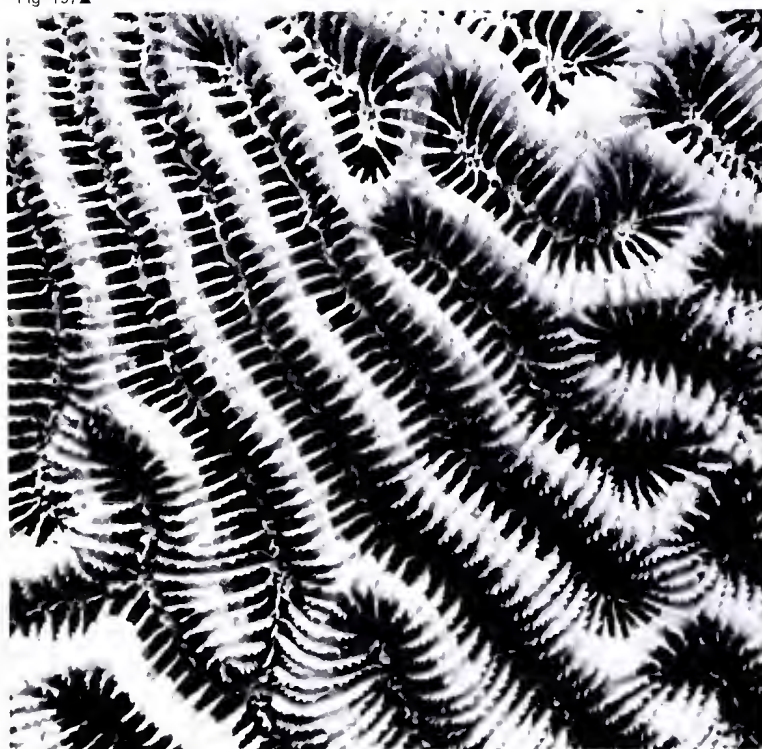


Fig. 199▲



Fig. 200▲

Yonge Reef, Lizard Island (3 specimens), **Eagle Reef, Low Isles, Palm Islands** (46 specimens), **Wheeler Reef, Magnetic Island** (2 specimens), **Whitsunday Islands** (2 specimens), **Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex** (2 specimens), **Swain Reefs** (4 specimens), **Solitary Islands**.

These localities include collecting stations 2, 5, 9, 13, 17, 19, 23, 33, 34, 36, 38, 40, 41, 42, 43, 45, 54, 55, 56, 57, 60, 67, 69, 75, 79, 80, 83, 85, 90, 91, 92, 97, 100, 103.

Previous records from Eastern Australia

Murray Islands, (as *Maeandra lamellina*) Vaughan (1918); **Low Isles**, (as *Coeloria lamellina*) Matthai (1928), (as *Coeloria lamellina*) Crossland (1952), Stephenson & Wells (1955); **Heron Island**, Salter (1954); **Moreton Bay**, Wells (1955b); **Solitary Islands**, Veron *et al.* (1974); **Lord Howe Island**, Veron (1974).

Characters

Colonies are massive and rounded, occasionally flat. Valleys are almost always elongated except on concave surfaces where they may become short, even monocentric (Fig. 200). The walls are characteristically thick (1-1.5 x the valley width). Septa are continuous across the walls and are only slightly exsert. They are evenly spaced, with successive cycles usually indistinguishable. Septal dentations are usually evenly distributed around the septa and, as with other *Platygyra* species, they may form tiny horizontal plates. There are no paliform lobes. The columellae are usually narrow and not significantly different from those of *P. daedalea*. There is little tendency to form a recognisable centre.

Colonies have the same wide colour variations as *P. daedalea*. However, those from far southern localities (e.g. Solitary Islands) tend to have much brighter colours than those from the southern Great Barrier Reef.

Affinities

Platygyra lamellina is usually distinguished from the much more common *P. daedalea* by the presence of a much thicker wall and markedly more rounded, less exsert septa. These differences are prominent in colonies from the same biotope (Figs. 453-455) but become increasingly obscure in collections from diverse biotopes.

Colonies of *P. lamellina* which have short valleys are readily distinguished from *P. sinensis* by the much thicker wall and differences in septal structure, as described. They are distinguished from *P. pini* by the absence of paliform lobes and differences in the structure of the columella.

Underwater, *P. lamellina* is sometimes difficult to distinguish from *Goniastrea australensis*, as these species tend to have markedly parallel growth form modifications within the same biotope. Coralla of the latter species are distinguished by the normal presence of well defined centres and abundant paliform lobes.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to Polynesia.

***Platygyra sinensis* (Edwards & Haime, 1849)**

Synonymy (partly after Chevalier, 1975)

Astroria sinensis Edwards & Haime, 1849.

Astroria stricta Edwards & Haime, 1849.

Coeloria sinensis Edwards & Haime, 1857; Studer (1881); Ortmann (1892); Gardiner (1899, 1904); Bernard (1900); Matthai (1924).

Coeloria stricta Edwards & Haime, 1857; Studer (1881); Quelch (1886); Matthai (1924).

Coeloria delicatula Ortmann, 1888.

Maeandra stricta (Edwards & Haime); Vaughan (1918).

Platygyra ryukyuensis Yabe & Sugiyama, 1935; Yabe, Sugiyama & Eguchi (1936).

Platygyra sinensis (Edwards & Haime); Wells (1954); Ma (1959); Chevalier (1968, 1975); Wijsman-Best (1972, 1976).

Platygyra stricta (Edwards & Haime); Chevalier (1968).

This synonymy lists only those authors who appear to have used the name *P. sinensis* or *P. stricta* correctly. In some cases this has not been confirmed. Synonymies of species by earlier authors have been very varied; for example, Stephenson & Wells (1955) made *P. sinensis* a provisional junior synonym of *P. lamellina*, along with all other then accepted nominal species of *Platygyra*.

Matthai (1928) was incorrect in synonymising *P. sinensis* with *P. daedalea*, as also was Umbgrove (1940) who included it with *P. rustica* (a synonym of *P. daedalea*).

Chevalier's (1975) inclusion of *P. ryukyuensis* with *P. sinensis* is supported by this study although the type of the former has not been examined.

Material studied

Darnley Island, Yorke Island, Murray Islands, Great Detached Reef (6 specimens), **Tijou Reef** (6 specimens), **Bewick Island, Houghton Island** (4 specimens), **Jewell Reef, Yonge Reef, Lizard Island, Three Isles** (11 specimens), **Hope Island** (2 specimens), **Low Isles** (10 specimens), **Palm Islands** (19 specimens), **Keeper Reef, Wheeler Reef, Rattlesnake Island, Magnetic Island** (23 specimens), **Swain Reefs** (2 specimens).

These localities include collecting stations 1, 2, 5, 6, 9, 12, 13, 18, 27, 31, 33, 34, 36, 40, 41, 43, 45, 51, 61, 77, 79, 84, 85.

Previous records from Eastern Australia

Murray Islands, (as *Maeandra stricta*) Vaughan (1918); **Low Isles**, (as *Coeloria* or *Coeloria daedalea*) Stephenson & Stephenson (1933), Manton (1935), (as various synonymyms of *P. lamellina*) Stephenson & Wells (1955).

Characters

Colonies are massive and rounded, occasionally flat. Valleys are usually very short, mostly monocentric, but some colonies do have long meandering valleys (Fig. 206). Septa are thin and only slightly exsert. Viewed from above they are evenly spaced. Their greatest radial dimension occurs approximately half way down the theca, at which point they descend vertically or near vertically. As with all *Platygyra* species, there are fine granulations on the sides of the septa and well formed dentations down their margins. There are no paliform lobes, although large septal dentations may occur where the septa descend vertically. Columellae are narrow and largely composed of loosely intertwined trabeculae. Living colonies (Fig. 457) have a wide variety of colours, often bright, as is the case with some other *Platygyra* species.

Skeletal variation

This species frequently forms microatolls. Otherwise, colonies usually grow towards (but seldom attain) a spherical growth form. The diameter of colonies decreases rapidly with increasing depth of water.

Figs. 201-206 *Platygyra sinensis* ($\times 2.5$).

Fig. 201 From Three Isles, showing very heavy calcification.

Fig. 202 From Hope Island, showing valley lengths most commonly found and well developed columellae.

Fig. 203 From Swain Reefs, collecting station 77, showing short valleys with reduced columellae.

Fig. 204 From Three Isles, showing monocentric valleys.

Fig. 205 From Bushy Island-Redbill Reef, collecting station 86 (intertidal), showing some tendency to form centres.

Fig. 206 From Fantome Island, Palm Islands, collection station 34, showing extremely meandroid valleys.

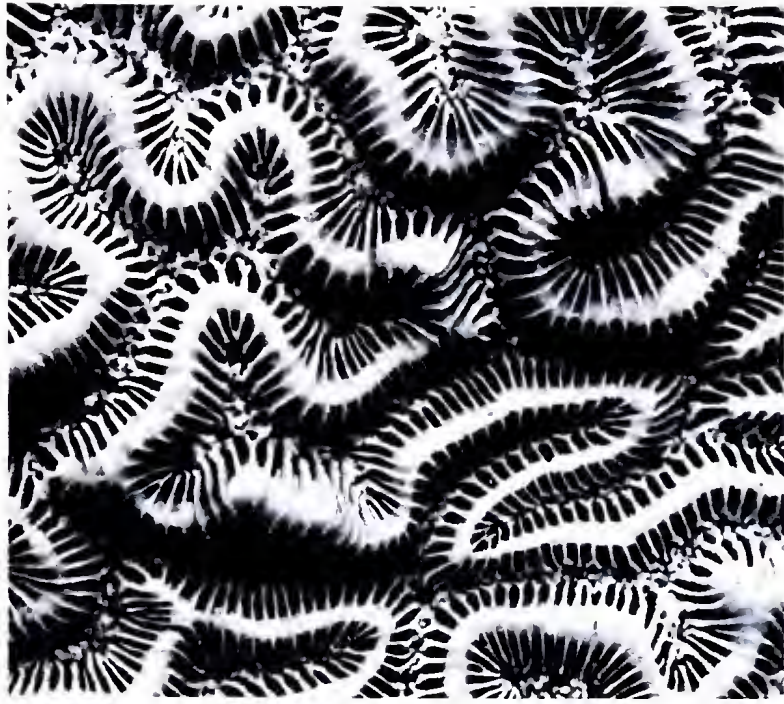


Fig. 206▲



205▲

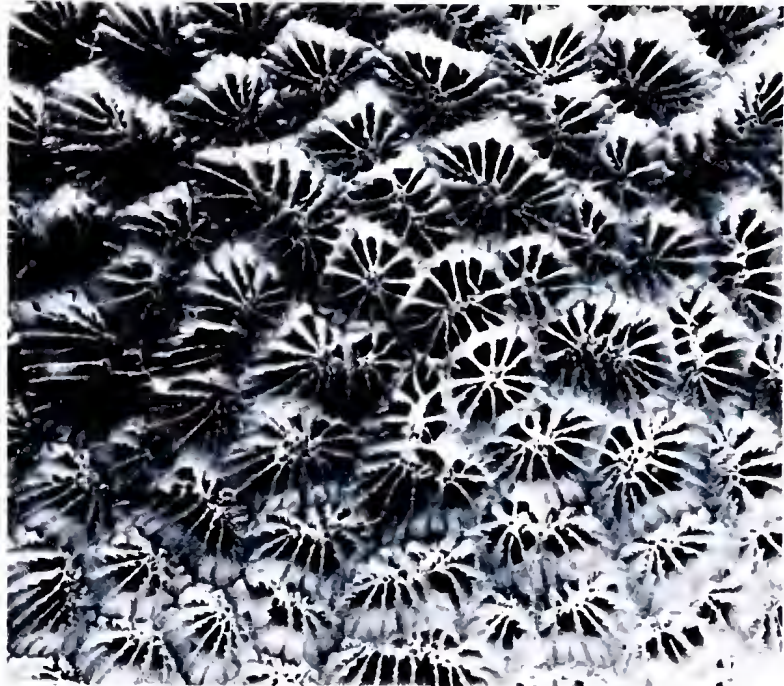
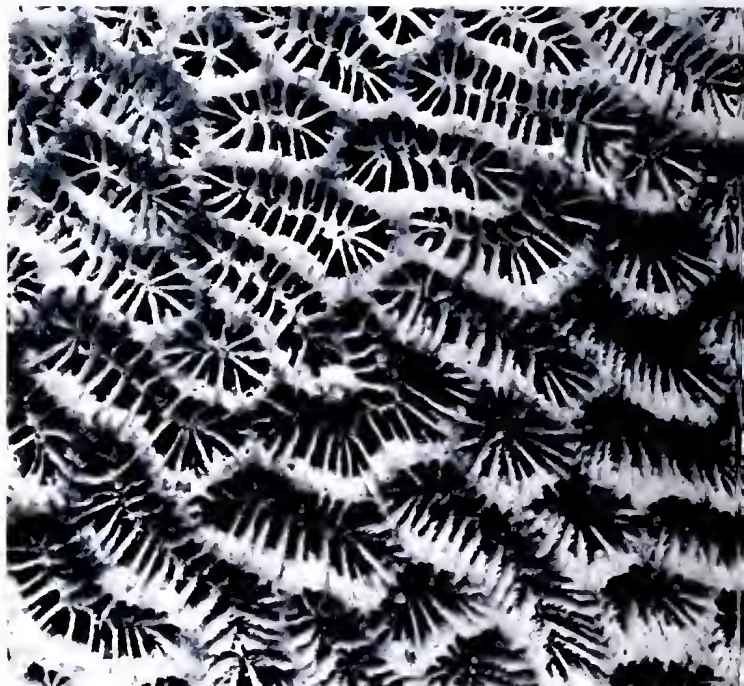


Fig. 204▲



203▲

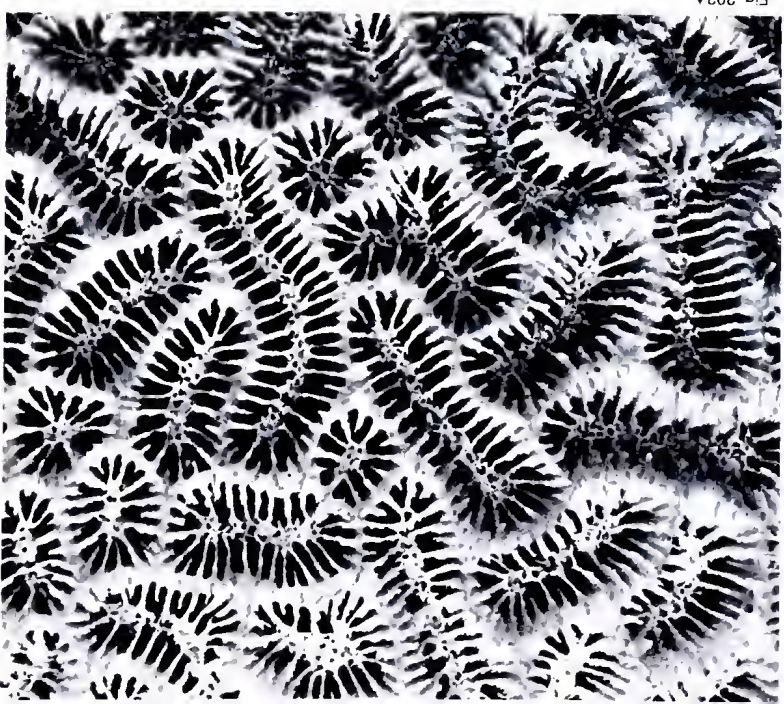


Fig. 202▲



201▲

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to Samoa.

Platygyra pini Chevalier, 1975

Synonymy

Platygyra pini Chevalier, 1975; Wijsman-Best (1976).

Failure to recognise the existence of this widespread species in earlier collections has probably contributed much to the uncertainties expressed by earlier workers in their treatment of *Platygyra*. *Platygyra pini* has many skeletal characteristics which overlap with the extremes of variation of the other major species of *Platygyra* and if not recognised, makes delineation of these species completely arbitrary.

Material studied

Great Detached Reef (5 specimens), **Tijou Reef** (2 specimens), **Bewick Island** (2 specimens), **Houghton Island**, **Jewell Reef** (3 specimens), **Yonge Reef**, **Lizard Island** (12 specimens), **MacGillivray Reef** (4 specimens), **Ribbon Reef**, **Three Isles** (3 specimens), **Hope Island** (9 specimens), **Low Isles** (10 specimens), **Bowl Reef**, **Palm Islands** (50 specimens), **Wheeler Reef**, **Bushy Island-Redbill Reef**, **Pompey Complex** (5 specimens), **Swain Reefs** (4 specimens).

These localities include collecting stations 1, 5, 6, 9, 10, 32, 34, 35, 36, 37, 39, 40, 42, 43, 45, 51, 55, 56, 60, 61, 63, 66, 74, 77, 80, 90, 91, 93, 103, 104.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are massive and are rounded or flat, sometimes encrusting. Valleys are short, usually with one or two recognisable centres. The walls are usually relatively thick, although this is variable. Septa are usually thin but may be greatly thickened in colonies with greatly thickened walls. As with other *Platygyra* species, the septa are dentate and have fine granules on their sides. The dentations sometimes form tiny horizontal plates fringed with granulations, presumably sclerodermites. Such granules may also be present on vertical dentations, in which case they form distinct synapticular rows.

One or sometimes several rows of dentations form distinctive paliform lobes. The trabecular columellae are usually well developed, with centres tending to form at the ends of valleys.

Living colonies are usually a uniform grey-grown or yellow-brown with green centres (Fig. 458.)

Affinities

Platygyra pini may closely resemble *P. sinensis* in having very short valleys, but is readily distinguished by the presence of thick walls, paliform lobes and much greater development of the columella. It may also resemble certain growth forms of *P. daedalea* (especially

Figs. 207-213 *Platygyra pini* ($\times 2.5$).

- Fig. 207 From Barber Island, Palm Islands, collecting station 83.
- Fig. 208 From Curaçoa Island, Palm Islands, collecting station 56.
- Fig. 209 From Low Isles, collecting station 12.
- Fig. 210 From Pelorus Island, Palm Islands, collecting station 90.
- Fig. 211 From SE Cape, Great Palm Island, collecting station 38.
- Fig. 212 From Great Detached Reef, collecting station 5.
- Fig. 213 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.

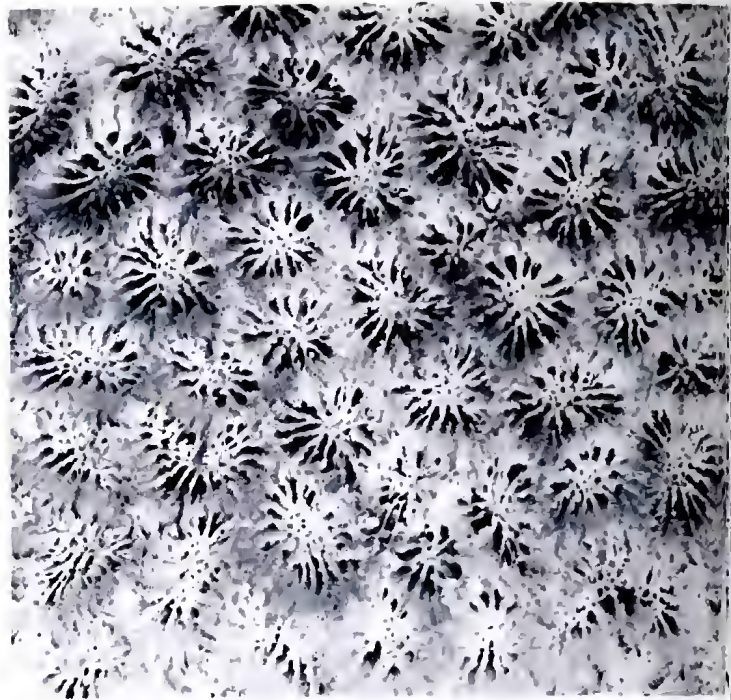


Fig 212

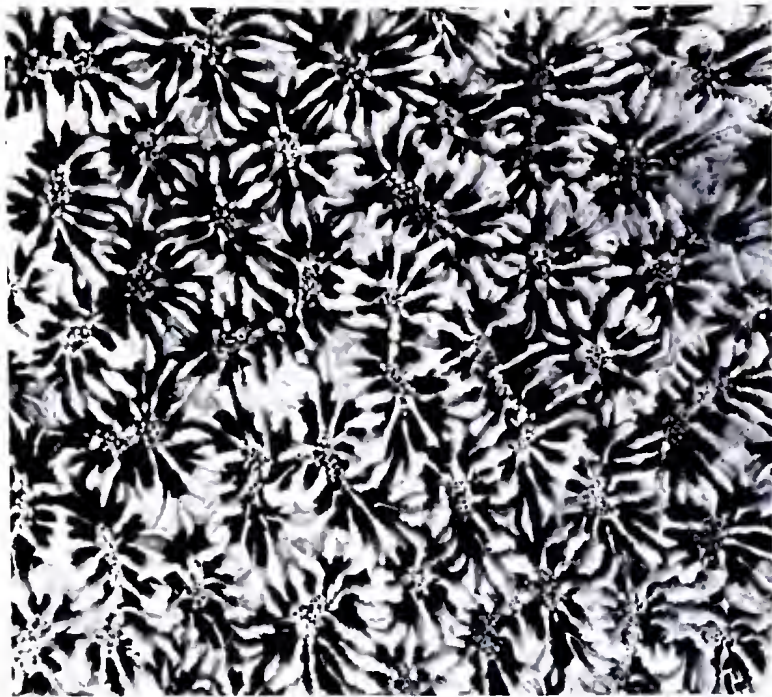


Fig 213



Fig 209



Fig 210

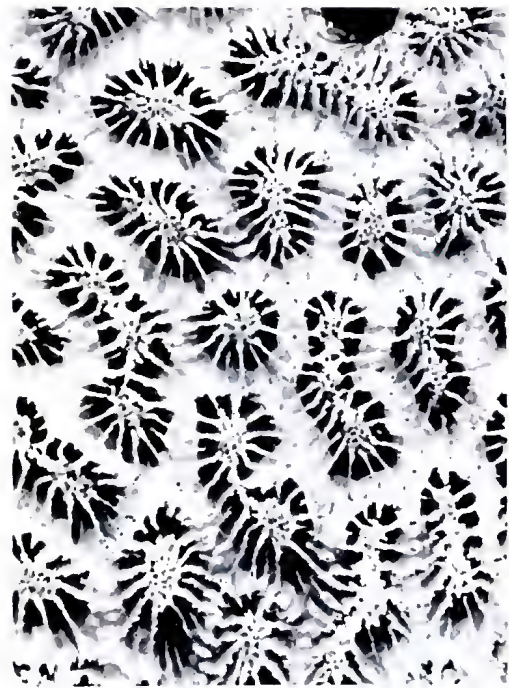


Fig 211

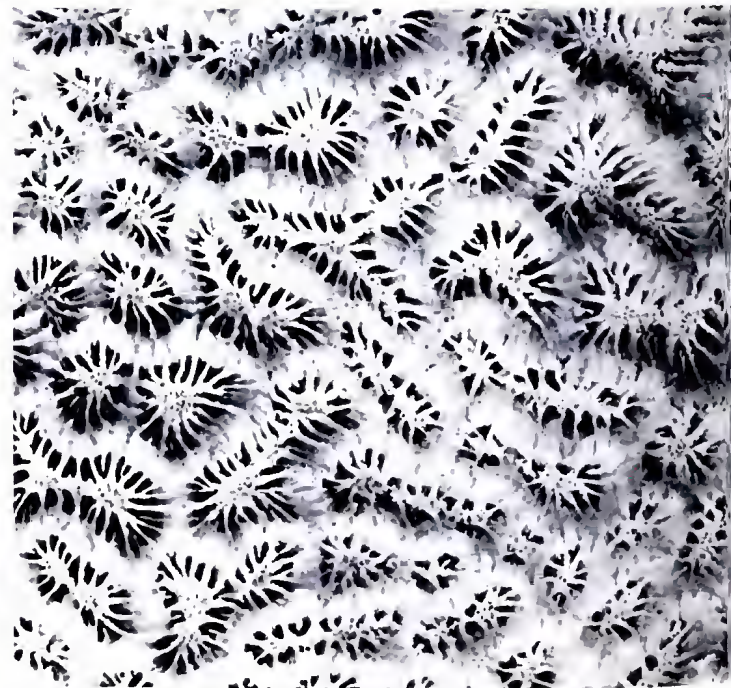


Fig 207

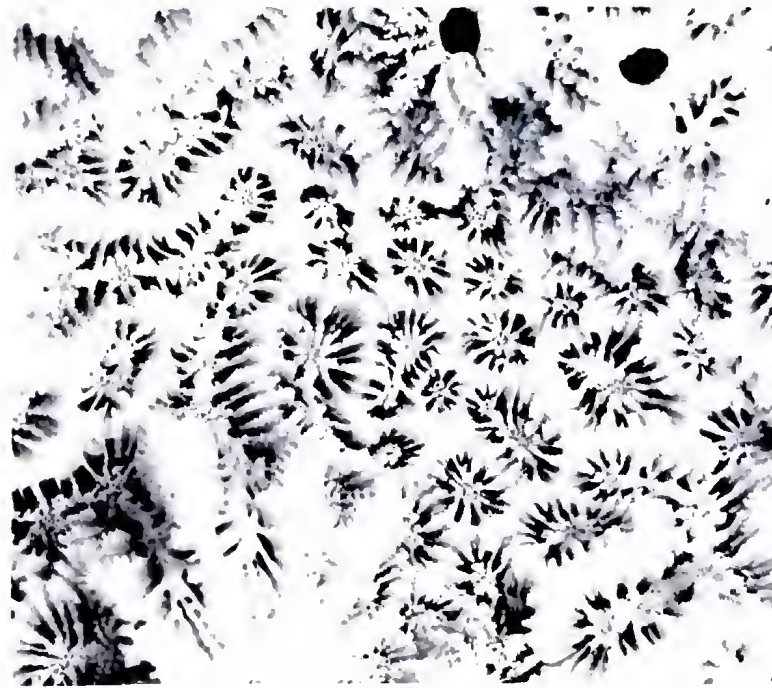


Fig 208

astraeiformis-like *P. daedalea*) and *P. lamellina*, which have short or monocentric valleys. In collections from a single biotope or a series of similar biotopes, these growth forms are normally distinguished from *P. pini* by comparison with other growth forms having elongated valleys. However, in collections from diverse environments or those made without record of environmental conditions, distinctions may sometimes be difficult and unreliable.

Distribution

Although recorded only from New Caledonia, Indonesia, the Chesterfield Islands (Chevalier, 1975) and the Great Barrier Reef, this species is probably widespread, at least throughout the tropical western Pacific Ocean.

***Platygyra zelli* n.sp.**

Material studied

Lizard Island (3 specimens), **Palm Islands** (13 specimens), **Pompey Complex**.

These localities include collecting stations 34, 35, 45, 55, 59, 75, 99.

Previous records from Eastern Australia

Not previously recorded.

Characters

This species differs from all other *Platygyra* in having a ramose growth form. There is little or no tendency towards massive or flat habits and hence this species, alone among *Platygyra*, can be distinguished solely on growth form (Fig. 459). Colonies are up to 25 cm high (Fig. 214) and have main branches 1.5-3cm in diameter. Actively growing branch ends (Figs. 218, 219, 221) are composed of intricate arrays of thecae and elongated septa reminiscent of branch tips of *Hydnophora rigida* on a larger scale. Dead skeleton forms the base of most colonies. The valleys are short (Figs. 215, 220) and usually monocentric. The walls are thick (2-4mm) especially towards the base of colonies where skeletal parts are heavily calcified. Valleys are usually shallow with smooth blister-like floors (Fig. 219). There is usually no sign of a columella, although elongated, recurved septal dentations are occasionally found and occasionally these form a distinct columella (Fig. 218). The septa (Figs. 218-221) are similar to those of *P. daedalea* and *P. lamellina*. They are dentate and have fine granulations on their sides. Some dentations are twisted to form tiny horizontal plates fringed with granulations, presumably sclerodermites.

Individual colonies are mostly uniform in colour with bases of branches usually slightly darker than the tips (Fig. 459). Colour ranges from an inconspicuous grey-green to grey-brown and is usually very uniform within colonies of the same biotope.

This species is seldom found around platform or barrier reefs, but is much more common in the relatively turbid water associated with high islands. In some areas, e.g. the north end of Eclipse Island (collecting station 59), it may dominate extensive areas (Fig. 222).

Affinities

The ramose growth form of this species, combined with the normal lack of a columella, separates it from all other *Platygyra* and makes its generic affinities obscure. It is placed in the genus *Platygyra* because (1) where a columella is formed, it resembles those of other *Platygyra* species, (2) the septa resemble those of other *Platygyra* and (3) there are no other skeletal structures, e.g. paliform lobes, which suggest closer affinity with any other genus.

Alternatively, there is a case for creating a new genus for this species, especially if another species were to be found with close affinities to it.

Skeletal variation

Most of the variation of the present series is found within single biotopes and it appears that this species shows little variability in growth form within the narrow range of habitats it occupies.

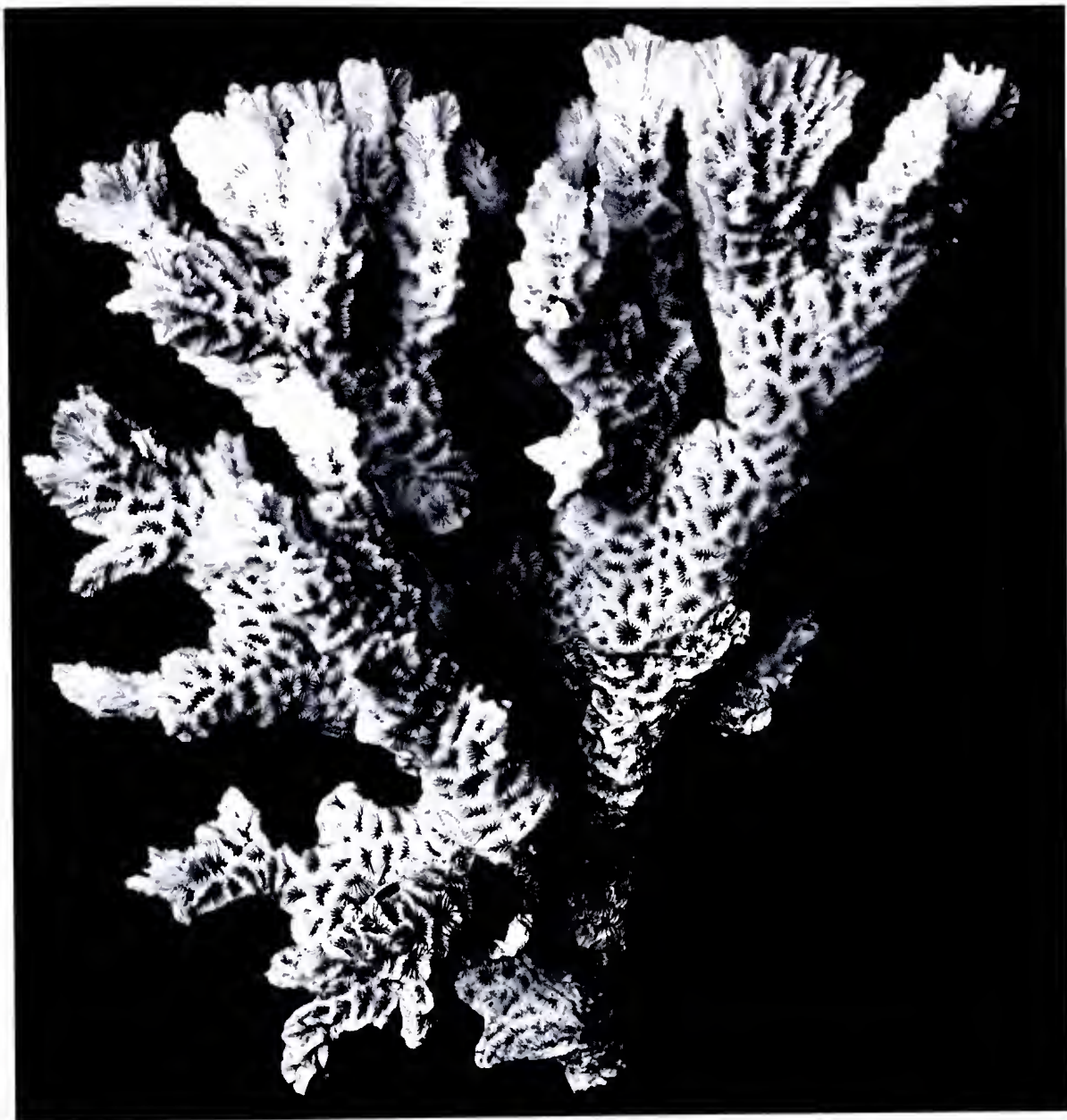


Fig. 214 Paratype of *Platygyra zelli* from Eclipse Island, Palm Islands, collecting station 59 ($\times 0.4$).

Fig. 215-217 *Platygyra zelli* ($\times 1.0$).

- Fig. 215 (Paratype) from Eclipse Island, Palm Islands, collecting station 59, showing a piece of the base of a large colony.
 Fig. 216 (Paratype) from Lizard Island, collecting station 100, showing an actively growing branch end.
 Fig. 217 (Holotype) from Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91, showing a heavily calcified branch end.

Figs. 218-221 *Platygyra zelli* ($\times 2.5$).

- Fig. 218 A branch end of the corallum illustrated in Fig. 214 showing partial development of a columella.
 Fig. 219 A branch end of the corallum illustrated in Fig. 217 (holotype) showing shallow valleys without development of a columella.
 Fig. 220 The same corallum as Fig. 215.
 Fig. 221 A branch end of the corallum illustrated in Fig. 216 showing *Hydnophora*-like development of the terminal septa and thecae.



Fig. 215



Fig. 216



Fig. 217



Fig. 218



Fig. 219

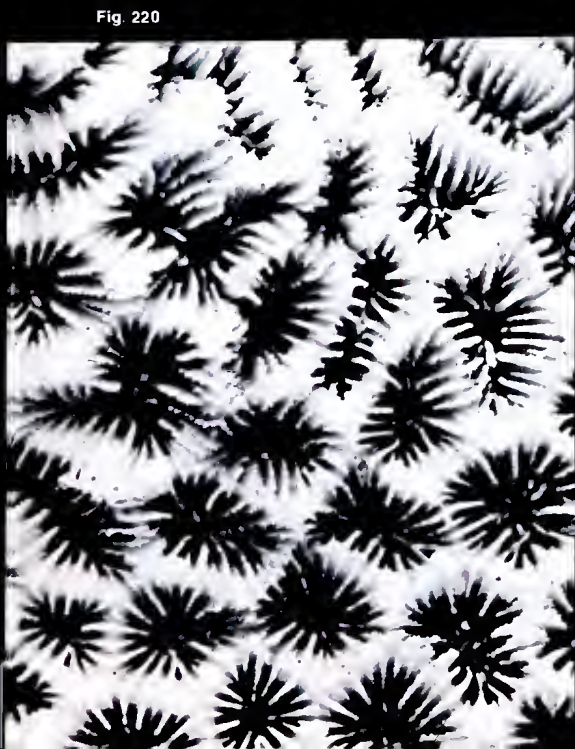


Fig. 220



Fig. 221

Etymology

Named after Mr L. D. Zell of the Australian Institute of Marine Science.

Holotype (Figs. 217, 219)

Dimensions: Maximum dimension is 20.5cm, including approximately 5cm of base overgrown with encrusting algae.

Locality: Pioneer Bay, Orpheus Island, Palm Islands.

Depth: 3m.

Collector: J. E. N. Veron.

Holotype: British Museum (Natural History) 1977.1.1.4.

Paratypes (Figs. 214-216)

Figs. 214, 215. Australian Institute of Marine Science.

Fig. 216. Queensland Museum, Australia.

Rijksmuseum van Natuurlijke Historie, Leiden, Nederland, No. 10736.

Distribution

Known only from the Great Barrier Reef.

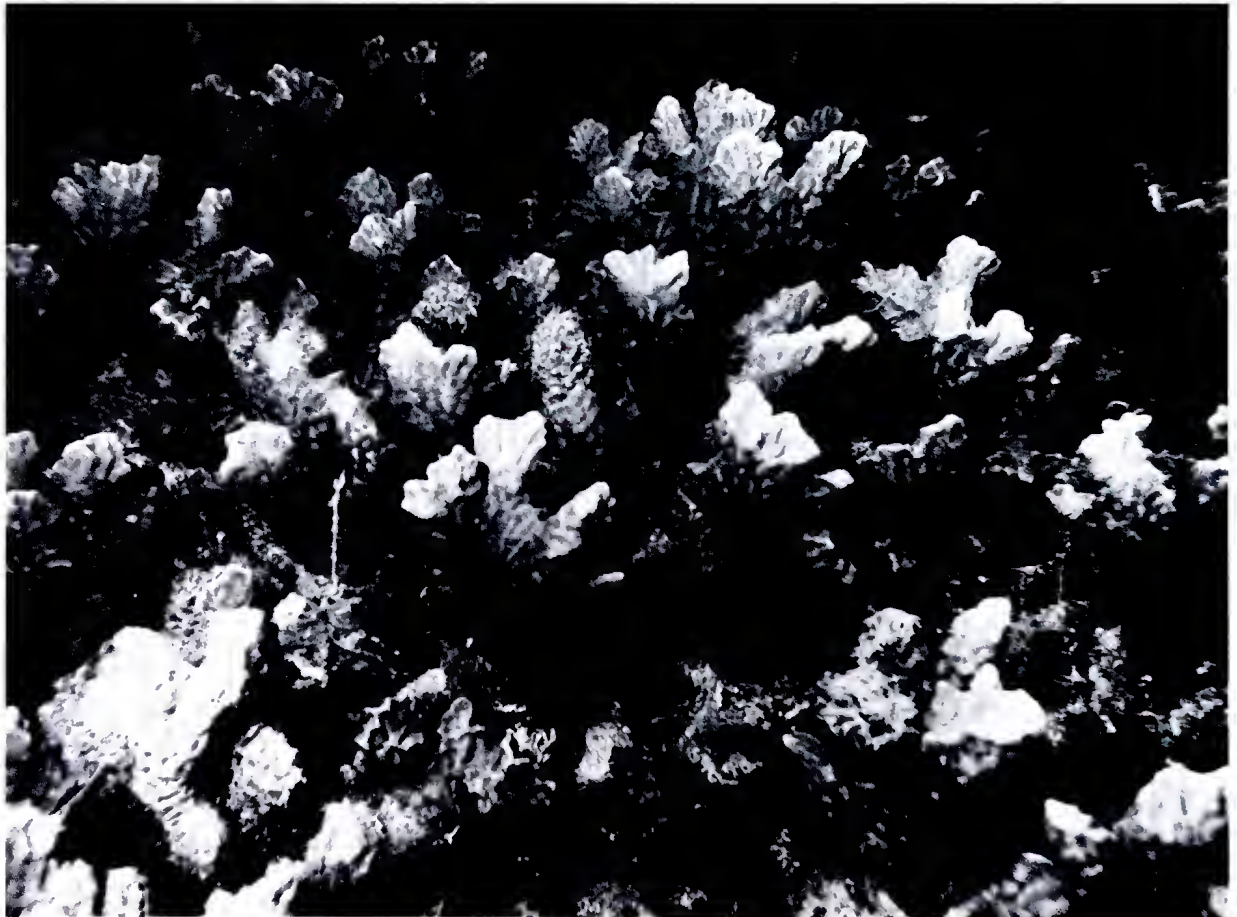
GENUS *LEPTORIA* EDWARDS & HAIME, 1848

Generic synonymy

Madrepora Ellis & Solander, 1786.

Maeandrina (*pars*); Dana, 1846.

Fig. 222 A large *Platygyra zelli* colony near Eclipse Island, Palm Island, collecting station 59.



Leptoria Edwards & Haime, 1848; Vaughan (1918), Matthai (1924); Vaughan & Wells (1943); Wells (1956).

Platygyra (pars) Matthai (1928); Yabe, Sugiyama & Eguchi (1936).

Type species *Madrepora phrygia* Ellis & Solander, 1786.

Leptoria phrygia (Ellis & Solander, 1786)

Synonymy

Madrepora phrygia Ellis & Solander, 1786.

Maeandrina phrygia (Ellis & Solander); Dana (1846).

Maeandrina gracilis Dana, 1846.

Maeandrina tenuis Dana, 1846.

Leptoria phrygia (Ellis & Solander); Edwards & Haime (1857); Ortmann (1888); Bernard (1900); von Marenzeller (1901); Vaughan (1918); Matthai (1924); Hoffmeister (1925); Faustino (1927); Yabe & Sugiyama (1932, 1935); Eguchi (1935); Wells (1950); Crossland (1952); Stephenson & Wells (1955); Searle (1956); Ma (1959); Pichon (1964); Chevalier (1968, 1975); Rosen (1971); Scheer (1972); Wijsman-Best (1972, 1976); Scheer & Pillai (1974).

Leptoria gracilis (Dana); Edwards & Haime (1857); Klunzinger (1879); Ortmann (1888, 1889); Gardiner (1899, 1904); Vaughan (1918); Yabe & Sugiyama (1935); Chevalier (1968).

Leptoria tenuis (Dana); Edwards & Haime (1857); Brüggemann (1879a); Ortmann (1888); Gardiner (1899); Vaughan (1917, 1918); Hoffmeister (1925); Faustino (1927); Yabe & Sugiyama (1935).

Platygyra phrygia (Ellis & Solander); Matthai (1928); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939, 1940); Rossi (1954); Eguchi (1968).

Platygyra gracilis (Dana); Matthai (1928); Yabe, Sugiyama & Eguchi (1936).

The synonymy of the three nominal species above has been discussed in some detail by various authors (Vaughan, 1918; Hoffmeister, 1925; Matthai, 1928; Umbgrove, 1940; Crossland, 1952; Wijsman-Best, 1972; Chevalier, 1975), who arrived at differing conclusions. The present series, along with extensive underwater observations, support the findings of the latter three authors that only one species is involved.

Material studied

Yorke Island, Murray Islands, Great Detached Reef (14 specimens), **Tijou Reef** (4 specimens), **Houghton Island, Lizard Island, Eagle Reef** (2 specimens), **Hope Island** (2 specimens), **Low Isles** (4 specimens), **Lodestone Reef, Palm Islands** (20 specimens), **Swain Reefs**.

These localities include collecting stations 1, 2, 6, 19, 26, 32, 34, 36, 37, 40, 41, 45, 55, 57, 60, 76.

Previous records from Eastern Australia

Murray Islands, (as *L. gracilis*) Mayor (1918), Vaughan (1918); **Low Isles**, (as *Platygyra phrygia*) Yonge (1930), (as *Platygyra*) Stephenson *et al.* (1931), (as *Platygyra* and *Platygyra phrygia*) Manton (1935), Crossland (1952), Stephenson & Wells (1955); **Heron Island**, (as ?*L. gracilis*) Salter (1954), Stephenson & Wells (1955); as 2 species as far south as **Lady Elliott Island** (Wells, 1955a).

Characters

Colonies are irregular in shape, usually having gently undulating surfaces. The skeleton is always very hard and dense. Valleys are of indefinite length with very regular appearance and constant width (Fig. 223), and are usually very deep. Septa are usually not segregated



Fig. 223▲

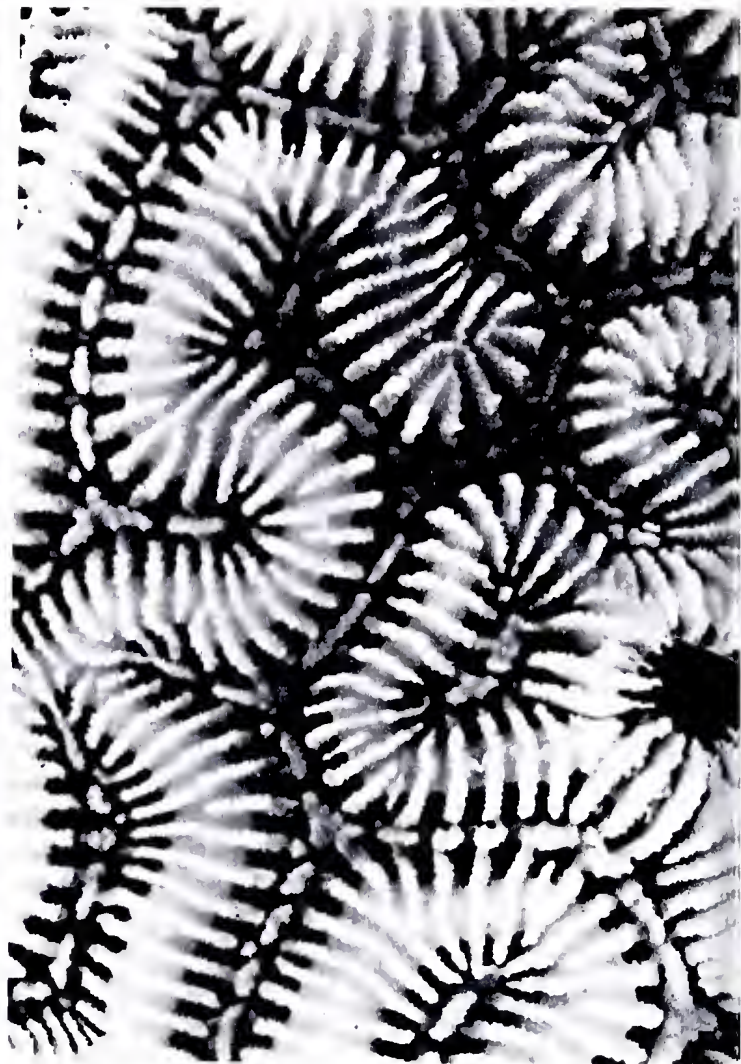


Fig. 224▲



Fig. 225▲



Fig. 226▲

into orders, but are of regular size and appearance, with constant interseptal distances. Septa have long horizontal lobes at the level of the columellae which form a series of bars connecting the septa to the columellae. The septa have fine dentations down their margins and fine granules down their sides; both are arranged in synapticular rows. The columellae characteristically have the form of a single vertical plate which is usually lobed, although very rarely completely discontinuous. Septa are regularly exsert with those of adjacent valleys usually adjoined. A thin epithelial ridge is often present in coralla from protected biotopes. The thecae are always thick and dense. There are no exothecal dissepiments; endothecal dissepiments are thin and widely spaced.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to the Fiji Islands, and to Japan in the north.

GENUS *OULOPHYLLIA* EDWARDS & HAIME, 1848

Generic Synonymy

Maeandrina (*pars*) Lamarck, 1816.

Oulophyllia Edwards & Haime, 1849.

Ulophyllia Edwards & Haime, 1857.

Coeloria (*pars*) Gardiner, 1904.

Coelogyra Nemenzo, 1959.

Type species *Oulophyllia crispera* (Lamarck, 1816).

Characters

The corallum is large, massive and meandroid. Valleys are discontinuous, wide and deep. Single corallites are very rare. Septa are thin, not very exsert, narrow in their upper part. Their margins bear numerous, irregular, small dentations. Centres are generally distinct. They are connected by loose trabecular processes or by valley septa. The endotheca is vesicular.

Affinities

Although the majority of specimens referred to *Oulophyllia* seem to be relatively uniform, the relationships of this genus with other genera of the Faviinae have not yet been well defined. Edwards & Haime (1848) remarked on a similarity with *Tridacophyllia* (= *Pectinia*), but this does not go beyond the stage of a superficial resemblance. Affinities with *Platygyra* are clearly more basic. Without hesitation, Gardiner (1904) merged both into the genus *Coeloria*. The two genera were again separated by Gravier (1910) and his opinion has prevailed amongst subsequent authors, including Crossland (1952) who reported both *Oulophyllia* and *Coeloria* from the Great Barrier Reef, despite his statement that he 'has every sympathy with Gardiner's arrangement'.

Figs. 223-226 *Leptoria phrygia*, Figs 224-226 ($\times 5.0$).

Fig. 223 *In situ*, with polyps retracted, from Swain Reefs, collecting station 79 ($\times 3.0$).

Fig. 224 From Great Detached Reef, collecting station 1, showing thickening of skeletal structures associated with exposed biotopes.

Fig. 225 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91.

Fig. 226 From Hope Island.

The generic affinities of *Oulophyllia* are further complicated by two peculiar species, *Coeloria* (?) *gigantea* Yabe & Sugiyama, and *Coelogyra laevis* Nemenzo. Wijsman-Best (1972) expressed the opinion that both species were related to *Goniastrea australensis*, whereas Chevalier (1975) considered *Coeloria* (?) *gigantea* a true *Oulophyllia*, an opinion which is supported by this study.

The type of *Coelogyra laevis* appears to be lost; however, Nemenzo's description and figure, combined with observations on specimens collected by one of the authors near the type locality, permit this species, along with *C. gigantea*, to be included in *Oulophyllia*. The latter is distinguished from *Platygyra* by its wider valleys and the existence of clear calicular centres.

This genus is here considered to be monospecific, the characters of which are the characters of *O. crispera*. It is usually considered to be uncommon and previous collections have included only a few specimens at most. However, although it is seldom found at the surface of reefs, it is by no means rare in many Great Barrier Reef biotopes, and this appears to be the general case throughout the tropical Indo-Pacific.

***Oulophyllia crispera* (Lamarck, 1816)**

Synonymy

Maeandrina crispera Lamarck, 1816; de Blainville (1823, 1830, 1834); Edwards & Haime (1848).

Oulophyllia crispera Edwards & Haime, 1857; Verrill (1901).

Oulophyllia stokesiana Edwards & Haime, 1857.

Oulophyllia aspera Quelch, 1886.

Fig. 227 *Oulophyllia crispera* at Lizard Island, collecting station 100.



Ulophyllia cellulosa Quelch, 1886; von Marenzeller (1907).

Ulophyllia stuhlmanni Rehberg, 1892.

Ulophyllia maxima Rehberg, 1892.

Ulophyllia bonhourei Gravier, 1910; Gravier (1911).

Coeloria cooperi Gardiner, 1904.

Coeloria magna Gardiner, 1904.

Oulophyllia crispa Matthai, 1928; Yabe, Sugiyama & Eguchi (1936); Crossland (1952); Scheer (1964); Wijsman-Best (1972, 1976).

wulophyllia aspera Matthai, 1928; Scheer & Pillai (1974); Chevalier (1975); Wijsman-Best (1976).

Coeloria gigantea Yabe & Sugiyama, 1935; Yabe, Sugiyama & Eguchi (1936).

Coelogyra laevis Nemenzo, 1959.

Material studied

Yorke Island, Murray Islands (3 specimens), **Sue Island, Waining Reef** (2 specimens), **Lizard Island** (2 specimens), **Eagle Reef, Hope Island** (2 specimens), **Low Isles, Palm Islands** (46 specimens), **Whitsunday Islands** (12 specimens), **Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex, Swain Reefs** (18 specimens).

These localities include collecting stations 13, 17, 19, 23, 32, 34, 35, 36, 38, 42, 43, 45, 50, 55, 57, 58, 59, 60, 62, 67, 69, 70, 79, 80, 81, 90, 91, 93, 94, 97, 98, 102.

Previous records from Eastern Australia

Low Isles (?), Crossland (1952), Stephenson & Wells (1955); **Heron Island**, Stephenson & Wells (1955); **Great Barrier Reef**, Ma (1959).

Characters

Colonies are usually large and massive, rarely encrusting, tending to become hemispherical. Valleys are comparatively short, with few distinct calicular centres. The average width of valleys is 9-20mm, the average depth 4-14mm. Septa are thin, usually compact, occur in two to three orders, and are continuous between valleys (biseptal laminae). First order septa are generally exsert above the common wall. The wall is usually thin and perforate on its upper part, above the endothecal dissepiments. The free upper margin of the septa bear numerous small dentations decreasing in size from the periphery to the centre, except for one or two taller ones which may sometimes be replaced by a paliform lobe. Dentations of the inner margin usually curve at right angles to give pseudosynapticulae. The sides of the septa are covered with numerous small granules, sometimes arranged in line and even fusing together following the direction of septal trabeculae. The endothecae are well developed and

Figs. 228-235 *Oulophyllia crispa* Figs 229-235 ($\times 2.0$).

Fig. 228 From Sue Island, collecting station 17 ($\times 0.6$).

Fig. 229 From Pioneer Bay, Orpheus Islands, Palm Islands, collecting station 91, showing thin thecae flat collines and irregular valleys. The endothecae are mostly deep and irregularly developed.

Fig. 230 From the Palm Islands, showing very narrow, meandroid valleys. The paliform lobes and endothecae are well developed.

Fig. 231 From Hazard Bay, Orpheus Island, Palm Islands, collecting station 45, showing narrow and deep valleys, few septa and no paliform lobes.

Fig. 232 From SW Swain Reefs, collecting station 69, showing valleys with well developed septa.

Fig. 233 From the Palm Islands, showing long straight valleys, thick paliform lobes and an alternating order of narrow septa.

Fig. 234 From Dido Rock, Palm Islands, collecting station 58, showing large valleys, well developed endotheca, flat, superficial corallities.

Fig. 235 From Yorke Island, collecting station 13, showing flat upper septal margins similar to *Coeloria gigantea* Yabe, Sugiyama & Eguchi, and *Coelogyra laevis* Nemenzo.

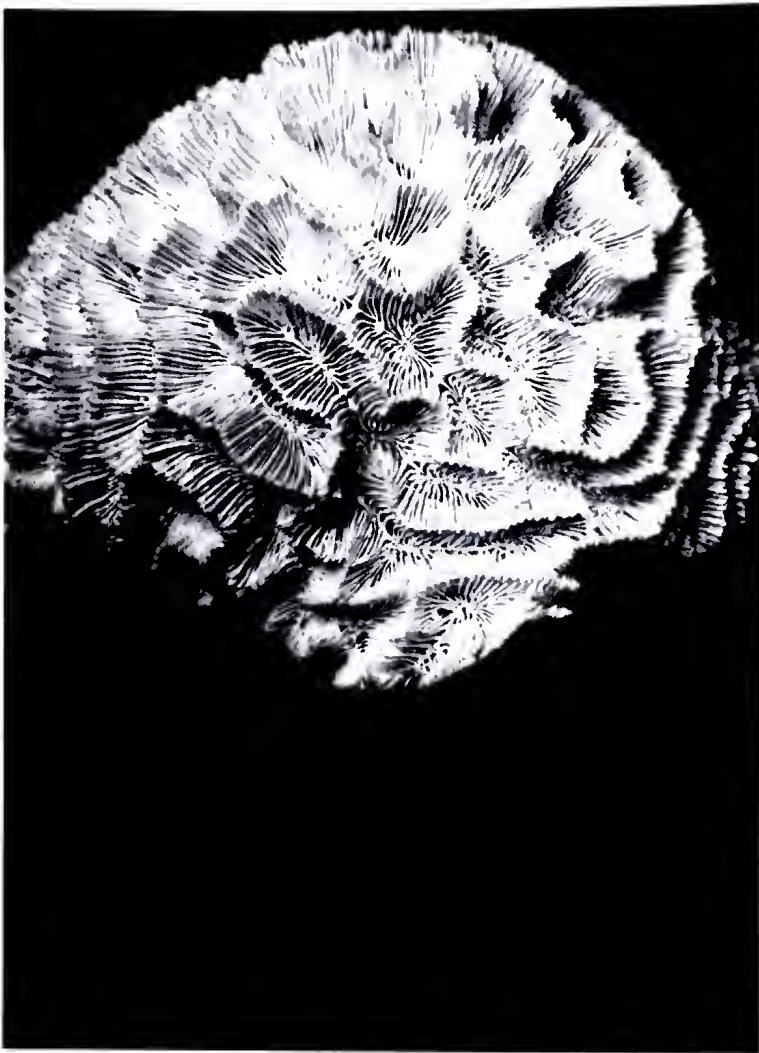


Fig. 228▲

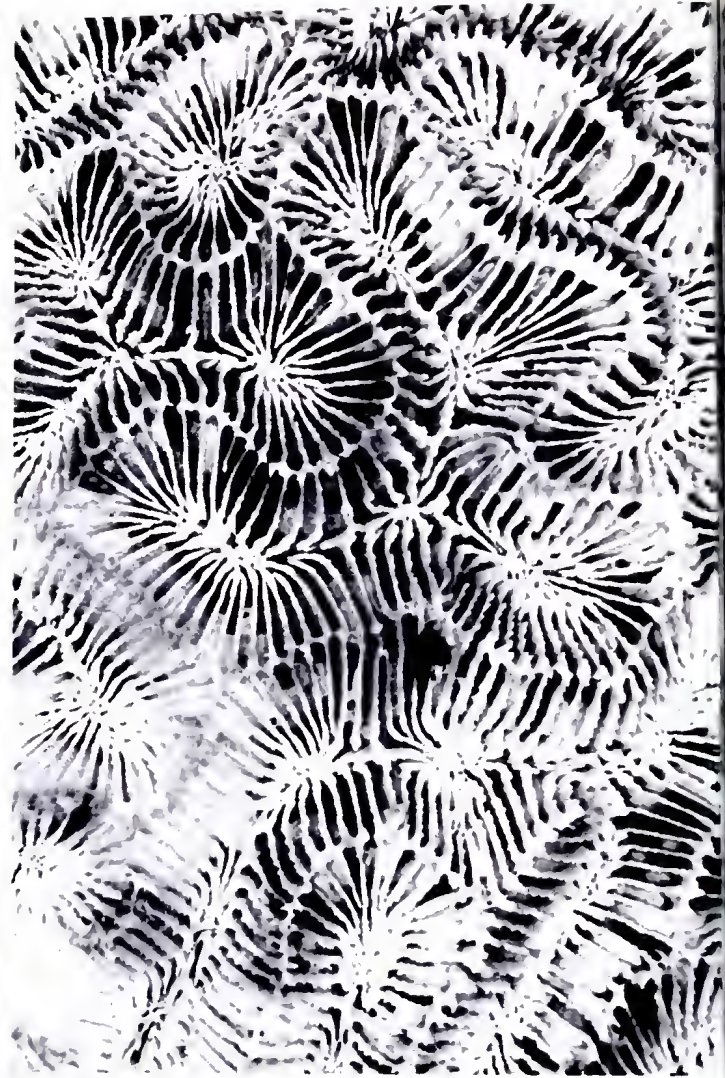


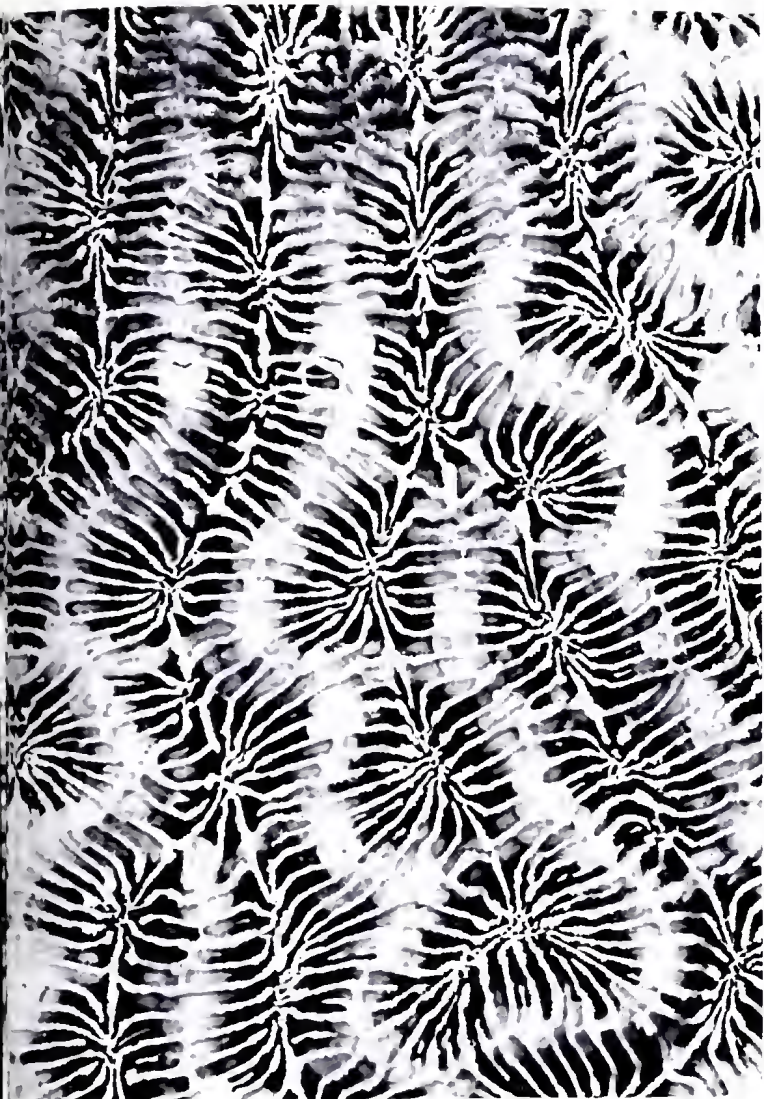
Fig. 229▲



Fig. 232▲



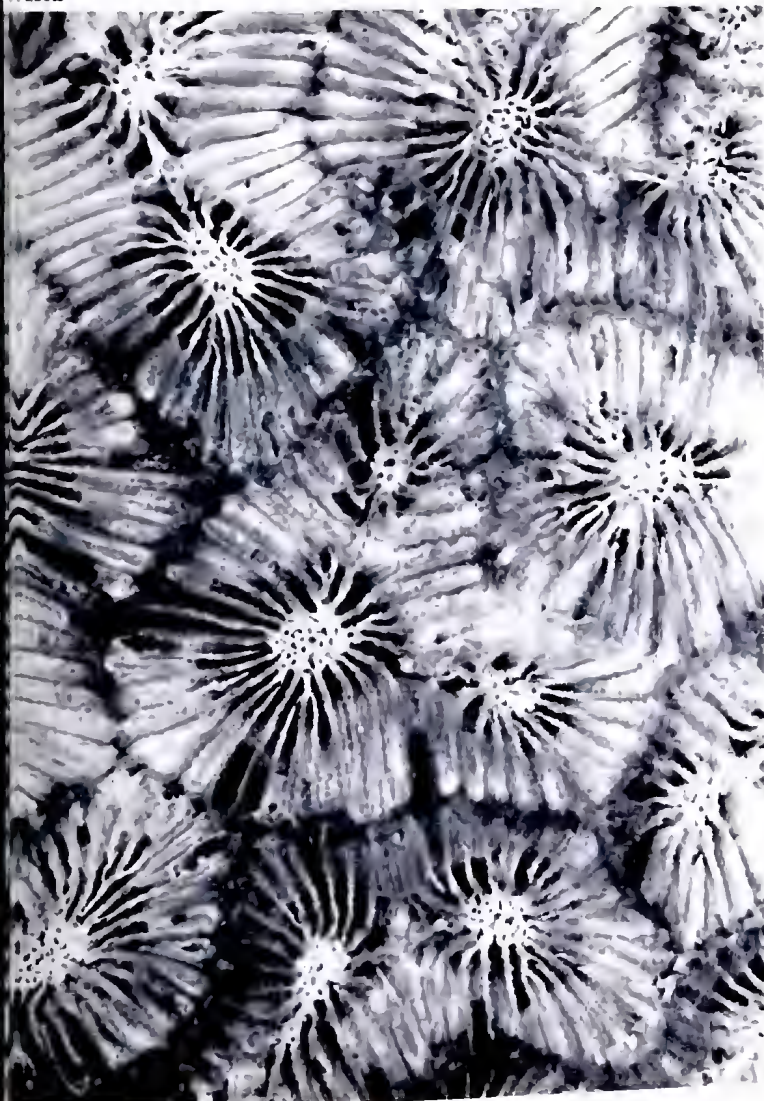
Fig. 233▲



230A



Fig. 231A



234A

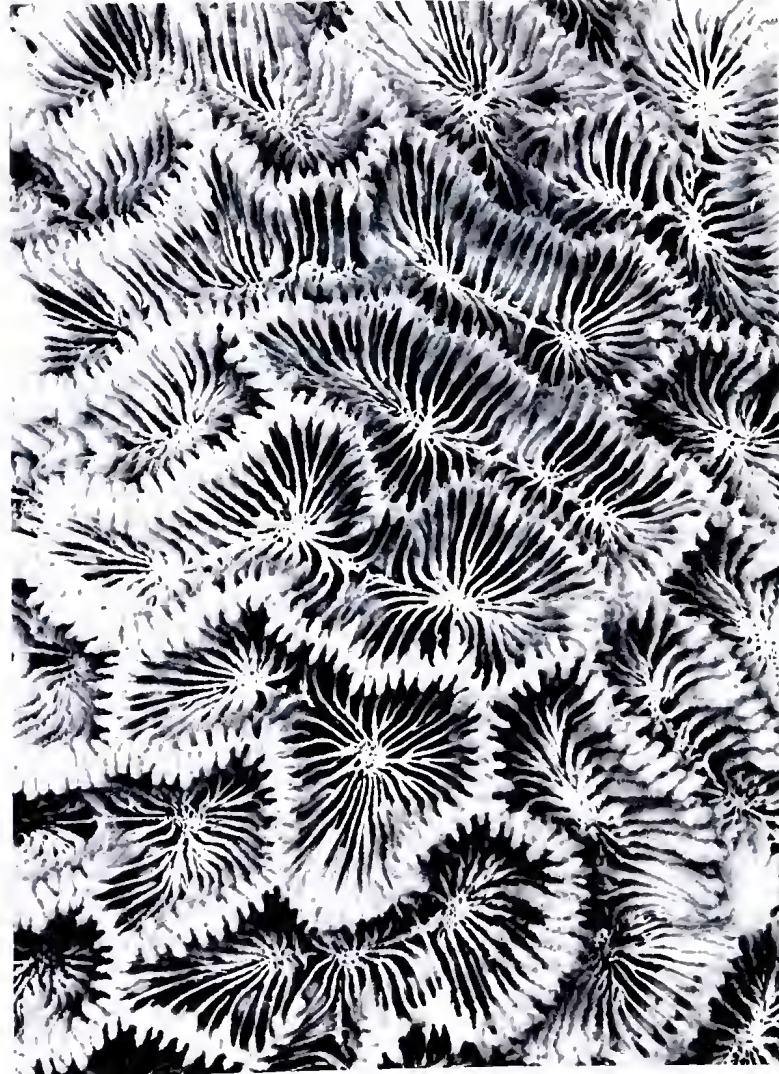


Fig. 235A

vesicular. The columellae are well developed, spongiose, with papillae at the top. Columellar centres are connected by a more or less compact axial process, ranging from a trabecular network to a solid lamina. The common walls are costate, the costae being thin and laminar and occasionally embedded in vesicular exotheca. Sometimes the costae bear a few flattened, triangular spines.

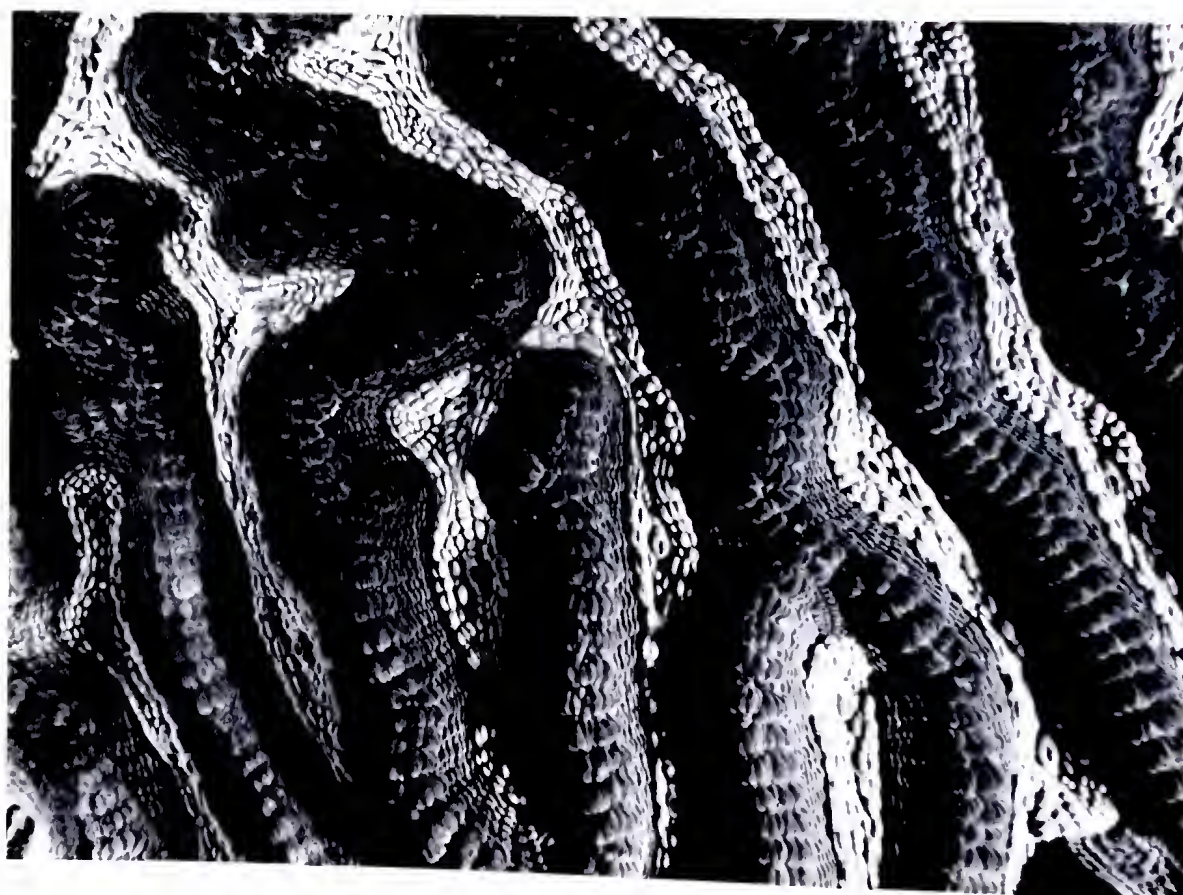
Skeletal variations

Oulophyllia crista is a highly plastic species and most characters of the corallum show a great range of variation. As mentioned earlier, the average width of the valleys varies from 9.5 to 20mm (extremes 4 and 30mm). They tend to be wider at the level of a terminal centre. The depth varies between 4.5 and 13.5mm (extremes 3 and 18mm), giving a marked difference in the appearance of the specimens, from a flat, even surface with superficial collines to high, narrow and acute collines. The number of centres per valley ranges from one to about twenty. In some coralla, corallites are mostly monocentric with a meandrisation index

$$Im = \frac{\text{Number of centres}}{\text{Number of valleys}} \text{ of } 1.88;$$

in others, valleys are mostly long with an Im of >5.5 . Wall perforations vary in number with the height of the collines and the development of the endothecae. However, this character varies greatly within the one colony. The general shape of the septa is largely dependent upon the height of the collines. In flat coralla, the intracalicular upper margin is almost horizontal; in others with high collines, it is strongly inclined towards the centres. In some specimens of the latter category, the bisepal lamina have a horizontal flattened top (Fig. 235). The number of septa varies from 5 to 12 per cm, with an average of 6 to 7 septa of the first order. The thickness of the septa is also variable but this is not correlated with the number of septa. Often the septa are thickened towards their inner margins. This may also apply to the paliform lobes which range, even in the one corallum, from obsolete to very well developed (*Goniastrea-*

Fig. 236 *Oulophyllia crista*, *in situ* at the Palm Islands ($\times 2.0$).



like processes. With very few exceptions, the columellar centres are conspicuous, but the axial skeleton connecting them shows all intergrading stages between loosely intermingled, twisted trabeculae (sometimes originating from the fusion of the dentations of the inner septal margin) and a thick lamina (porous or solid), with a dentate upper margin. All intermediate situations, such as those described by Chevalier (1975), occur in the present series and much of this variation occurs in individual coralla.

The endotheca is always present, although it may be inconspicuous and developed only deeper in the valleys, giving them an empty appearance. Conversely, the endotheca may entirely fill up the intracalicular space, from the centres almost to the top of the walls, a situation in which the visible part of the septa is reduced to a low, narrow lamina, just below the free upper septal margin.

There appear to be few correlations between variations in the above-mentioned characters or group of characters and no well defined ecomorphs can be distinguished in the present series. This species occupies a relatively narrow range of biotopes and appears to respond in a very plastic manner to fluctuations in microenvironmental conditions.

Affinities

The genus *Oulophyllia* illustrates the dangers of describing or identifying coral species from a small number of specimens without accurate data on their intraspecific variability. The types of *O. crispa* and *O. aspera* display a number of differences, but fall well within the range of the variations described above. This range clearly covers all characters which were previously used (e.g. by Scheer & Pillai, 1974, and Chevalier, 1975) to separate these two nominal species. The synonymy of *Coeloria* (?) *gigantea* and *O. crispa* has been referred to above. As far as *Coelogyra* is concerned, Nemenzo himself mentioned its resemblance with *Coeloria* (?) *gigantea* but did not attempt to compare it with *Oulophyllia* which at that time was not known from the Philippines. As previously noted, *Coelogyra* appears to be an

Fig. 237 *Oulophyllia crispa*, *in situ* at the Swain Reefs, showing expanded polyps at night ($\times 2.0$).



Oulophyllia, identical with the specimens which have a comparatively poorly developed axial organ, and relatively narrow valleys and high collines.

The relationships and affinities of *Coeloria magna* Gardiner are hardly more certain. Matthai (1928) and Scheer & Pillai (1974) have considered this species to be identical with *O. aspera*. However, Chevalier (1975) later expressed doubts of this. The present authors have not examined the type, but the description and figure published by Gardiner show that his *Coeloria magna* is close to the specimens of the present series, exhibiting flat, superficial valleys with relatively abundant endotheca.

Distribution

Red Sea, East Africa, Madagascar, Chagos, Maldives, Nicobar, Singapore, Moluccas, Duke of York Island, Great Barrier Reef, New Caledonia, Philippines, Taiwan, Japan.

GENUS *HYDNOPHORA* FISCHER DE WALDHEIM, 1807

Generic synonymy

Hydnophora Fischer de Waldheim, 1807.

Monticularia Lamarck, 1816; de Blainville (1830, 1834); Dana (1846).

Merulina (*pars*) Dana, 1846.

Hydnophorella Delage & Herouard, 1901.

Type species *Hydnophora demidovii* Fischer de Waldheim, 1807 (= *Madrepora exesa* Pallas, 1766).

Affinities

Hydnophora is primarily characterised by the presence of conical collines (referred to as monticules or hydnae) which make this genus one of the easiest to distinguish. Confusion with other genera only occurs with *H. rigida*, when the monticules lose their typical appearance and assume the form of *Merulina laxa*, incorrectly considered a distinct species ever since Dana's original description. However, *Hydnophora*, in particular *H. rigida*, does have affinities with the Merulinidae, in particular the genus *Clavarina*. These will be discussed in Part III of the present series.

Hydnophora is a widespread genus throughout the Indo-Pacific and is fairly common on reefs. Curiously, comparatively few specimens are present in museum collections and this situation is certainly responsible for the confusion so far prevailing in the taxonomy of the genus.

Hydnophora rigida (Dana, 1846)

Synonymy

Merulina laxa Dana, 1846; Edwards & Haime (1851, 1857); Matthai (1924, 1928); Faustino (1927); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939); Nemenzo (1959); Scheer & Pillai (1974).

Merulina rigida Dana, 1846.

Hydnophora rigida (Dana); Edwards & Haime (1857); Studer (1881); Ortmann (1888); Vaughan (1918); Faustino (1927); Matthai (1928, 1948); Yabe, Sugiyama & Eguchi (1936);

Figs. 238-241 *Hydnophora rigida* ($\times 0.5$)

- Fig. 238 From Sue Island, collecting station 17, showing thick cylindrical branches with blunt ends.
Fig. 239 From Yorke Island, collecting station 13, showing a lax growth form.
Fig. 240 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91.
Fig. 241 From Sue Island, collecting station 17, showing a bushy corallum with numerous anastomosing branches, the terminal parts of which have been fused, and inclined monticules.

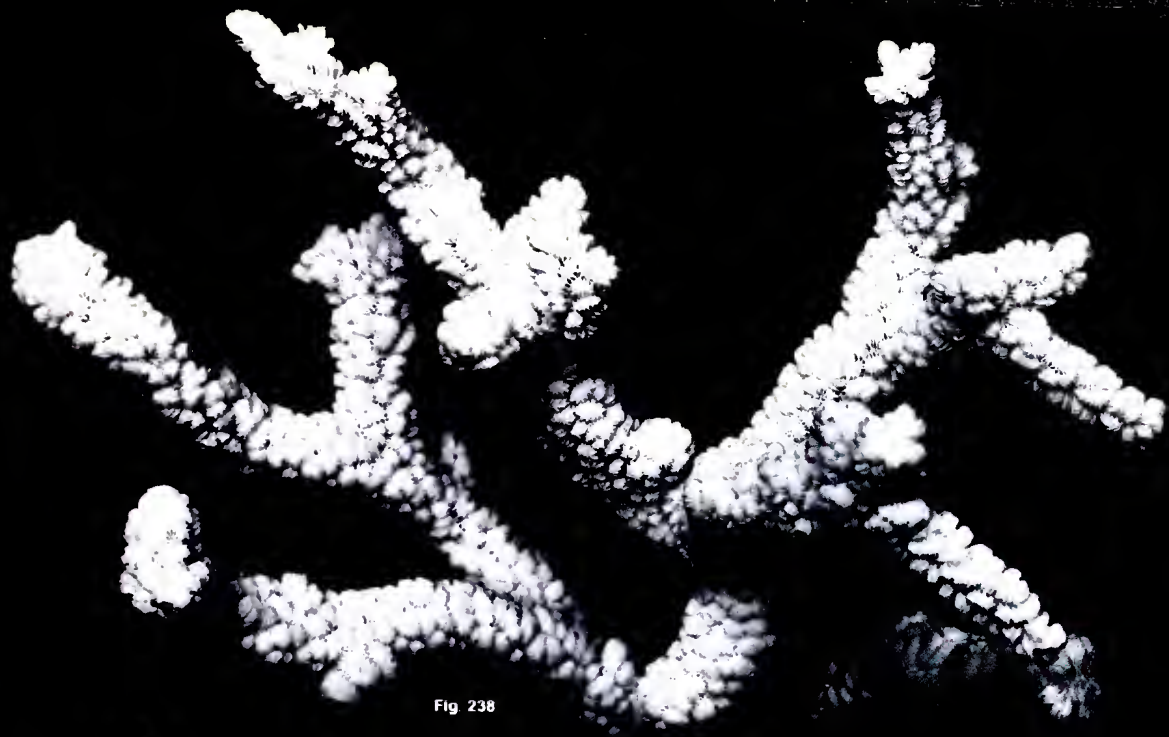


Fig 238



Fig 239



Fig 240



Fig 241

Umbgrove (1939); Stephenson & Wells (1955); Searle (1956); Nemenzo (1959); Wijsman-Best (1972, 1976); Chevalier (1975).

Merulina prolifera Quelch, 1886; *non* Gardiner, 1904.

Hydnophora columellata Rehberg, 1892.

Clavarina composita Rehberg, 1892.

Hydnophora mayori Hoffmeister, 1925.

Hydnophora cf. *mayori* Hoffmeister; Umbgrove (1939).

Hydnophora ramosa Nemenzo, 1959.

Dana (1846) described *Merulina laxa* before *M. rigida* and hence the former has page priority. However, in accordance with Article 24(a) and recommendation 24A of the International Code of Zoological Nomenclature, *Hydnophora rigida* is selected as the name of the taxon which best ensures stability and universality of nomenclature.

Figs. 242-244 *Hydnophora rigida* ($\times 2.5$).

Fig. 242 From Eclipse Island, Palm Islands, collecting station 59, showing a branch of a corallum where the monticules have almost completely disappeared and centres are well defined, with thick radial elements.

Fig. 243 From Lizard Island, collecting station 32, showing a branch of a corallum where the monticules are low and centres well marked and separate.

Fig. 244 Same corallum as Fig. 238, showing wide, low monticules with flat tops and well developed columella centres or axes.



Fig. 242▲



Fig. 243▲



Fig. 244▲

Material studied

Yorke Island (2 specimens), NE of **Murray Islands**, **Sue Island** (6 specimens), **Tijou Reef** (4 specimens), **Bewick Island** (2 specimens), **Yonge Reef** (2 specimens), **Lizard Island** (5 specimens), **Hope Island**, **Palm Islands** (25 specimens), **Pompey Complex** (2 specimens).

These localities include collecting stations 2, 6, 7, 9, 11, 13, 17, 18, 32, 43, 44, 45, 55, 56, 57, 59, 60, 75, 90, 91, 105.

Additional material from Queensland Museum: **Lizard Island**, **Low Isles** (2 specimens), **Big Broadhurst Reef** (2 specimens), **Bowden Reef**, **Bushy Island-Redbill Reef**, **Lady Musgrave Island**. Additional material from the Australian Museum: **Low Isles**, **Loop Island** (Coral Sea).

Previous records from Eastern Australia

Low Isles, Stephenson & Wells (1955).

Characters

The growth form is always ramose, without any massive or encrusting base. The average diameter of branches varies greatly among different coralla; it is usually between 6 and 40mm. Branches remain approximately cylindrical along their whole length, with the exception of the last few centimetres. The ends can be either blunt or slightly tapering. Monticules are generally present over the whole surface of the corallum, tending to be arranged in irregular rows along the branches. They have a circular or slightly elongated section (up to 6mm in diameter for the circular ones) and flat tops (as in *H. microconos*), particularly in specimens with thick branches. They are more conical towards the tips of the branches and their axes tend to be inclined in that direction. The monticules tend to fuse with each other on branch tips, thus forming ridges or collines, often with an acute upper edge, giving an angular appearance with 'winged' terminations. (These peculiarities produce the 'oblique lamina' character which has long been considered as typical of *Merulina laxa*.)

There are 8-14 septa radiating around the monticules, sometimes more on elongated ones. An alternating row of secondary septa is almost always present. The columellar centres are well defined, with 6-8 thick septa meeting at each centre. These centres are disposed in circles when the monticules are distant from each other, or in line along valleys when these are apparent. Septal dentations are obsolete or minute, except occasionally on the lower part of first order septa, close to the columellae. The septal sides are spinose.

Skeletal variations

Although all colonies are typically branching, they nevertheless display a considerable range of variation in their habits. As already mentioned, the thickness of the branches varies from 6 to 20mm. Their extremities can be either blunt or, more often, with tapering terminal branchlets. Distances between branches and angles of branching are also variable. In most specimens with thick branches (tall colonies, up to 35cm high), the branches remain generally distant, and there are few anastomoses. This situation also prevails in the colonies with the thinnest branches. Colonies with branches averaging 10-14mm in diameter usually have numerous branches in close proximity with numerous anastomoses, giving the corallum a bushy habit.

Monticules vary in shape (cylindrical, flat-topped, or conical) and dimension. In colonies with thick cylindrical branches, the monticules tend to be wide and relatively low, with a flat top. They become smaller but higher in thinner branched colonies. However, the latter may occasionally also exhibit low and flat topped monticules. The characters of the monticules also vary within the one colony, being more conical towards the apex of the branches than at the base, where they tend to remain lower and wider, sometimes also with a flat top. It has already been pointed out that at the tip of the branches the monticule axis tends to be inclined on the surface of the corallum, and that series of monticules have a strong

tendency to fuse together. Valleys between adjacent rows of fused monticules range from irregular and discontinuous to well defined, long and linear.

Allinities

Matthan (1928) pointed out the allinities of several forms then considered as distinct species: *H. rigida*, *H. mayori*, *H. columellata* and *Clavaria composita*. The descriptions and excellent photographs published for the two latter, and the examination of the holotype of *H. mayori* show that these are only intraspecific variations of one and the same polymorphic species, *H. rigida*.

Hollmeister (1925) considered that his species, *Hydnophora mayori* could be separated from *H. rigida* by the distinct serration of the septal margin. It is difficult to assess the constancy of this character for Hollmeister based his description on only one specimen. In our series, a few specimens also have a tendency to exhibit distinct septal dentations, particularly towards the valleys. These specimens (which do not differ from *H. mayori*) fit very well in the *H. rigida* series according to all other characters and are not here considered as distinct. It should be noted that the only specimen of *H. mayori* comes from a tidal pool. This represents a rather extreme type of environment, where deviations from the average range of skeletal variation would be expected.

The skeletal characters of Dana's *Merulina laxa* are as follows: 'ridges small, acute, elongate conical, oblique and lax septa and angular branches'. As previously mentioned, these characters fall within the range of variation of *H. rigida*. They are realised in specimens with narrow branches, where monticules are markedly inclined on the surface of the corallum and have fused together into more or less continuous ridges, hence the disappearance of true monticules and the appearance of the 'angular branches with oblique lamellae'. Indeed

Figs. 245, 246 Branch tips of *Hydnophora rigida* ($\times 50$) Fig. 245 from the Chesterfield Reefs, Fig. 246 from Yonge Reef, collecting station 9



Fig. 245

Fig. 246

M. laxa conditions are to be observed at the tip of every branch of practically all typical coralla of *H. rigida* and, with few exceptions, even the thick-branched ones. Actually, there is very little difference between the holotypes of these species, *M. laxa* having characteristic but flat monticules still clearly visible in some parts of the corallum. In the present series, a number of specimens have such characters much better developed than the holotypes. There is therefore every reason to consider *M. laxa* (including *M. prolifera* from Quelch) and *H. rigida* synonymous.

Hydnophora ramosa Nemenzo, the type and only specimen of which has been examined, should clearly be considered a synonym of *H. rigida*.

Distribution

Nicobar, Singapore, Moluccas, Philippines, Yap, Palau, Taiwan, Ryukyu, Great Barrier Reef, New Caledonia, Fiji.

Hydnophora exesa (Pallas, 1766)

Synonymy

Madrepora exesa Pallas, 1766; (*pars*) Esper (1789); *non* Ellis & Solander (1786).

Monticularia exesa (Pallas); Schweigger (1820).

Hydnophora exesa (Pallas); Verrill (1864); Studer (1881); Gardiner (1899); Matthai (1924, 1928, 1948); Vaughan (1918); Faustino (1927); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1939); Searle (1956); Nemenzo (1959); Wijisman-Best (1972, 1976); Scheer & Pillai (1974).

Hydnophorella exesa (Pallas); (*pars*) Bedot (1907).

Hydnophora contignatio (Forskål); Klunzinger (1879); von Marenzeller (1907); Matthai (1928, 1948); Umbgrove (1939).

Hydnophora demidovii Fischer de Waldheim, 1807; Fischer de Waldheim (1830-1837); Edwards & Haime (1848, 1849, 1857); Quelch (1886).

Hydnophora pallassii Fischer de Waldheim, 1807.

Hydnophora lobata (Lamarck); Lamouroux (1821); Dana (1846); Edwards & Haime (1849, 1857); Klunzinger (1879); Gardiner (1899, 1904).

Hydnophora polygonata (Lamarck); Dana (1846); Edwards & Haime (1849, 1857).

Monticularia meandrina Lamarck, 1816.

Monticularia folium Lamarck, 1816; de Blainville (1830, 1834).

Merulina folium (Lamarck); Dana (1846).

Hydnophora ehrenbergi Edwards & Haime, 1849; Edwards & Haime (1857).

Hydnophora gyrosa Edwards & Haime, 1849; Edwards & Haime (1857).

Hydnophora tenella Quelch, 1886; Matthai (1928); Umbgrove (1940, as *Hydnophora tenella* var. *applanata*).

Hydnophora grandis Gardiner, 1904; Matthai (1928); Yabe, Sugiyama & Eguchi (1936).

Hydnophora maldivensis Gardiner, 1904.

Hydnophorella microconus (Lamarck); *sensu* Gravier (1911); *non* *Monticularia microconus* Lamarck, 1816.

Material studied

Darnley Island, Yorke Island (2 specimens), **Sue Island, Thursday Island, Great Detached Reef, Tijou Reef** (4 specimens), **Bewick Island, Lizard Island, Eagle Reef, Low Isles, east of Bowl Reef, Palm Islands** (41 specimens), **Whitsunday Islands**.

These localities include collecting stations 2, 5, 13, 17, 19, 31, 32, 34, 36, 37, 38, 41, 42, 45, 48, 54, 55, 57, 60, 91, 98.

Additional material from the Queensland Museum: **Murray Islands; Green Islands; Low Isles; Bowden Reef; Lupton Reef; Bushy Island-Redbill Reef** (3 specimens), **Heron Island** (2 specimens), **Lady Musgrave Island, Moreton Bay; Flinders Reef** (3 specimens), **Tryon Reef** (4 specimens), **Peel Island**.

Additional material from the Australian Museum: **Heron Island; One Tree Island; Coral Sea; West Cay** (Diamond Islet).

Previous records from Eastern Australia

Murray Islands, Vaughan (1918); **Low Isles**, Yonge (1930, 1940); **Heron Island**, Salter (1954); **Palm Islands, Port Essington, Roebuck Bay, Rocky Island, Lark Passage**, Matthai (1928); **Port Denison**, (as *Hydnophora grandis*) Matthai (1928).

Characters

The growth form is usually primarily massive or encrusting, eventually becoming subsequently ramose (digitate or branching). The monticules are well developed, typically conical, up to 8mm high and 5mm wide at their base. These monticules are evenly distributed over the corallum, in some parts arranged in regular rows, 3-6mm apart, separating continuous valleys. In branching colonies, the monticule axis, which is normally perpendicular to the general surface of the corallum, tends to become increasingly inclined towards the tips of the branches. Ridges or collines which arise from the fusion of adjacent monticules are well developed in some specimens.

The number of septa reaching the top of the monticules varies from 6 to 12, with an average of ten. Some secondary intermediate septa can be observed at the base of the monticules, in the intervals between the first order septa. The septa are thin and narrow on the monticules, but they thicken and broaden in the valleys. Septal dentations are obsolete

Fig. 247 *Hydnophora exesa* from Lizard Island, collecting station 100.



on the monticules, but better developed on the lower part of the septa. The septal sides are slightly granular on the monticules, more granular in the valleys.

The columellar structure is irregularly developed, absent in places. It consists of a few twisted trabeculae marking the corallite centres, but frequently becomes laminar partly or wholly surrounding the monticules.

Skeletal variation

Hydnophora exesa is a highly polymorphic species with a correspondingly complex synonymy. Major variations affect the growth form, the development of the monticules and their degree of fusion.

The growth form is basically laminar or encrusting, and although the corallum can be very thick (up to 7cm) towards its centre, it never becomes genuinely massive, with a more or less hemispherical habit. On the other hand, the laminar corallum may tend to become extremely thin and foliate, adhering more or less closely to the substratum. A majority of specimens show a tendency to develop branches, which first appear as swollen areas of corallum. These branches are irregularly cylindrical, 7.5 to 4cm in average diameter, and up to 20cm high. They are sometimes larger towards the tip, but some specimens have conical branches with markedly tapering extremities. Occasionally, branches may anastomose.

Both width and height of the monticules are variable from one corallum to another. In one corallum, a given category of monticule is generally dominant, although considerable variation may occur, particularly in branching specimens. In that latter case, the monticules are smaller and flatter on the lower encrusting base of the corallum than on the branches themselves.

At the tip of the branches, or towards the free margin of laminar colonies, the monticules are more elongated than the average, and, as already mentioned, their axis is no longer

Fig. 248 *Hydnophora exesa* from Lizard Island, collecting station 99.



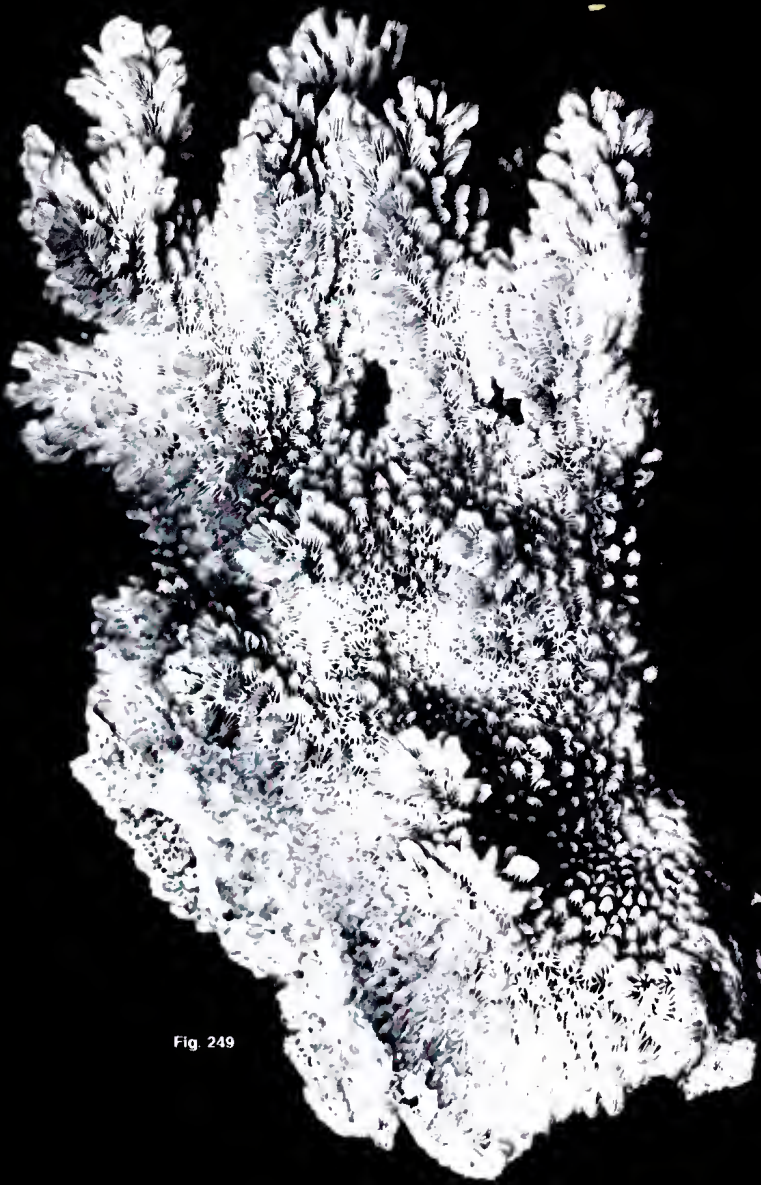


Fig. 249



Fig. 250

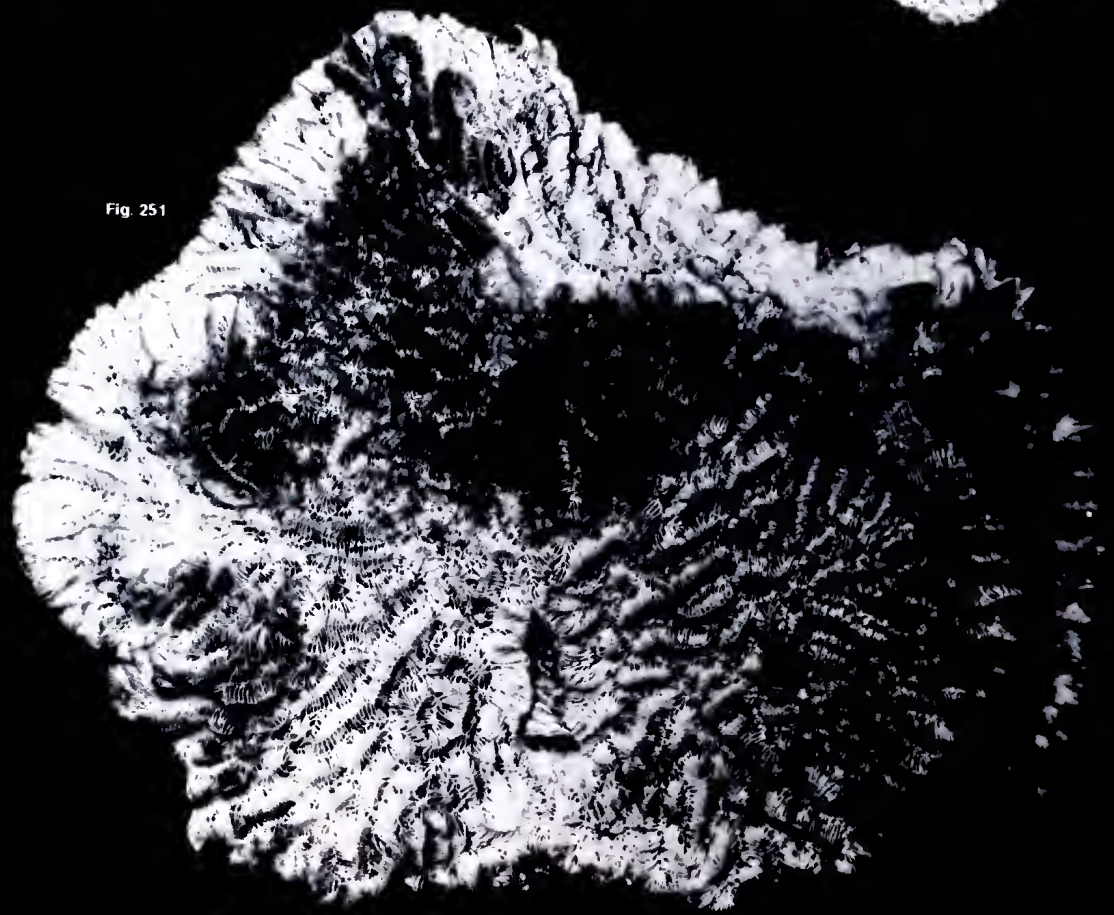


Fig. 251

perpendicular to, but is inclined on, the general surface of the corallum. Also, the normally isolated monticules tend to be arranged in well defined rows, and they even fuse together to form more or less continuous ridges, as noted in *H. rigida*.

Affinities

Although generally badly represented in most collections, *H. exesa* is a fairly common species. The range of skeletal variations largely explains why so many supposed 'species' of *Hydnophora* have been described. Nevertheless, *H. exesa* is easily recognised underwater and in heterogeneous collections, with or without ecological data.

Figs. 249-251 *Hydnophora exesa* ($\times 0.7$).

- Fig. 249 From Thursday Island, collecting station 54, showing characteristic fusion of the monticules towards the branch tips.
Fig. 250 From Bowl Reef, collecting station 48.
Fig. 251 From Palm Islands, showing a flat, encrusting growth form with monticules fused into ridges giving a meandroid appearance.

Figs. 252, 253 *Hydnophora exesa* ($\times 2.5$).

- Fig. 252 Same corallum as Fig. 251.
Fig. 253 From SE Cape, Great Palm Island, collecting station 38, showing tall, very acute monticules.

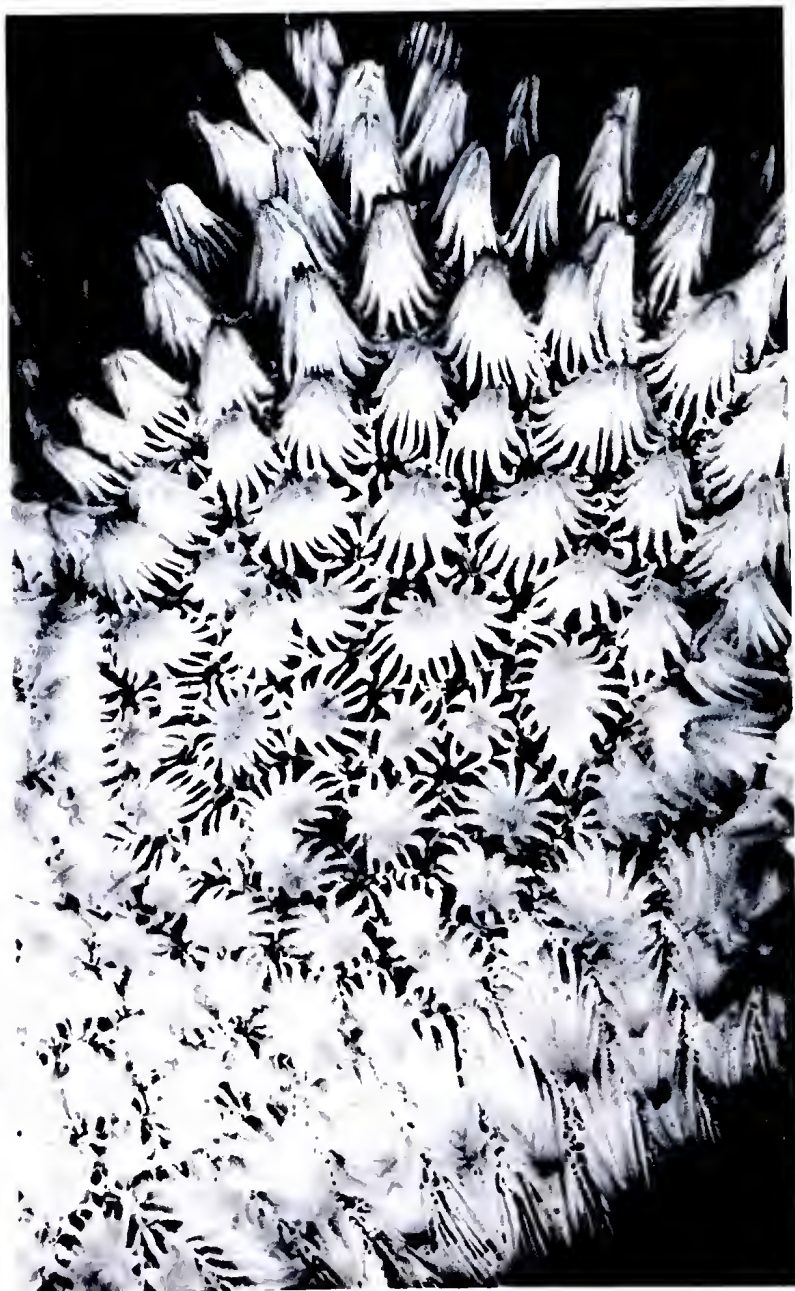


Fig. 253▲

In order to describe variation in the species, Wijsman-Best (1972) distinguished four 'types' as follows: *gyrosa*-type (massive corallum with a tendency to form branches and high conical monticules, from lagoon reefs and fringing reefs, in relatively shallow water and fairly protected conditions); *tenella*-type (with flatter monticules and wider valleys from the deeper outer slope); *grandis*-type (light textured corallum, with large flat hydnae, on sandy lagoon bottom); *maldivensis*-type (thick foliaceous colony, with extremely broad and flat monticules, often forming ridges, in bays with sandy-muddy bottom and highly turbid waters).

The present series of *H. exesa* (72 specimens) clearly illustrates that, whereas these 'types' may describe some of the diversity of the species, they are not based on any natural division within the species and cannot be considered as ecomorphs. The characters used to define these different forms do not appear to be connected (e.g. high conical monticules (*gyrosa*-type) are also found in laminar or encrusting colonies, and flatter monticules (*tenella*-type) also occur in branching colonies). Rather, they tend to vary independently of each other, hence the multiplicity of possible combinations which indeed accounts for the polymorphism of the species. Also there is no clear correlation between the morphological characters and the type of environment.

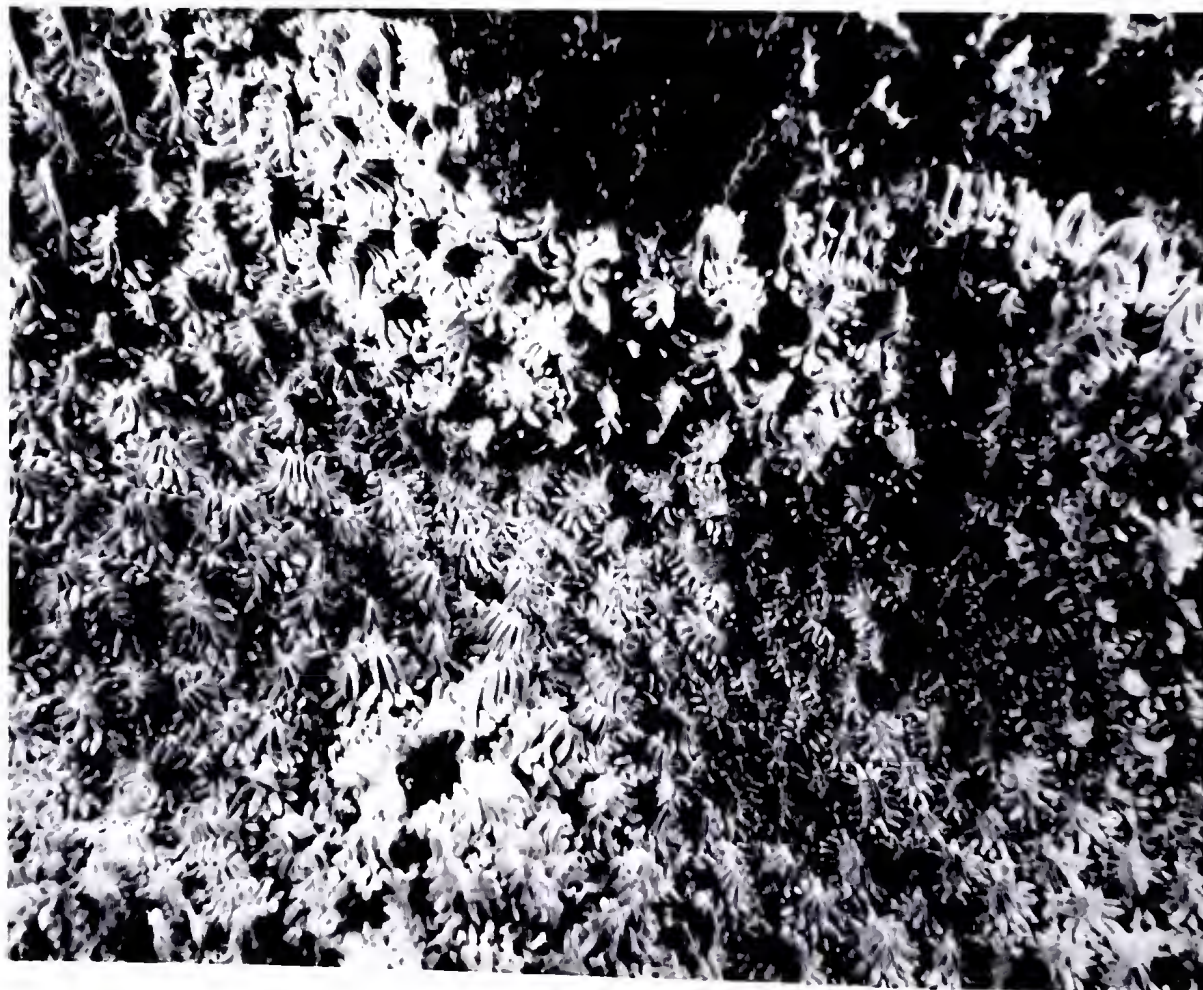
Several ecotype morphologies can be found on different parts of the same colony. Thus it is common to have a *gyrosa* aspect at the top of branching colonies, and *tenella* on the base, or *tenella* on the top and *maldivensis* on the base. Figs. 247 & 248 illustrate some of this diversity.

At the specific level *Hydnophora exesa* is a well defined species, without strong affinities with the other species of the genus.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to the Ellice Islands.

Fig. 254 *Hydnophora exesa*, *in situ* at the Palm Islands with tentacles expanded at night ($\times 2.0$).



Hydnophora microconos (Lamarck, 1816)

Synonymy (the spellings *microconos*, *microconus*, *microcona* are not separated)

Madrepora exesa Ellis & Solander, 1786; *non* *Madrepora exesa* Pallas, 1766.

Monticularia microconos Lamarck, 1816; Lamouroux (1821); Dana (1846).

Monticularia exesa (Ellis & Solander); de Blainville (1830).

Hydnophora microconos (Lamarck); Edwards & Haime (1849, 1857); Klunzinger (1879); Quelch (1886); Gardiner (1899, 1904); Vaughan (1918); Matthai (1924, 1926, 1928); Hoffmeister (1925); Faustino (1927); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939, 1940); Crossland (1952); Wells (1954); Nemenzo (1959); Scheer (1964); Chevalier (1968); Wijisman-Best (1972, 1976); Scheer & Pillai (1974).

Hydnophorella microconos (Lamarck); Bedot (1907); *non* Gravier (1911).

Hydnophora klunzingeri Rehberg, 1892.

Figs. 255, 256 *Hydnophora microconos* ($\times 2.5$).

Fig. 255 From Darnley Island, collecting station 31, showing the presence of an incomplete cycle of secondary septa.

Fig. 256 From Great Detached Reef, collecting station 47, showing monticules with flat tops and encircling columella.

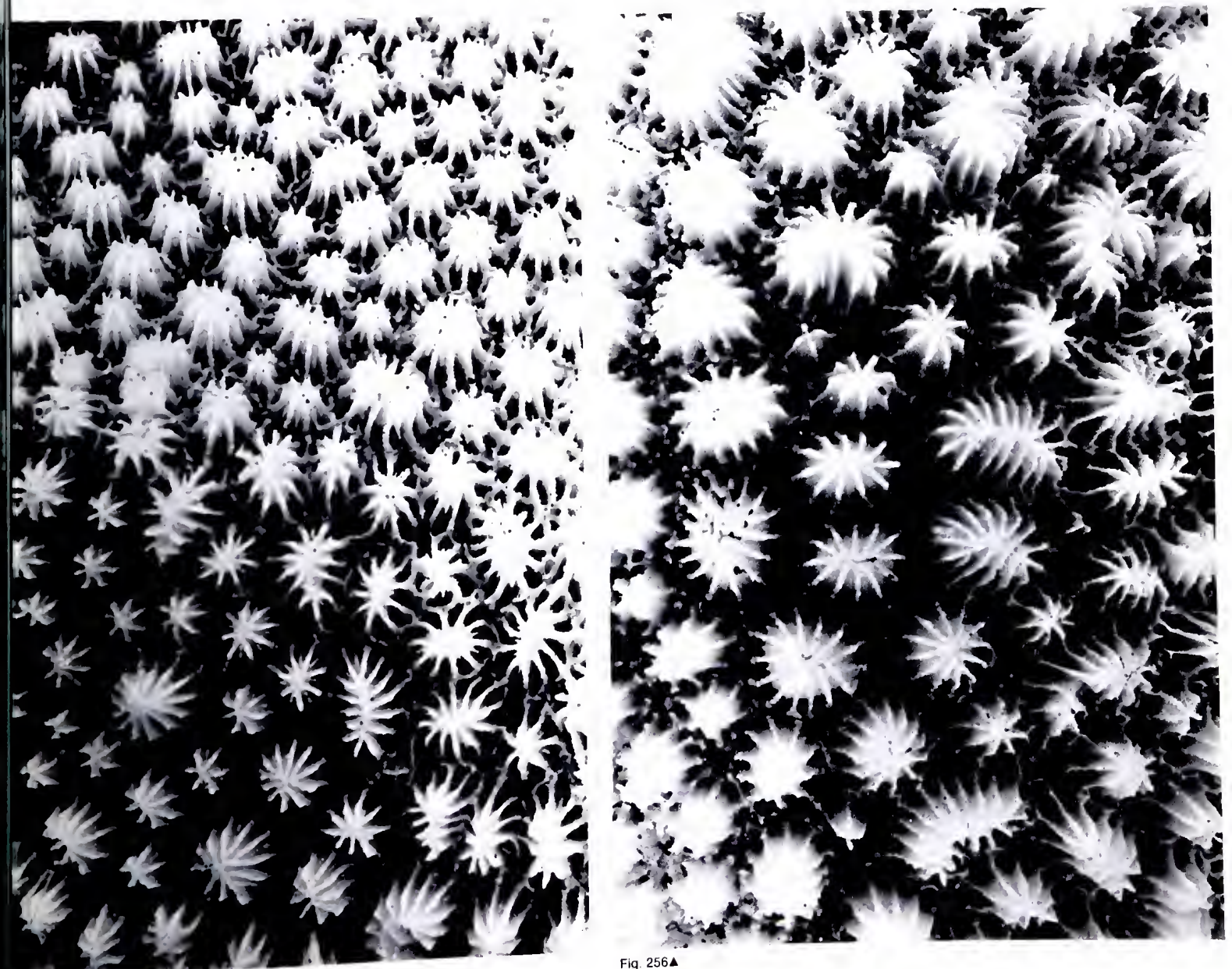


Fig. 256▲

Material studied

Darnley Island, Great Detached Reef (5 specimens), Tijou Reef, Bewick Island, Houghton Island, Three Isles, Hope Island, Palm Islands (2 specimens), Wheeler Reef (6 specimens).

These localities include collecting stations 1, 2, 5, 31, 36, 40, 45.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918), Mayor (1918); Low Isles, Crossland (1952), Stephenson & Wells (1955).

Characters

Colonies are always massive, usually with a convex surface. In shallow water (reef flats), the species often forms microatolls. Valleys are comparatively narrow with an average width of 2 to 3mm. The monticules are regularly conical, and only rarely elongated. They are smaller than those of other *Hydnophora*, with an average diameter of 2 to 3mm. Six to ten first order septa are found on each monticule. An incomplete cycle of secondary septa is usually present, but on the lower part of the monticules and rarely reaching the top. First order septa are horizontal at the top of the monticules, giving them the characteristic star-shape mentioned by Wijsman-Best (1972). They then fall steeply, often almost vertically, towards the valley giving the flat topped monticules a somewhat cylindrical aspect. The septal dentations are obsolete except on the lower part of the septa close to the columella, where a few fine dentations are sometimes developed. The septal margins are covered with scattered, small granules. The columellae are of a lamellar type, generally continuous, encircling the monticules.

Hydnophora microconos is a well characterised species, showing very little intraspecific variation. Slight variation occurs in the size and shape of the monticules, varying from almost cylindrical flat-topped to perfectly conical. These differences have no taxonomic or ecological significance.

Although the holotype of Rehberg's *Hydnophora klunzingeri* is destroyed, it seems likely that this species is a synonym of *H. microconos*, as already stated by Matthai (1928) (who had seen Rehberg's type) and Wijsman-Best (1972).

Distribution

Widely distributed throughout the Indian Ocean, Red Sea and western Pacific to the Cook Islands.

GENUS *MONTASTREA* DE BLAINVILLE, 1830

Generic synonymy

Montastrea de Blainville, 1830; Wells (1956); Chevalier (1971).

Orbicella Dana, 1846.

Heliastrea Edwards & Haime, 1857.

Type species *Astraea guettardi* DeFrance, 1826.

Affinities

The relationships of *Montastrea* have been discussed by Chevalier (1971) who gives an alternative to Wells' (1956) view that the genus is restricted to the Atlantic Ocean. The present study supports Chevalier's conclusions, particularly his delineations of *Montastrea* and *Plesiastrea* (see p.4). However, *Montastrea* is a particularly difficult genus to define. It is grouped with the Faviidae characterised by the predominance of extratentacular budding but its characters are primarily the relatively minor characters of the species included in it. Thus

Montastrea is separated from *Favia*, *Favites* and *Goniastrea* by the predominance of extratentacular budding and is separated from *Cyphastrea*, *Diploastrea*, *Leptastrea* and *Echinopora* by the separate, discrete characters of each of these genera. Confusion with *Plesiastrea*, as already discussed, is the primary source of instability in *Montastrea* and the resulting taxonomic history is complex.

***Montastrea curta* (Dana, 1846)**

Synonymy

The historical synonymy of this species was originally made complex by the multiplicity of names given to it by Edwards & Haime (1849) and later by Gardiner (1899). Confusion followed, especially with *Favia* species and *Plesiastrea versipora* (see Matthai, 1914; Crossland, 1952; Chevalier, 1971). The following synonymy therefore is largely incomplete.

Orbicella curta Dana, 1846; Gardiner (1899, 1904); Vaughan (1917, 1918); Hoffmeister (1925); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1940); Crossland (1952).

Orbicella coronata Dana, 1846; Gardiner (1899).

Astraea lamarckiana Edwards & Haime, 1849.

Astraea laperousiana Edwards & Haime, 1849.

Astraea solidior Edwards & Haime, 1849; Gardiner (1899); Matthai (1914).

Astaea quadrangularis Edwards & Haime, 1849.

Orbicella wakayana Gardiner, 1899; Matthai (1914).

Orbicella rotumana Gardiner, 1899.

Orbicella funafutensis Gardiner, 1899.

Orbicella vacua Crossland, 1952.

Montastrea curta (Dana); Chevalier (1971); Wijsman-Best (1977).

The present study shows that *Orbicella vacua* Crossland is a synonym of *O.* (= *Montastrea*) *curta*, as previously concluded by Chevalier (1971). *Orbicella* (= *Montastrea*) *annuligera* is, however, a valid species and not a synonym of *M. curta* (cf. Chevalier, 1971) (see below).

Material studied

Darnley Island (2 specimens), **Murray Islands** (3 specimens), **Thursday Island**, reef between **Yule Reef** and **Triangle Reef**, **Triangle Reef** (2 specimens), **Great Detached Reef** (17 specimens), **Tijou Reef** (9 specimens), **Bewick Island** (2 specimens), **Yonge Reef** (5 specimens), **Lizard Island** (3 specimens), **Ribbon Reef**, **Eagle Reef**, **Bowl Reef**, **Lodestone Reef**, **Palm Islands** (24 specimens), **Wheeler Reef** (3 specimens), **Whitsunday Islands**, **Bushy Island-Redbill Reef**, **Pompey Complex** (7 specimens), **Swain Reefs** (6 specimens), **Lord Howe Island** and vicinity.

These localities include collecting stations 1, 2, 3, 4, 5, 6, 9, 18, 19, 22, 27, 31, 35, 36, 37, 41, 45, 51, 53, 55, 56, 60, 65, 68, 69, 71, 75, 77, 79, 80, 91, 92, 98, 103, 104, 105.

Previous records from Eastern Australia

Murray Islands, (as *Orbicella annularis* and *O. vacua*) Mayor (1918), **Low Isles**, (as *Orbicella curta* and *O. vacua*) Crossland (1952).

Characters

Colonies are usually massive, tending to have a spherical or flat growth form; they are occasionally encrusting. Mature corallites are moderately exsert and usually circular; sometimes they are squeezed into irregular shapes. Calices are 2.5-7.5mm in diameter. Septa are regularly arranged in three orders, although the first and second orders are frequently

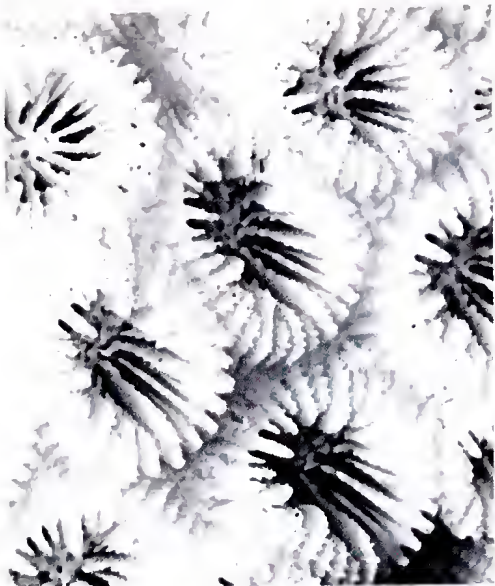


Fig. 257▲

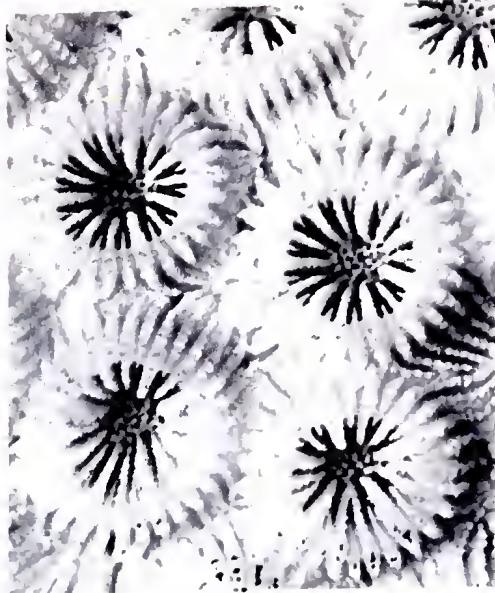


Fig. 258▲



Fig. 259▲

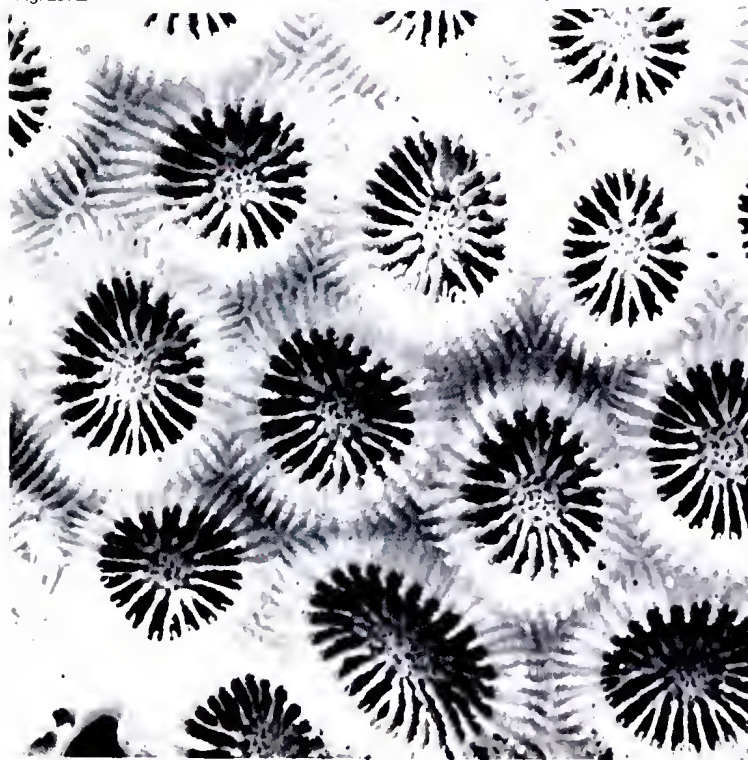


Fig. 260▲

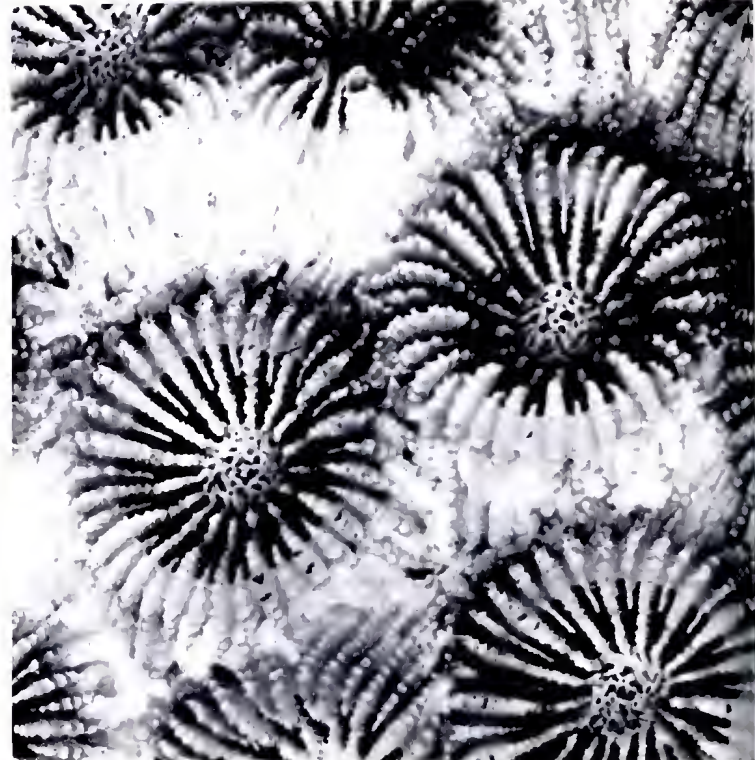


Fig. 261▲

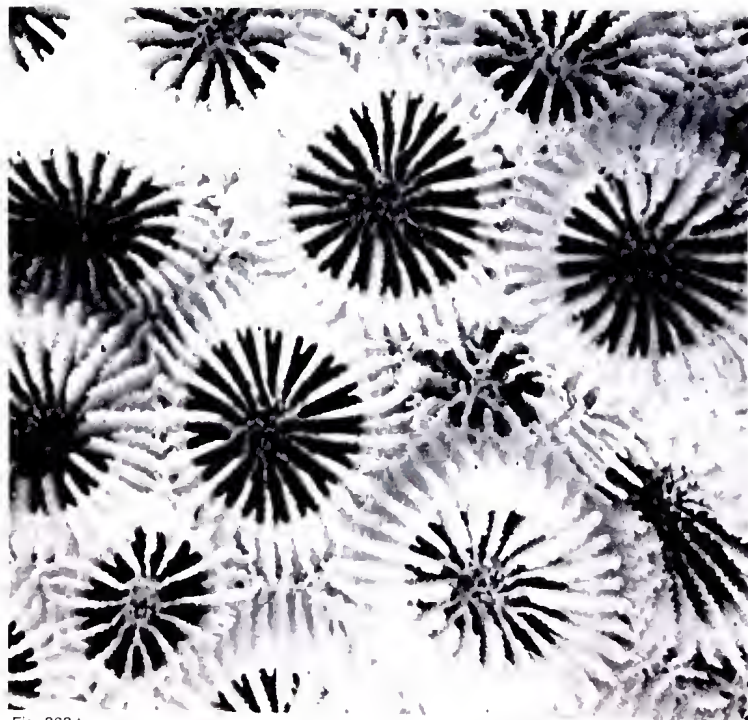


Fig. 262▲

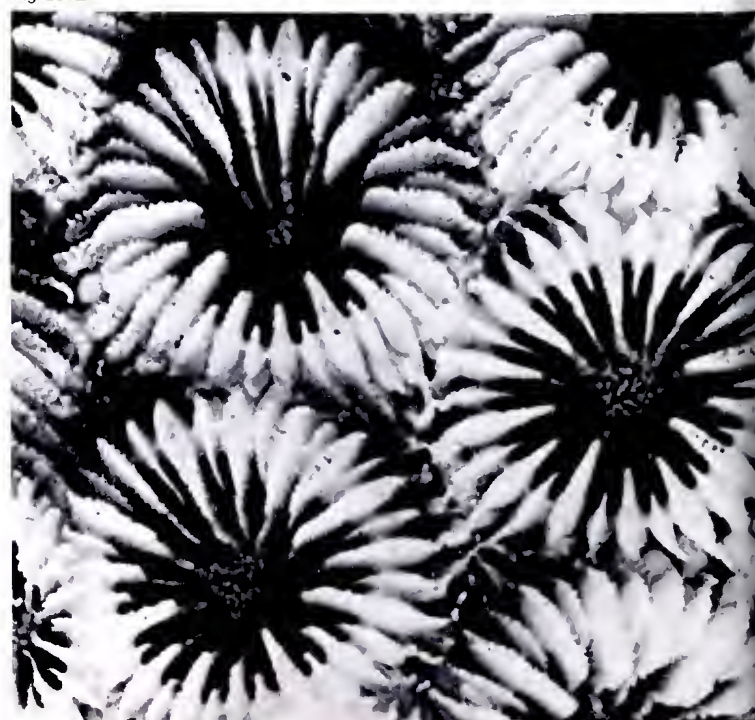


Fig. 263▲

indistinguishable. Inner margins of first order septa descend vertically just inside the theca, then curve inwards deep within the calice. The columellae are usually surrounded by paliform crowns which have a vertical inner margin descending to the columellae. If second order septa are distinguished from the first, they are uniformly less exsert and smaller, and sometimes do not reach the columella. They usually have paliform lobes. Third order septa are always present, sometimes only as ridges. They do not reach the columellae, do not form paliform lobes, and are less exsert. All septa have well formed, usually horizontal dentations and are granulated. The columellae are small, trabecular or spongy and compact. Costae are well formed, beaded, and equal or sub-equal. Beads on adjacent costae are aligned to form concentric circles. There are no intercostal ridges. Costae of adjacent corallites are not adjoined. Budding is entirely extratentacular.

Skeletal variation

Coralla from within the same biotope are usually very similar. Those from different biotopes show a wide range of phenotypic variation which can be separated into two intergrading ecomorphs:

Montastrea curta from exposed biotopes (Figs. 257-259).

Coralla from exposed biotopes are massive, usually small and spherical. Corallites are small and thick walled. Three septal cycles are usually present and sometimes a hexameral symmetry can be distinguished. Paliform lobes are frequently absent. The columella is small, frequently consisting of only a few twisted trabeculae.

Montastrea curta from protected and semi-protected biotopes (Figs. 260-263).

Coralla from reef lagoons, back reef slopes or turbid water have a variable, massive or encrusting growth form. Corallites become larger, and more widely separated in more sheltered biotopes. Giant corallites are occasionally formed. Calices are more open and septa more numerous. Usually only two orders of septa are distinguishable, the first order having a well developed paliform crown. Costae are well developed; the coenosteum of the intercostal grooves is frequently blistered.

Colonies found where light availability is poor have large, widely separated corallites. Such colonies are usually dark brown in colour.

Distribution

Widely distributed throughout the Indo-Pacific, from Madagascar to the Tuamotu Archipelago. This species is usually more abundant than *M. annuligera* in the Pacific, while the reverse usually applies in the Indian Ocean and Red Sea.

Montastrea annuligera (Edwards & Haime, 1849)

Synonymy

Orbicella annuligera Edwards & Haime, 1849; Gardiner (1904); Gravier (1907, 1911).
Montastrea annuligera (Edwards & Haime); Wijsman-Best (1977).

Figs. 257-263 *Montastrea curta* ($\times 5.0$).

- Fig. 257 From the outer slope, Great Detached Reef, collecting station 1.
- Fig. 258 From the outer slope, Tijou Reef, collecting station 2.
- Fig. 259 From the inner slope, Yonge Reef, collecting station 9.
- Fig. 260 From Maer Island, Murray Islands, collecting station 27.
- Fig. 261 From Bullumbooroo Bay, Great Palm Island, collecting station 35. This corallum is close to the type of *M. vacua* (cf. Crossland (1952), Plate III, Fig. 2).
- Fig. 262 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91.
- Fig. 263 From Bushy Island-Redbill Reef, collecting station 80.

Material studied

Murray Islands (2 specimens), reef between **Yule Reef** and **Triangle Reef** (2 specimens), **Triangle Reef**, **Yonge Reef**, **Lizard Island** (2 specimens), **Palm Islands**, **Pompey Complex** (3 specimens), **Swain Reefs**.

These localities include collection stations 3, 27, 32, 34, 77, 104.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are irregular, massive or encrusting. Mature calices are circular, uniform in size, 3-4mm in diameter. Septa are in three orders which are usually distinct. The 6-10 septa of the first order are relatively erect and thickened over the theca. They drop abruptly into the calice and usually taper towards their inner edge. They have well developed, thick paliform lobes which form a conspicuous crown. The paliform lobes have vertical inner margins and are usually adjoined deep within the calice by a pseudo-synapticular ring. Enlarged septal granules occasionally form pseudo synapticulae between first and second order septa. Second order septa are usually, though not always, distinct from those of the first order, being less erect and thickened above the thecae. They may reach the columellae and may form paliform lobes, which are usually vertical but which are sometimes inwardly projecting. Some may be joined at their inner margins, either to each other or to first order septa. Third order septa are of relatively uniform appearance. They extend inward one-quarter to one-third of the septal radius and do not form paliform lobes. All septa are dentate and granulated. The columellae are small, compact and spongy, although occasionally trabecular (in coralla from turbid water). The costae are well formed and beaded. The beads frequently have a transverse border of granules. Shallow intercalicular grooves usually separate costae of adjoining corallites.

Corallites of most colonies are separated by deep grooves usually containing tubercles of epitheca as described for *M. valenciennesi* (Fig. 268). This groove and tubercle formation, however, is never well developed. Budding is entirely extratentacular.

Skeletal variation

The present series of coralla is too small to indicate much about skeletal variation other than that calicular structures tend to be uniform (Figs. 265-267). This is a rare, although well-defined, species and is readily recognisable underwater.

Affinities

In many respects, this species is very close to species of *Leptastrea*, especially *L. immersa* Klunzinger and *L. bottae*. The small, rounded corallites separated by intercalicular grooves, the development of the theca and the thickened, erect septa above it are all *Leptastrea*-like. However, the paliform crown, the compact spongy columella, the lack of inward sloping paliform lobes, and the well developed costae closely resemble other *Montastrea* species, especially *M. curta*. It is important to note here, however, that none of these skeletal characters are entirely diagnostic and that coralla obtained from protected turbid waters have a tendency towards *Leptastrea*-like development.

Figs. 264-268 *Montastrea annuligera* ($\times 5.0$).

Fig. 264 Holotype of *Montastrea annuligera*.

Fig. 265 From Lizard Island, collecting station 32.

Fig. 266 From a barrier reef between Triangle Reef and Yule Entrance.

Fig. 267 From Yonge Reef, collecting station 3.

Fig. 268 From the Pompey Complex, collecting station 104, showing the characteristic invasion of the intercalicular grooves by the epitheca.

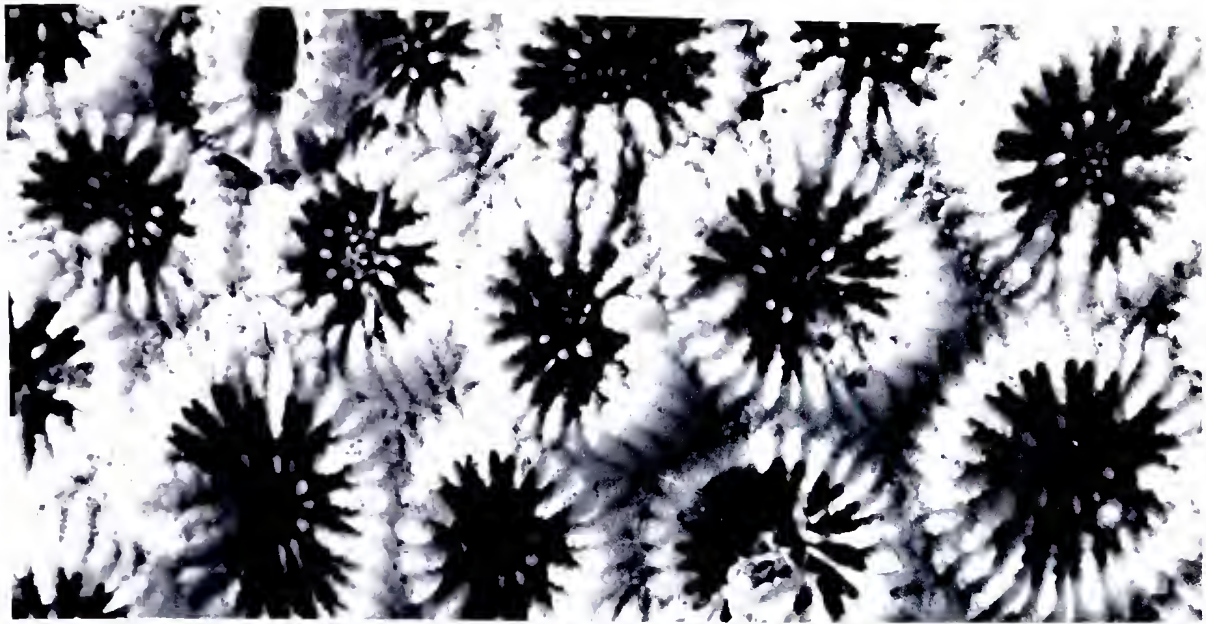
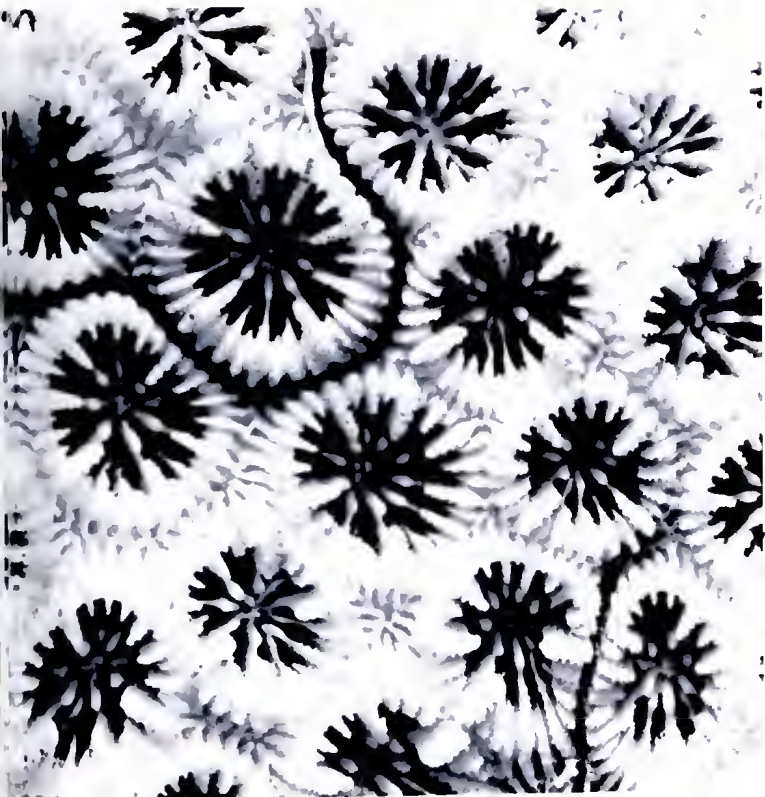


Fig. 264▲



265▲

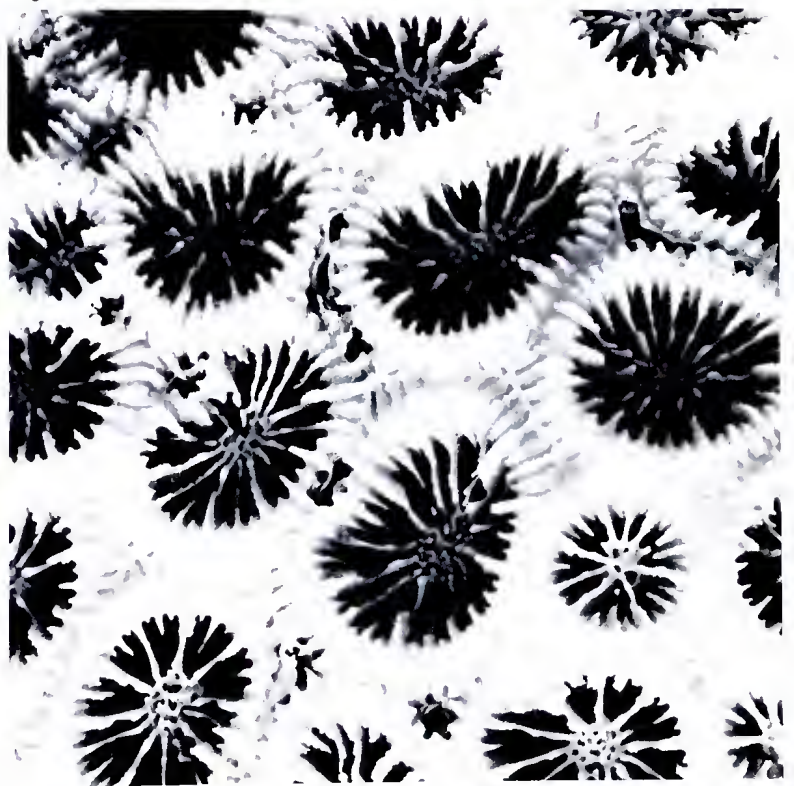
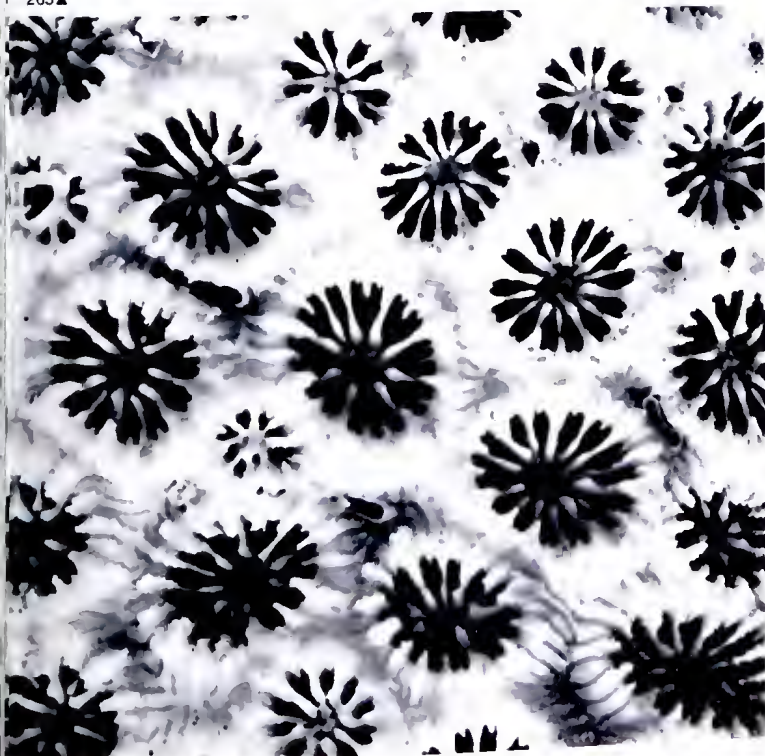


Fig. 266▲



267▲



Fig. 268▲

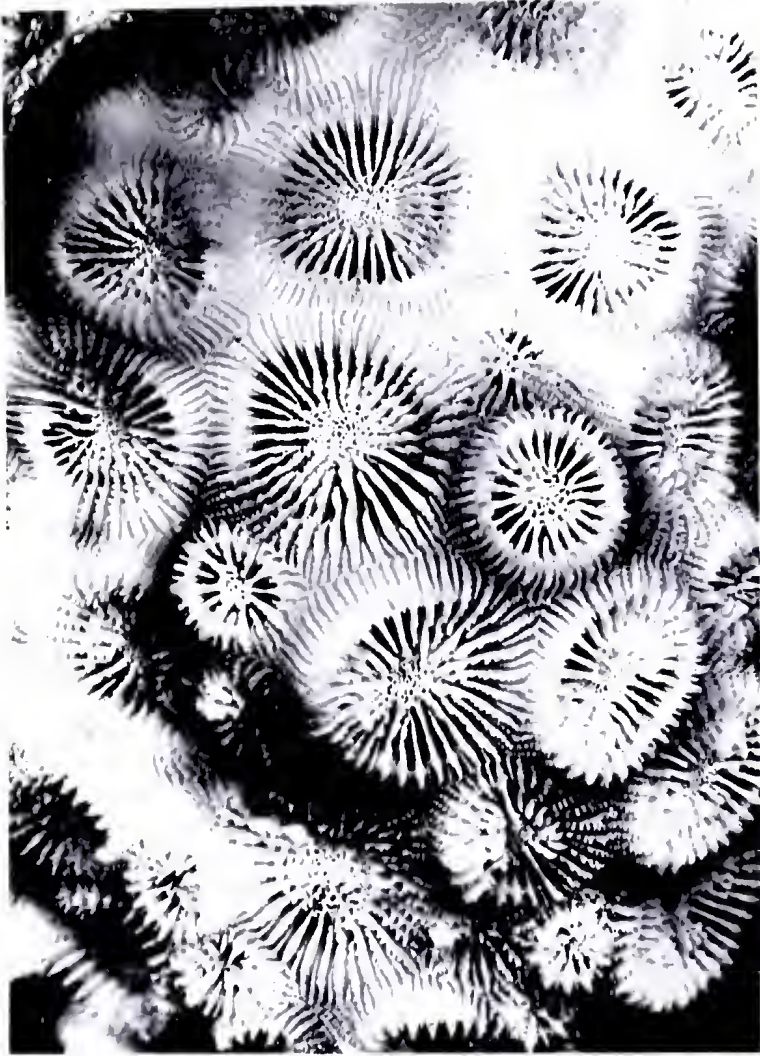


Fig. 269▲

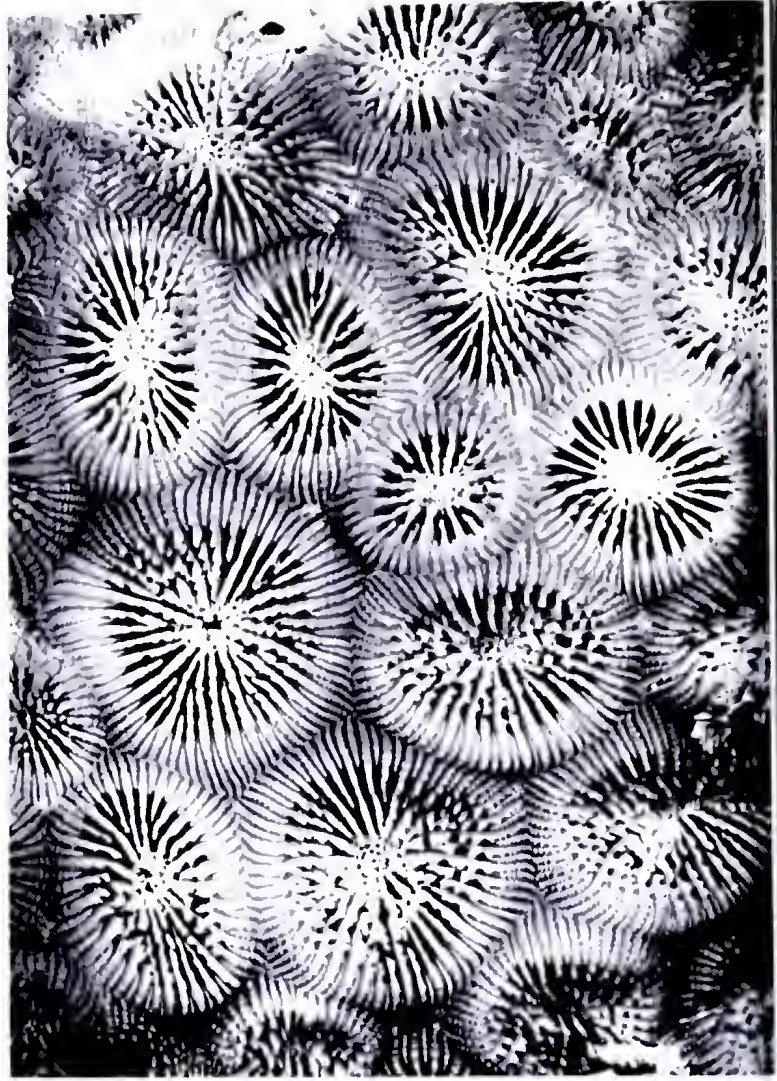


Fig. 270▲

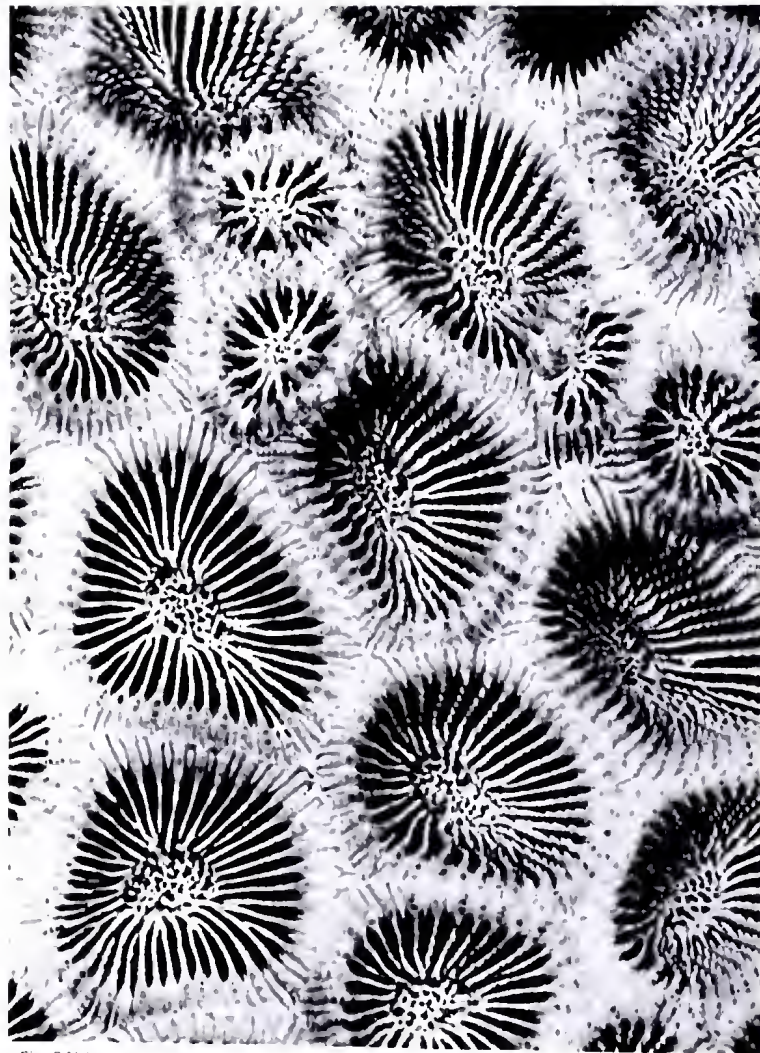


Fig. 271▲

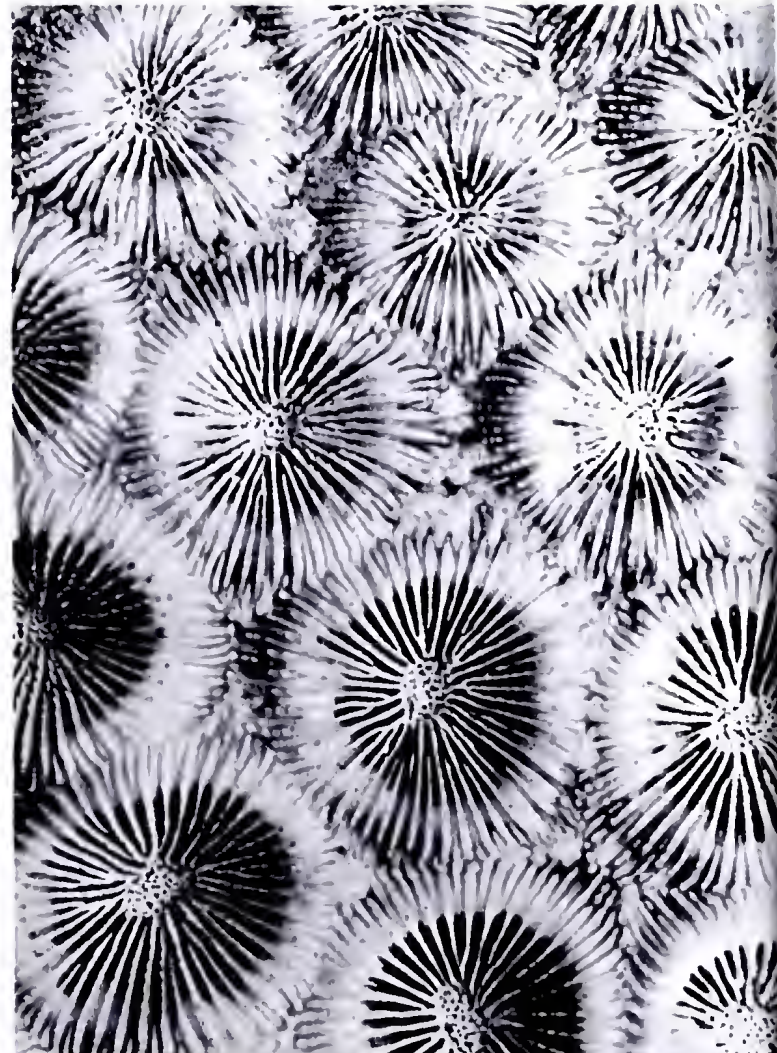


Fig. 272▲

Distribution

This species has been observed or recorded from the Red Sea to the western Pacific, including Indonesia, the Philippines and New Caledonia.

Montastrea magnistellata Chevalier, 1971

Synonymy

Montastrea magnistellata Chevalier, 1971; Wijisman-Best (1977).

Material studied

Great Detached Reef (7 specimens), **Tijou Reef**, **Bewick Island** (2 specimens), **Lizard Island** (8 specimens), **Eagle Reef** (2 specimens), **Three Isles**, **Hope Island** (2 specimens), **Low Isles**, **Lodestone Reef**, **Palm Islands** (9 specimens), **Whitsunday Islands**, **Swain Reefs**.

These localities include collecting stations 1, 2, 5, 18, 19, 32, 35, 36, 37, 41, 55, 69, 92, 97, 99.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are massive, flattened or irregular in shape or are encrusting. Mature corallites are circular, 7.3-15.1mm in diameter and are usually slightly exsert. Septa are of two orders, arranged alternately, with very constant interseptal distances. First order septa slope gradually towards the columella in shallow calices or may have an initial steep slope inside the theca in deeper calices. The septal dentations are always large and conspicuous; in some corallites they extend uniformly across the full length of the septo-costae, in others the dentations become increasingly elongated and interwoven towards the calice centres to form trabecular columellae. A circle of paliform lobes can usually be distinguished. These usually have vertical or near vertical inner margins descending towards the columellae. Second order septa are small, frequently occurring only as ridges down the inner thecae. They are thinner than first order septa and less exsert. Costae are usually unequal and well developed. Those of adjacent corallites are not adjoined and may be separated by a small ridge. The septo-costae and septal dentations are granulated. The columellae may be trabecular, spongy or very compact.

Living colonies are dark coloured except when exposed to strong light, then they have a variety of pale colours, usually with darker sides.

Skeletal variation

Colonies from protected biotopes are encrusting and have large corallites with shallow calices and fine septa. They are invariably dark coloured. Coralla become more massive with increasing exposure to wave action and light, and the calices become deeper with more heavily calcified components. No specimens have been obtained from outer slopes of reef exposed to very strong wave action.

Distribution

Previously recorded only from New Caledonia and Indonesia.

Figs. 269-272 *Montastrea magnistellata* ($\times 2.5$).

- Fig. 269 From Yonge Reef, collecting station 9.
- Fig. 270 From Tijou Reef, collecting station 8.
- Fig. 271 From Three Isles.
- Fig. 272 From Yonge Reef, collecting station 9.

Montastrea valenciennesi (Edwards & Haime, 1848)

Synonymy (partly after Chevalier, 1971 and Wijsman-Best, 1972)

The spellings *valenciennesi* and *valenciennesii* are not separated.

Phymastrea valenciennesi Edwards & Haime, 1848; Edwards & Haime (1850); Duncan (1883); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Alloiteau (1957).

?*Phymastrea profundior* Edwards & Haime, 1848; Edwards & Haime (1857); Duncan (1883).

Favia bertholleti Edwards & Haime, 1857; Matthai (1914).

Phymastrea irregularis Duncan, 1883.

Phymastrea aspera Quelch, 1886.

Favia valenciennesi (Edwards & Haime); Matthai (1924); Gravely (1927); Faustino (1927); Umbgrove (1939); Crossland (1952); Wells (1954); Stephenson & Wells (1955); Nemenzo (1959); Ma (1959); Utinomi (1965); Chevalier (1971); Wijsman-Best (1972, 1974); Scheer & Pillai (1974).

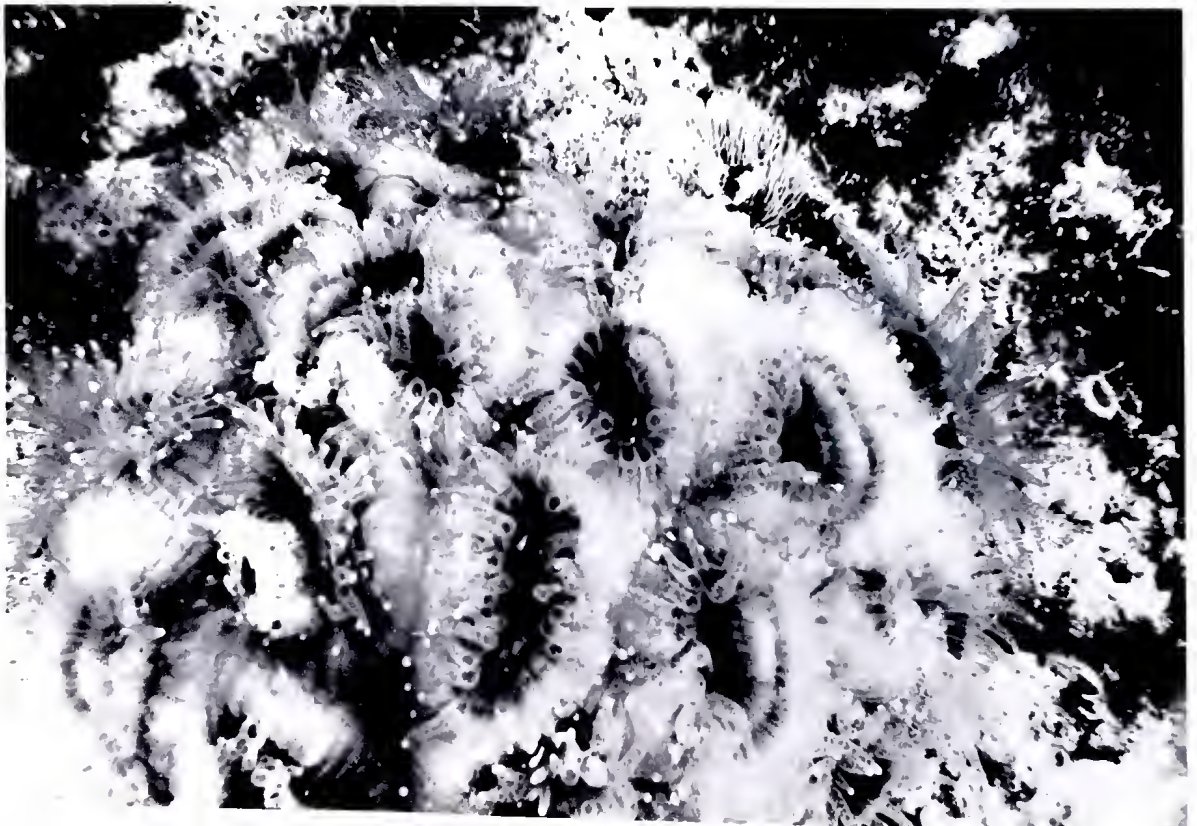
Favia eridani Umbgrove, 1940.

Plesiastrea ? valenciennesi (Edwards & Haime); Rosen (1968).

Material studied

Yorke Island, Murray Islands (3 specimens), **Sue Island, Thursday Island** (3 specimens), **Great Detached Reef** (2 specimens), **Jewell Reef** (3 specimens), **Yonge Reef** (3 specimens), **Lizard Island** (9 specimens), **Ribbon Reef, Hope Island** (3 specimens), **Low Isles, Palm Islands** (14 specimens), **Magnetic Island** (2 specimens), **Whitsunday Islands** (4 specimens), **Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex** (9 specimens), **Swain Reefs** (12 specimens), **Heron Island**.

Fig. 273 *Montastrea magnistellata*, *in situ* at the Palm Islands, with tentacles expanded at night ($\times 2.0$).



These localities include collecting stations 1, 5, 9, 13, 17, 27, 32, 33, 34, 36, 41, 45, 51, 54, 55, 57, 60, 65, 66, 68, 69, 70, 75, 76, 77, 79, 80, 85, 91, 96, 98, 99, 104, 105.

Previous records from Eastern Australia

Low Isles, (as *Favia valenciennesi*) Crossland (1952), Stephenson & Wells (1955); **Heron Island**, (as *Favia valenciennesi*) Salter (1954).

Characters

Colonies are usually massive, rounded or flattened, sometimes encrusting. Corallites are distinctly polygonal, usually hexagonal, 8-15mm in diameter (Figs. 276-281). Calice diameters are uniform in some colonies, very variable in others. Some colonies have an even, regular surface, while others have tightly interlocking, twisted calices giving a very convoluted appearance (Fig. 276).

Three orders of septa are usually present; sometimes six exsert primary septa can be distinguished from the others of the first order and occasionally a fourth order is present. First order septa are usually thickened over the theca and along their inner margins. They usually have well formed paliform lobes with vertical inner edges sometimes in two rows, and usually form a distinct crown. Second order septa may also be similarly thickened. They reach the columellae but do not form paliform lobes. The first two orders may be equally or subequally exsert; sometimes the first order septa are very thickened and very exsert. Third order septa usually extend approximately half the calice radius inwards, where they may fuse with second order septa. If a fourth order is present, it occurs only as a fine ridge, but has well formed corresponding costae. All septa are dentate, the dentations being large and conspicuous. The dentations and septa are always granulated. The columellae are usually small, compact and spongy; sometimes loosely trabecular (Fig. 278). Costae are prominently beaded, and are well developed in calices with well developed exotheca. Intercostal ridges are usually well formed.

This species is usually characterised by the presence of 'groove and tubercle' structures

Figs. 274, 275 *Montastrea valenciennesi*, showing the structural continuation between the 'groove and tubercle formation', the epitheca (Fig. 274) and the epithecal lining of a polychaete tube (Fig. 275) ($\times 8.0$).



Fig. 275▲

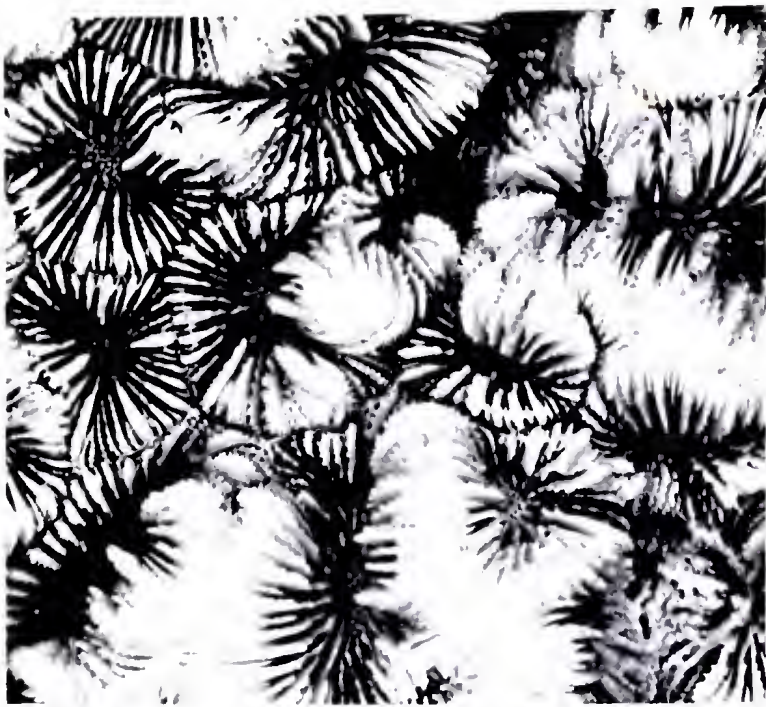


Fig. 276▲

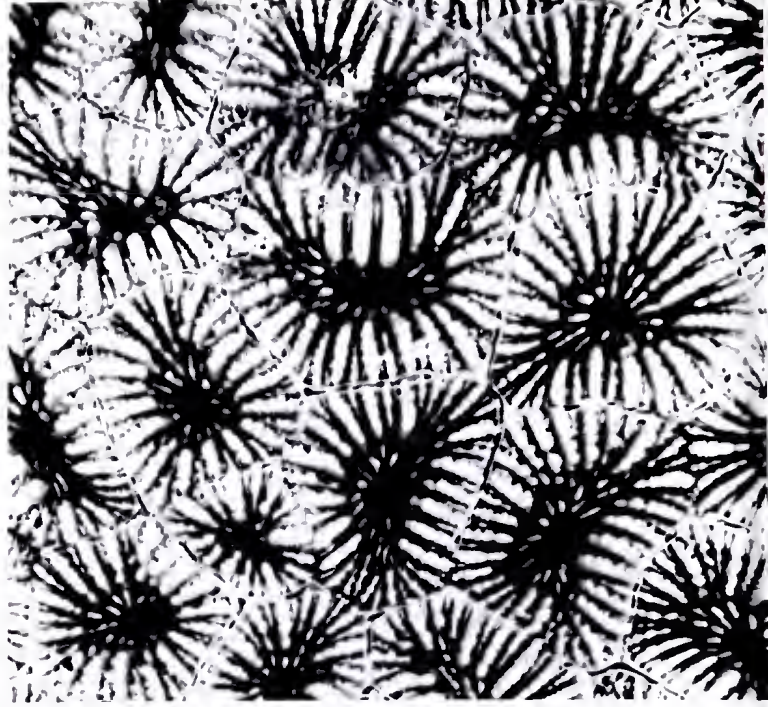


Fig. 277▲

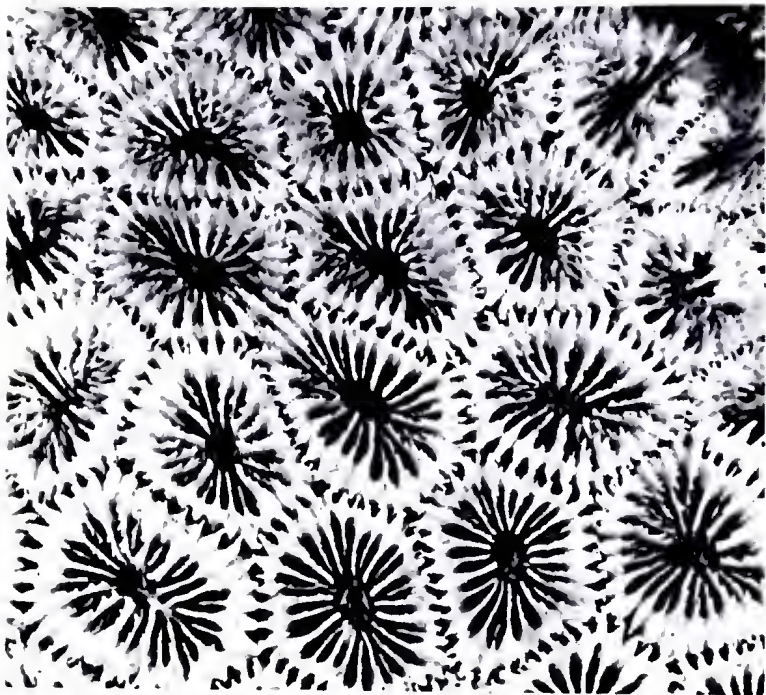


Fig. 278▲

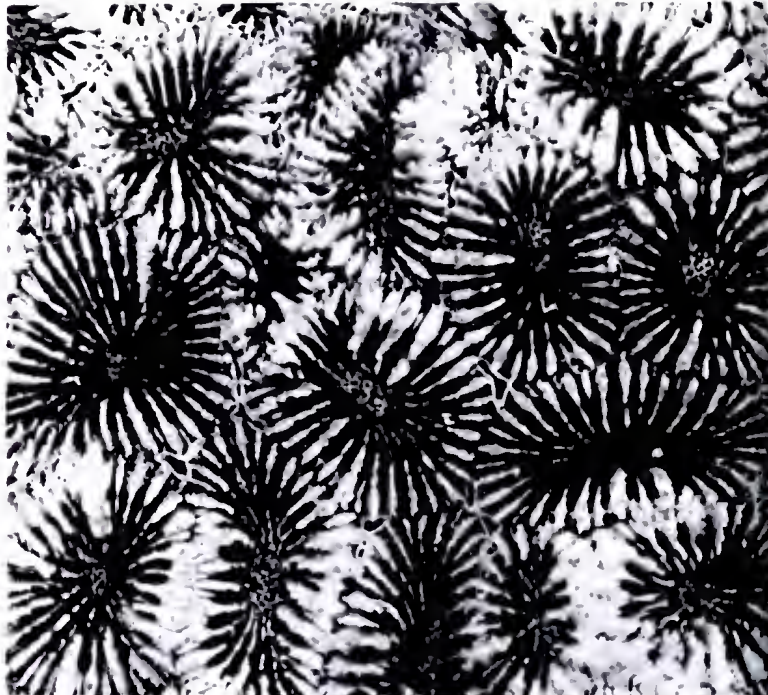


Fig. 279▲

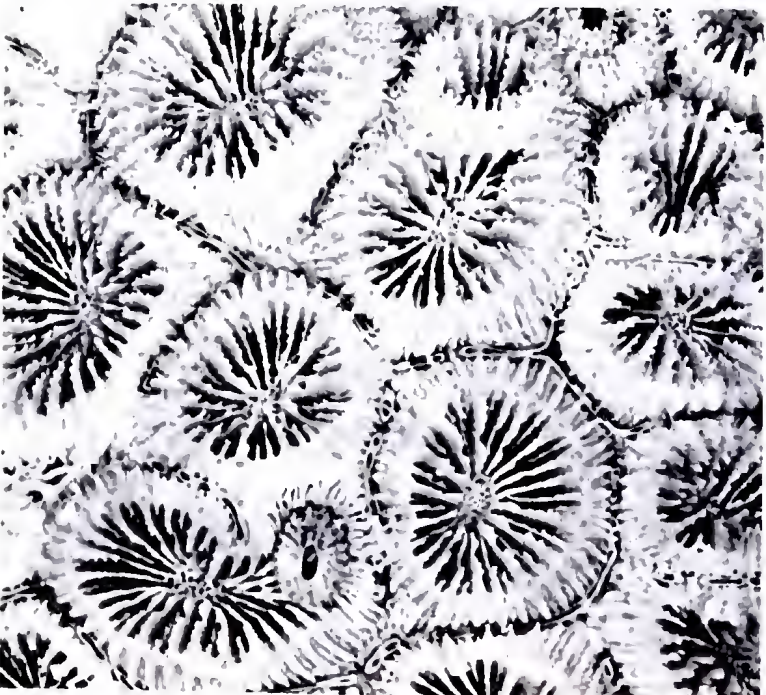


Fig. 280▲

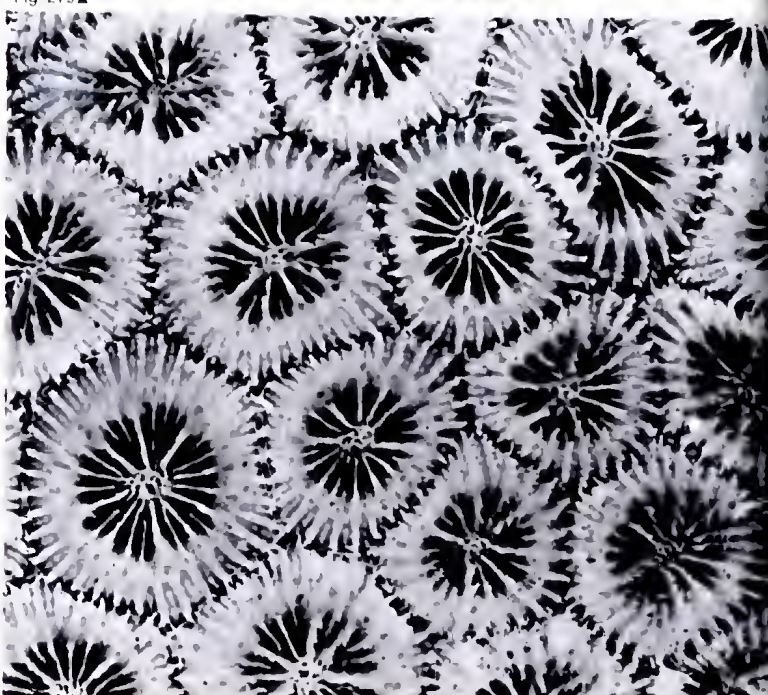


Fig. 281▲

which are interspersed between most calices. These structures consist of very thin walled tubes up to 0.5mm in diameter, which have circular or elongated openings at irregular intervals on their upper surfaces. They have calcareous walls identical to, and continuous with, the epitheca, which is normally visible as a fine lamina at the periphery of most colonies (Fig. 274).

These 'groove and tubercle' structures have been discussed in some detail in relation to this species by Rosen (1968) and Chevalier (1971), both of whom claimed that they have a primarily exothecal origin. Rosen suggested that primarily they develop directly from exothecal dissepiments, while Chevalier claimed that they develop from a fusion of costal dentations which are subsequently thickened by exothecal dissepiments. Thus, both authors considered that their origin is not associated with the epitheca. Rosen described them as 'pathologic' and Chevalier specifically suggested that they are a result of parasitism. Recent observations by Randall (in press), who found large numbers of polychaetes within them, confirm these suggestions.

Our observations indicate that these structures are epithelial in origin and, as well as being pathologic, appear partly to result from growth modes which are partly plocoid, partly phaceloid. This species, along with many others (e.g. *Blastomussa* species and *Leptastrea bottae*) frequently has deep divisions between its calices. In some specimens, these divisions are invaded by the epitheca, in others they are not. Thus, *L. bottae* has similar calice separations to this species (Figs. 300, 301) but without the 'groove and tubercle' formation of the epitheca. It should also be added that epithelial lamina frequently line the inside of large polychaete tubes and that these lamina are also continuous with the tubercles (Fig. 275).

As with other species of *Montastrea* the retracted polyps of living colonies are separated from each other by deep grooves in the coenosarc (Fig. 282). Colours are variable, most frequently greens and yellows, with the coenosarc and oral disc always being different (Fig. 465).

Skeletal variation

The wide variation in calicular structures in this species is best related to environmental influences by comparing coralla obtained from biotopes which are generally very favourable for rapid reef coral growth, and those obtained from turbid waters where calcification rates are low. The majority of coralla, however, come from biotopes within these extremes, both on a macro- and micro-environmental level.

Ecomorphs from biotopes with abundant coral growth (Figs. 276, 277, 280, 281).

Coralla obtained from shallow reef situations where the water is clear and illumination is maximal have relatively uniform skeletal characters. Degree of exposure to wave action appears to have little effect on growth form, although no specimens have been obtained from areas exposed to extreme wave action.

Coralla are massive and heavily calcified. Corallites are large, septa are thick and usually exsert. Paliform lobes are always well developed and form a well defined crown (Fig. 277). Extratentacular budding is dominant and in many colonies, exclusive.

Ecomorphs from deep or relatively turbid water (Figs. 278, 279).

Figs. 276-281 *Montastrea valenciennesi* ($\times 2.5$).

- Fig. 276 From Swain Reefs, collecting station 68, showing twisted, interlocking calices.
- Fig. 277 From Swain Reefs, collecting station 77, showing maximum development of the paliform lobes.
- Fig. 278 From Falcon Island, Palm Islands, collecting station 41, showing deep divisions between the corallites without superficial invasion of the epitheca.
- Fig. 279 From Lizard Island, collecting station 44, showing the variation in corallite size common to this species. Note the elongated septal dentations and the near absence of paliform lobes.
- Fig. 280 From Thursday Island, collecting station 54.
- Fig. 281 From Fantome Island, Palm Islands, collecting station 34, showing thickening of the thecae characteristic of coralla from shallow water.

Coralla obtained from deep water or from protected, turbid waters such as are normally found on the protected side of large high islands have skeletal characters which are essentially the reverse of the above and which appear to reflect low rates of calcification. Thus, coralla tend to be flat or encrusting. Calices are small with thin thecae, thin septa and little or no development of paliform lobes. The septa may sometimes be exsert, frequently very exsert in the first order. Both intra- and extratentacular budding are found, either being dominant in different coralla.

Living colonies (Figs. 282, 283, 465) are dark, pale or mottled but not brightly coloured.

Affinities

Previously accepted delineation of the Sub-families Faviinae Gregory, 1900 and Montastreinae Vaughan and Wells, 1943 is dependent on the dominant mode of budding. Thus, species of *Favia* have primarily intratentacular budding whilst budding in *Montastrea* is primarily extratentacular. *Montastrea valenciennesi*, however, does not clearly belong to either group. In their original description, Edwards & Haime (1848) said that budding was extratentacular; in 1857 they said it was intratentacular. Most subsequent authors (working from individual specimens or small series) have considered that intratentacular budding is dominant and that the species belongs to the genus *Favia*.

However, Duncan (1883) and Alloiteau (1957) have placed it in the genus *Phymastrea* and Rosen (1968) tentatively in the genus *Plesiastrea*, all on the basis that extratentacular bud-

Figs. 282, 283 *Montastrea valenciennesi*, from Bushy Island-Redbill Reef, collecting station 80, with polyps retracted by day (Fig. 282) and expanded by night (Fig. 283) ($\times 2.0$).



Fig. 282▲



Fig. 283▲

ding is dominant. Rosen and Chevalier (1971) discussed their differing conclusions in some detail.

In the present series, 35 colonies had dominantly extratentacular budding, 7 colonies dominantly intratentacular budding, and 10 had neither type discernibly dominant. Extratentacular budding was usually dominant in actively growing edges of colonies from exposed biotopes, or from highly convex growth surfaces, i.e. in situations of very active polyp divisions. Intratentacular budding occurred mostly on flat or concave surfaces and in coralla from protected biotopes, where the rate of calcification was evidently low.

Thus, mode of budding is a variable character in this species, which is provisionally placed in the genus *Montastrea* on the doubtful basis that extratentacular budding is usually more dominant than intratentacular budding. Rosen (1968) placed the species in genus *Plesiastrea* for similar reasons. In this study, the genus *Montastrea* is substituted for *Plesiastrea* following re-definition of these genera (p.4). However, it is emphasised that a taxonomic character as variable as this is not likely to have much phylogenetic significance and throws doubt on the validity of Sub-family Montastreinae.

Distribution

This species has been recorded from Madagascar and the Seychelles Islands, east to the Marshall Islands and New Hebrides.

GENUS *PLESIASTREA* EDWARDS & HAIME, 1848

Generic synonymy

Astraea (*pars*) Lamarck (1816).

Plesiastrea Edwards & Haime (1848).

Orbicella (*pars*) Vaughan (1907); Yabe, Sugiyama & Eguchi (1936).

Favia (*pars*) Matthai (1914).

Type species *Astraea versipora* Lamarck, 1816.

Characters of the genus

Coralla are sub-crioid to plocoid with round corallites produced by extra-tentacular budding. Like *Montastrea*, but corallites are smaller, with a better developed paliform crown composed of true pali.

Plesiastrea versipora (Lamarck, 1816)

Synonymy

Astraea versipora Lamarck, 1816; (*non* Dana, Whitelegge (1898); *non* Quelch (1886)).

Plesiastrea versipora (Lamarck); Edwards & Haime (1849, 1857); Crossland (1952); Wells (1954, 1955b); Stephenson & Wells (1955); Chevalier (1968, 1971); Eguchi (1968); Rosen (1971); Pillai & Scheer (1973); Scheer & Pillai (1974); Wijsman-Best (1977).

Plesiastrea urvillei Edwards & Haime, 1849; Edwards & Haime (1857); Tenison-Woods (1878); Quelch (1886); Folkson (1919).

Plesiastrea quatrefagiana Edwards & Haime, 1849; Edwards & Haime (as *P. quatrefagesana*) (1857); Brüggemann (1879a).

Plesiastrea peroni Edwards & Haime, 1857; Tenison-Woods (1878); Howchin (1924); Squires (1966).

Orbicella versipora (Lamarck); Gardiner (1899); Vaughan (1918); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1940).

Favia versipora (Lamarck); Matthai (1914, 1923, 1924); Gravely (1927).

Plesiastrea proximans Dennant, 1904.

Orbicella gravieri Vaughan, 1907; Vaughan (1918).

Favia ingolfi Crossland, 1931.

Plesiastrea salebrosa Nemenzo, 1959.

The genus *Plesiastrea* is represented on the Great Barrier Reef by a single species which has one of the widest geographic ranges along eastern Australia of any hermatypic coral. Wide morphological variation within this range has resulted in southern forms being considered as a separate species, *P. urvillei*, or, in the case of Dennant (1904), as *P. proximans*.

Material studied

Darnley Island (5 specimens), **Yorke Island** (2 specimens), **Murray Island** (2 specimens), **North West Reef** (2 specimens), **Thursday Island** (12 specimens), **Jewell Reef**, **Lizard Island** (9 specimens), plug reef south of **Ribbon Reef**, **Palm Islands** (15 specimens), **Whitsunday Islands** (5 specimens), **Bushy Island-Redbill Reef**, **Swain Reefs** (2 specimens), **St. Vincent's Gulf** (2 specimens).

These localities include collecting stations 13, 14, 28, 31, 32, 33, 34, 35, 53, 54, 61, 64, 69, 76, 78, 80, 90, 92, 97, 98.

Previous records from Eastern Australia

Low Isles, Stephenson *et al.* (1931), (as *Favia laxa*) Manton (1935), Crossland (1952), Stephenson & Wells (1955); **Heron Island**, Salter (1954); **Moreton Bay**, Wells (1955b); **Solitary Islands**, Veron *et al.* (1974); **Lord Howe Island**, Veron (1974); 20 localities south beyond Sydney, Wells (1955a); **Moreton Bay to St. Vincent's Gulf**, (as *P. urvillei*) Wells (1962), (as *P. urvillei*, *P. peroni* and *P. proximans*) Squires (1966); **St. Vincent's Gulf**, (as *P. proximans*) Dennant (1904), (as *P. urvillei*) Howchin (1909), (as *P. urvillei* and *P. peroni*) Howchin (1924); **Bass Strait**, (as *P. peroni*) Tenison-Woods (1878).

Characters

The present series shows clearly the continuity of variation of this species throughout eastern Australia and from one biotope to another. However, this variation is so great that, even among biotopes of similar latitude, the only truly diagnostic characters of the species are those which are diagnostic of the genus.

Colonies are massive or encrusting, sub-ceroid or plocoid. Corallites are round, approximately 2.5mm in diameter. Septa are in three orders, those of the first two sometimes being indistinguishable. First order septa are exsert to varying degrees and project inwards approximately two thirds of the calice radius. They have well developed pali which can have almost any form, varying from thick wedges to fine pinnacles. The pali always form well defined crowns around the columellae. Second order septa, if distinguishable, are similar to those of the first order except that they are smaller and may not have paliform lobes. Third order septa are much reduced; they do not have paliform lobes and do not reach the columellae. All septa and paliform lobes are granulated. The columellae are small, usually consisting only of a few pinnacles. First order costae are always present; those of other orders may be equal or absent. There are no intercostal ridges. The coenosteum may be smooth, or ornamented with granules. Budding is extratentacular.

Figs. 284-292 *Plesiastrea versipora* ($\times 5.0$).

Figs. 284, 285 From Thursday Island, collecting station 54.

Fig. 286 From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.

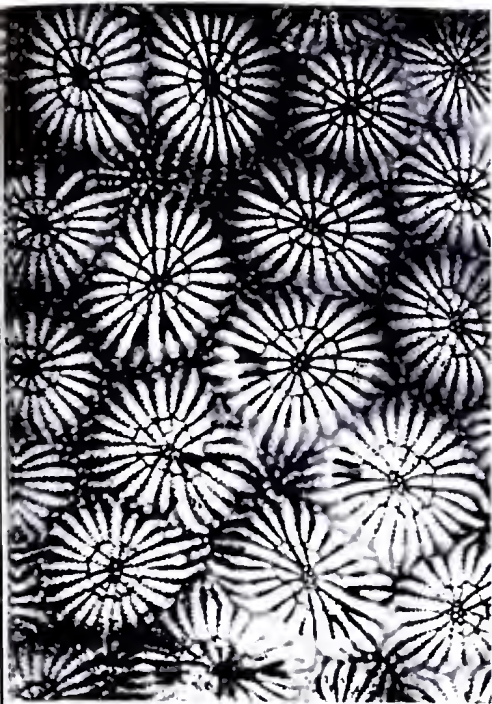
Figs. 287, 288 From St Vincent's Gulf, close to the holotype of *P. urvillei* Edwards & Haime.

Fig. 289 From Dewar Island, Murray Islands, collecting station 28.

Fig. 290 From Darnley Island, collecting station 31, close to the type of *P. quatrefagiana* Edwards & Haime and *Orbicella gravieri* Vaughan.

Fig. 291 From Bullumbooroo Bay, Palm Islands, collecting station 35.

Fig. 292 From Yorke Island, collecting station 13.



284A

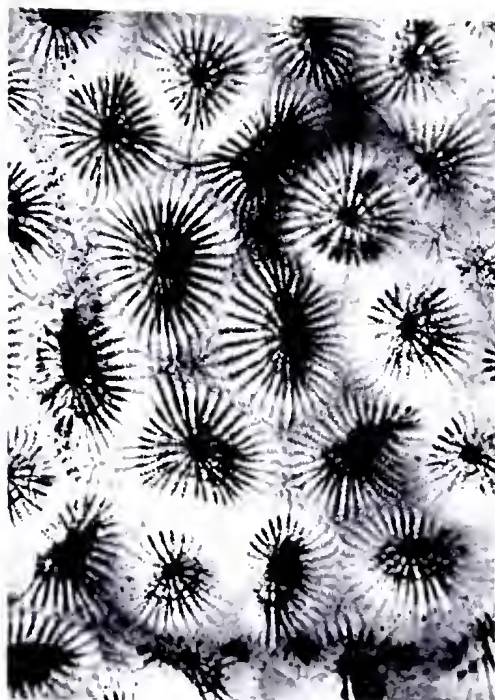


Fig. 285A

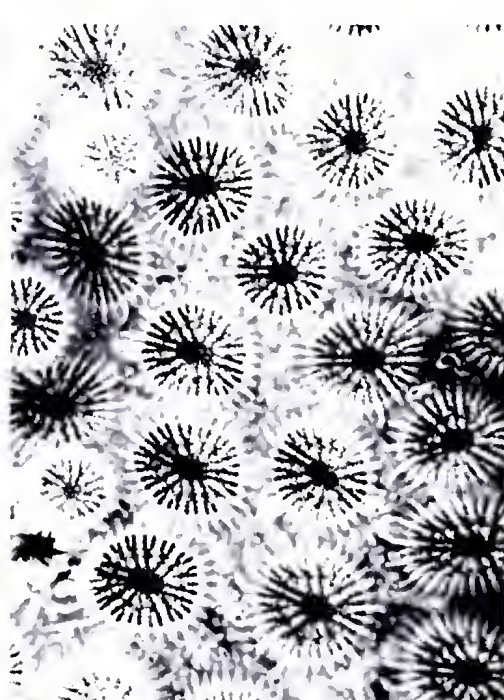
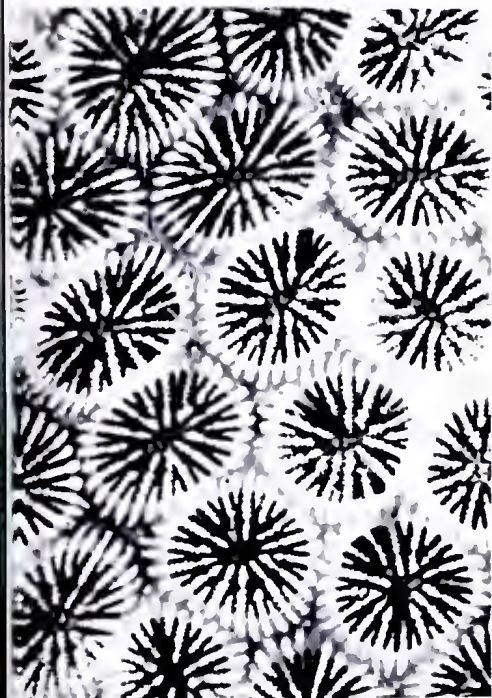


Fig. 286A



287A

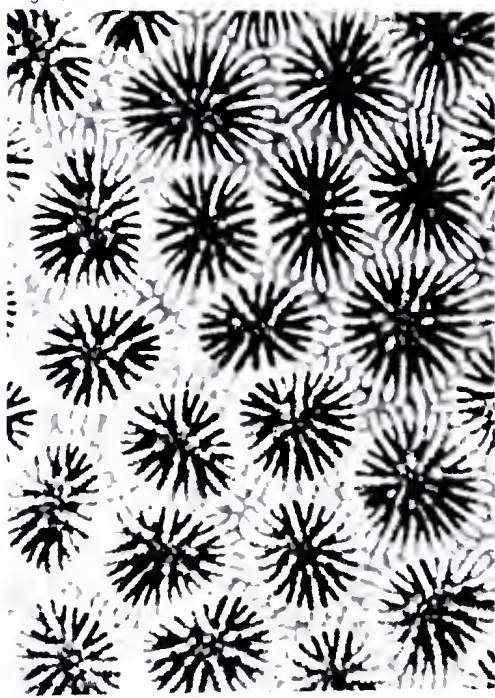


Fig. 288A

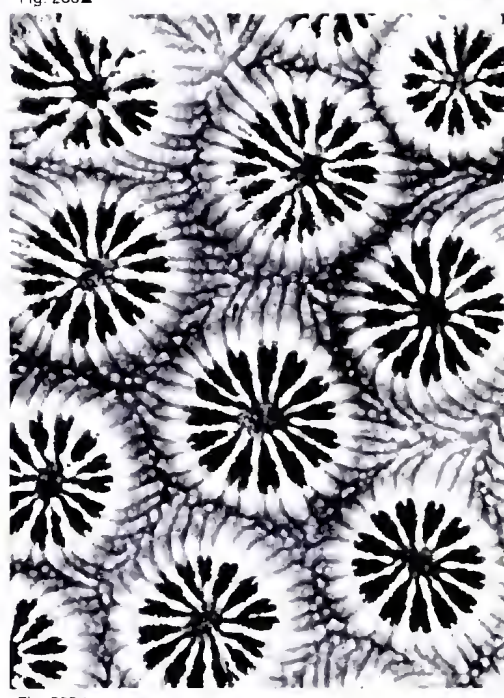


Fig. 289A



290A

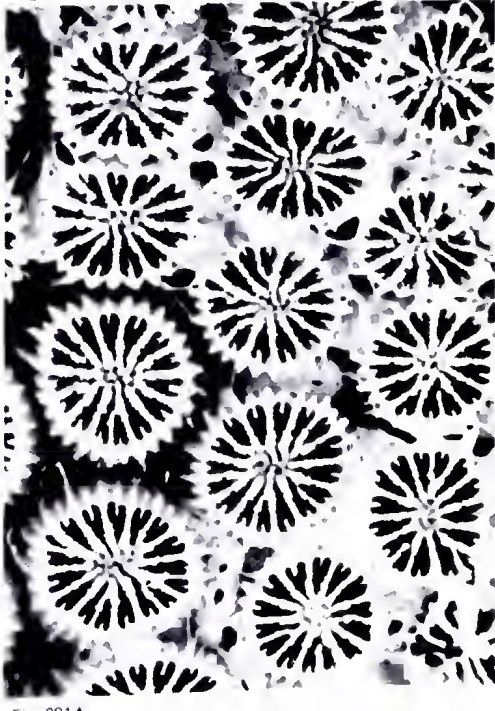


Fig. 291A



Fig. 292A

Living colonies are usually pale yellow, cream or brown in colour although they may be brightly coloured in exposed biotopes or far southern biotopes.

Skeletal variation

The above description applies to *P. versipora* from the vast majority of reef biotopes where coral growth is abundant. However, there are three ecomorphs:

Plesiastrea versipora from exposed biotopes (Figs. 284-286).

Colonies exposed to strong wave action, and to a lesser extent to strong currents, are massive and relatively dense. Corallites are frequently sub-ceroid and are often distorted into irregular shapes. Calices are shallow and densely packed with thick septa which have thick, wedge-shaped paliform lobes. Frequently there are two concentric circles of paliform lobes, both on the first order septa. Two orders of septa can be distinguished, both well developed and very granulated with granules of adjacent first order septa frequently forming a pseudosynapticular ring close to the columella. The columella is very dense and compact. The theca is thick and the exothecal dissepimental area reduced. The costae are thick, equal or subequal and beaded, the beads frequently being highly ornamented with transverse rows of granules.

Plesiastrea versipora from protected biotopes (Figs. 290-292).

Colonies from biotopes where light intensity is reduced but where water circulation is good and coral growth abundant usually show evidence of rapid growth, but low calcification rate. Coralla are usually massive and characteristically have a low density. They are primarily composed of very vesicular exothecal dissepiments. Like *Cyphastrea* species from similar biotopes, the corallites are set well apart and are relatively exsert. The theca is thin, the coenosteum is composed of smooth dissepimental blisters traversed by fine primary costae. All corallite structures are very granulated, adjacent septal granules frequently forming partial or complete pseudosynapticular rings.

Fig. 293 *Plesiastrea versipora*, *in situ*, at the Swain Reefs, showing the lobed growth form characteristic of shaded environments.

Fig. 294 *Plesiastrea versipora* at the Palm Islands with tentacles expanded at night ($\times 5.0$).

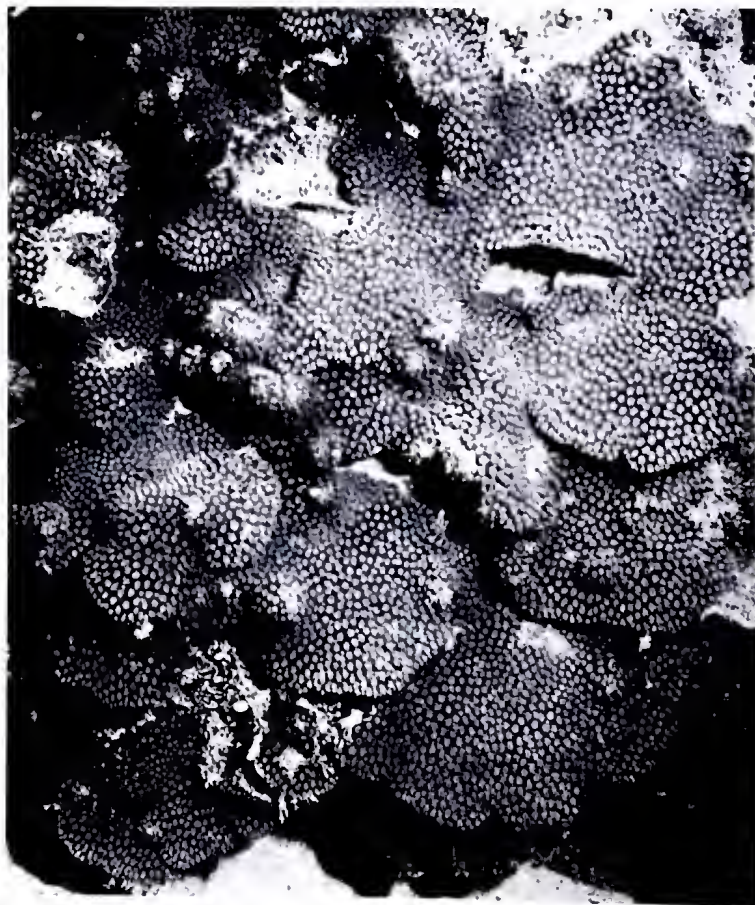


Fig. 293▲

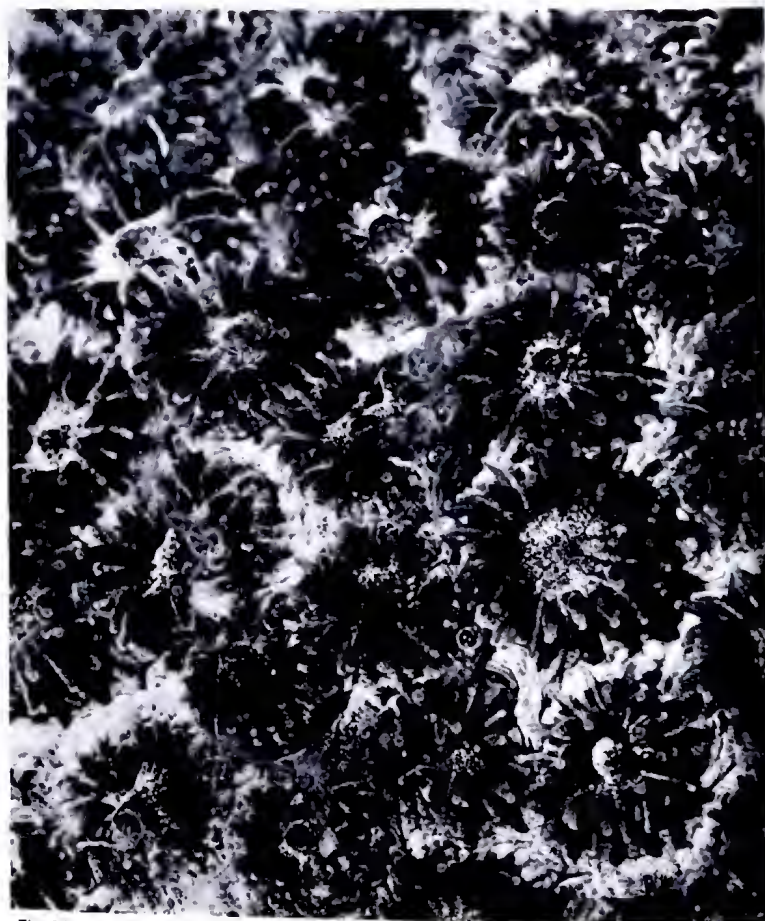


Fig. 294▲

Plesiastrea versipora ecomorph *urvillei* (Figs. 287, 288).

Coralla from far southern latitudes are usually encrusting. At the Solitary Islands, colonies are up to 1m across (Veron *et al.* 1974); Howchin (1909) records a single massive colony 3.1m long in St. Vincent's Gulf. Coralla are plocoid with corallites usually close together, and having characteristically thin thecae. The septa are thin; three orders are usually discernible. First order septa are moderately exsert, reach the columella and have paliform lobes. Some calices have a tendency towards hexamerous symmetry. Second order septa are those which do not reach the columella but which form a second, outer paliform crown. Third order septa are small, as with other ecomorphs. Costae are usually sub-equal. There is little exothecal ornamentation. The columella consists of a few pinnacles which are usually combined with the paliform lobes.

Distribution

Widely distributed throughout the tropical Indo-Pacific, from the Red Sea to the Marshall and Fiji Islands.

GENUS *DIPLOASTREA* MATTHAI, 1914

Generic synonymy

Astraea (*pars*) Lamarck, 1816 and others.

Diploastrea Matthai, 1914.

Type species *Astraea heliopora* Lamarck, 1816.

Characters of the genus (after Vaughan & Wells, 1943 and Wells, 1956).

Forms large plocoid colonies by extratentacular budding. Walls are mostly septothecate, but partially synapticulothecate and porous at the level of the calices. Septa are thick peripherally and thin internally. They are formed by compound trabeculae and have large dentations. The columella is well developed.

Diploastrea heliopora (Lamarck, 1816)

Synonymy

Astraea heliopora Lamarck, 1816.

Obicella heliopora (Lamarck) Gardiner (1899).

Diploastrea heliopora (Lamarck); Matthai (1914, 1924); Vaughan (1917, 1918); Hoffmeister (1925); Eguchi (1935, 1938); Yabe, Sugiyama & Eguchi (1936); Crossland (1952); Wells (1954); Searle (1956); Nemenzo (1962); Scheer (1964); Chevalier (1968); Pillai, Vine & Scheer (1973); Scheer & Pillai (1974).

Material studied

Murray Islands (2 specimens), **North West Reef, Bewick Island, Lizard Island, Hope Island** (2 specimens), **Low Isles, Palm Islands** (12 specimens).

These localities include collecting stations 14, 18, 26, 30, 34, 36, 37, 45, 55, 57, 60.

Previous records from Eastern Australia

Lizard Island, Stephenson *et al.* (1931); **Low Isles**, Crossland (1952); 5 localities south to 20° 20' S lat., Wells (1955a).

Characters

Crossland (1952) appropriately comments, 'This species is one of the few corals immediately recognisable, and which has been given this specific name by almost all authors. The numerous figures published show no striking variation: only the tothing of the septa may be more or less pronounced'.

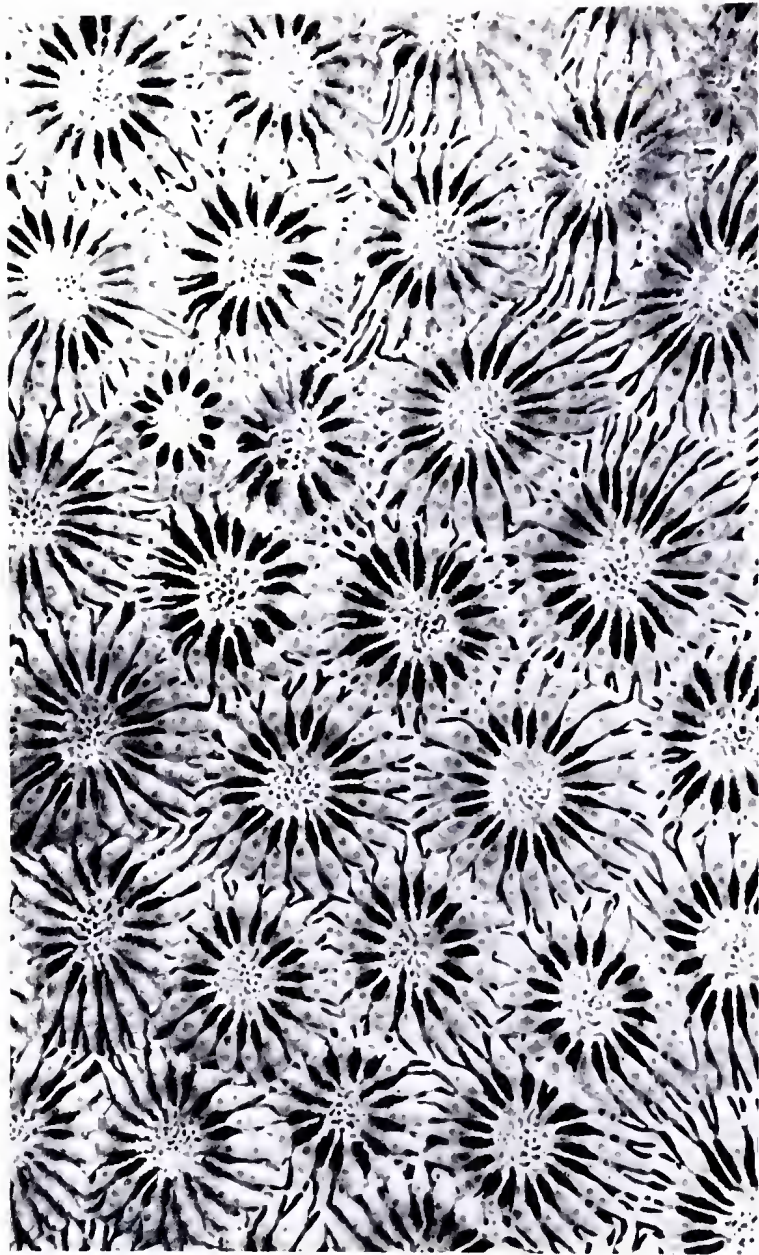


Fig. 295▲

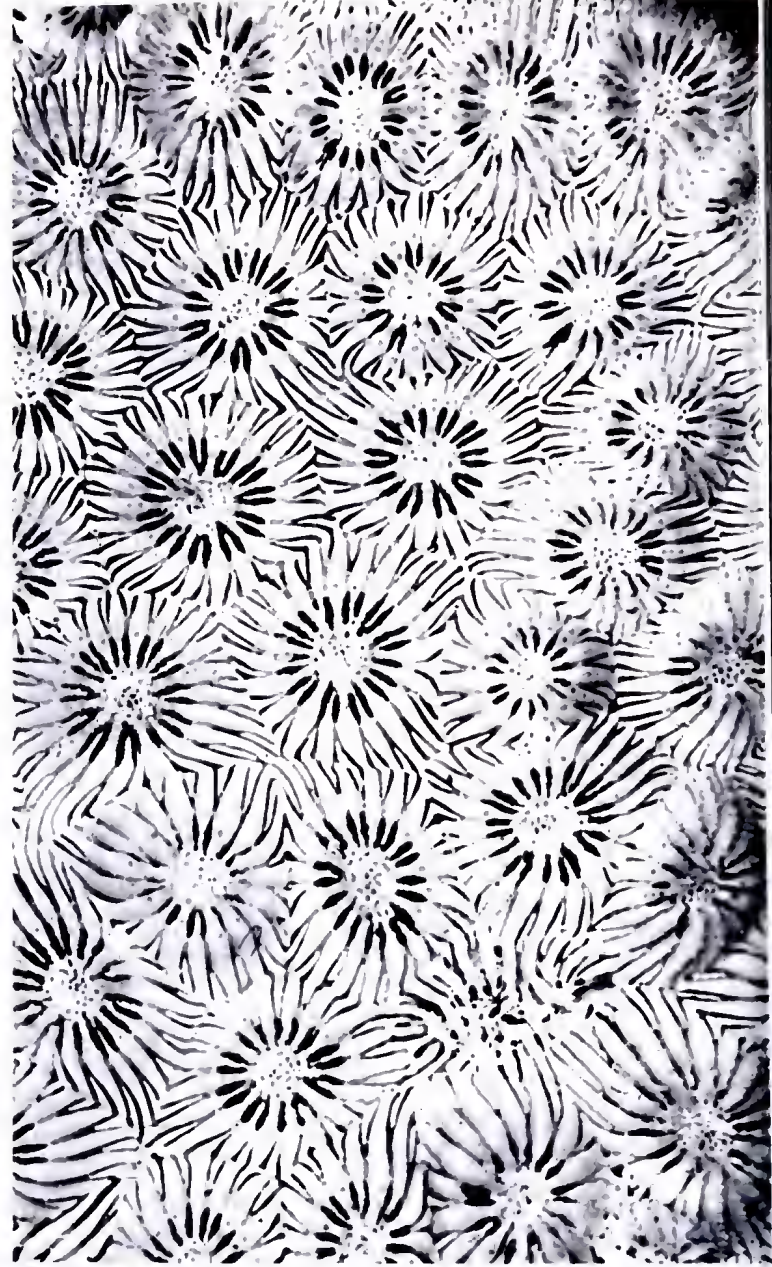


Fig. 296▲

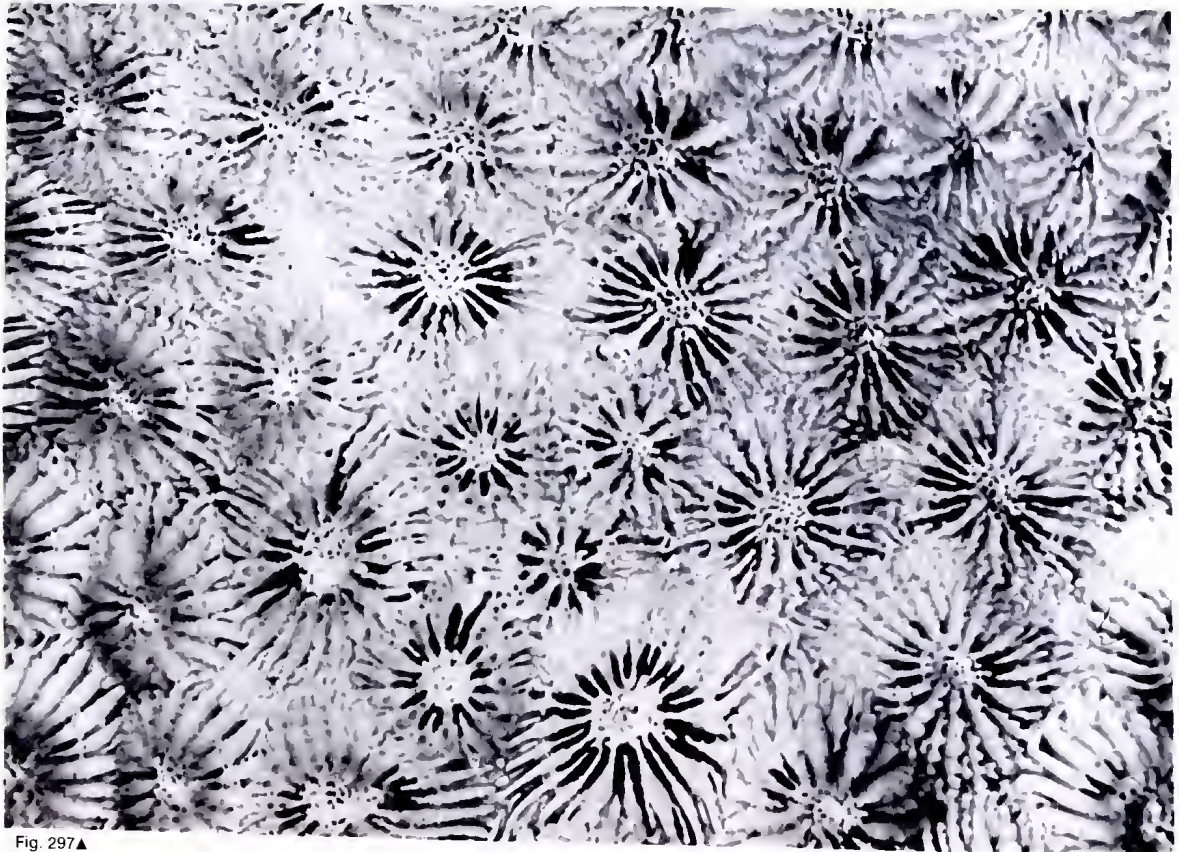


Fig. 297▲

Colonies are usually dome shaped and may be up to 2m high and 7m in diameter. They are characteristically symmetrical in shape, with a very uniform surface. The colour is a uniform pale cream and the skeleton is dense and very hard.

This species is much more abundant than has been indicated by previous authors. It occupies diverse habitats, ranging from the front of outer barrier reefs (exposed to extreme wave action) to protected sides of high islands. Large colonies are usually restricted to semi-protected and very protected localities; otherwise growth form variation is minimal throughout this range.

Distribution

Throughout the Indo-Pacific, from the Red Sea and Madagascar to Samoa.

GENUS *LEPTASTREA* EDWARDS & HAIME, 1848

Generic synonymy

Leptastrea Edwards & Haime, 1848.

Baryastrea Edwards & Haime, 1848.

Type species *Leptastrea roissyana* Edwards & Haime, 1848.

Characters of the genus

Leptastrea is similar to *Montastrea* but is distinguished from it by the absence or near absence of costae, by the presence of a columella usually consisting of vertical pinnacles and by, usually, inwardly projecting dentations on the septa.

Similarities between *Leptastrea* and species of *Montastrea* are mentioned above (p. 140).

Leptastrea cf. *bottae* (Edwards & Haime, 1849)

Synonymy

Cyphastrea bottae Edwards & Haime, 1849.

Leptastrea inaequalis Klunzinger, 1879; Gravier (1907, 1911) (as *Orbicella* (*Leptastrea*) *inaequalis*).

Leptastrea bottae Klunzinger, 1879; Ortmann (1888) (as *L. bottai*); Vaughan (1918); Faustino (1927); Crossland (1948, 1952); Wells (1950); Chevalier (1968); Rosen (1968); non Yabe, Sugiyama & Eguchi (1936); Nemenzo (1959).

Orbicella (*Leptastrea* (or *Leptastreaea*)) *bottae* Gardiner (1904); Vaughan (1907); Gravier (1911).

?*Leptastrea agassizi* Vaughan (1907).

?*Leptastrea hawaiiensis* Vaughan (1907).

Leptastrea solida Matthai (1914).

The holotype of the species (Figs. 298, 299) differs substantially from coralla of the present series and also from most other published accounts where the name *L. bottae* is used. Retention of the name for the present species is subject to further study and is therefore provisional only.

Figs. 295-297 *Diploastrea heliopora* ($\times 2.5$).

- Fig. 295 From Hope Island.
Fig. 296 From Wyer Island, Murray Islands, collecting station 30.
Fig. 297 From Maer Island, Murray Islands, collecting station 26.

The holotypes of *L. inaequalis* and *L. bottae* are more clearly synonymous. Relationships between *L. agassizi*, *L. hawaiiensis* and *L. bottae* are uncertain, the former two names being attributable to a single species of Hawaiian *Leptastrea* which differs substantially from Red Sea *L. bottae*.

Material studied

Murray Islands (2 specimens), reef between **Yule Reef** and **Triangle Reef**, **Great Detached Reef** (3 specimens), **Jewell Reef** (3 specimens), **Lizard Island** (3 specimens), **Bowl Reef**, **Palm Islands** (3 specimens), **Whitsunday Island**, **Swain Reefs** (2 specimens).

These localities include collecting stations 4, 5, 26, 27, 32, 33, 34, 35, 61, 77, 78, 97.

Previous records from Eastern Australia

Low Isles, (as *L. agassizi*) Yonge (1930), Crossland (1952).

Characters

Coralla are massive and plocoid. Calices on flat surfaces are mostly of uniform diameter (about 3mm), while those at the base of depressions are usually much smaller. Occasionally giant calices are present. Thecae are frequently higher on one side of calices, or row of calices than on the other.

The septa of an average sized calice are in three distinct cycles. The primary cycle is usually very exsert, much thicker than the others and reaches the columella. The secondary cycle is usually much less exsert and extends inwards approximately half the calice radius. The tertiary cycle is usually much smaller than the second and frequently appears as a thin ridge only. Giant calices may have an irregularly developed fourth cycle; some calices have

Figs. 298, 299 Holotype of *Leptastrea bottae*, Fig. 298 ($\times 1$), Fig. 299 ($\times 5.0$).

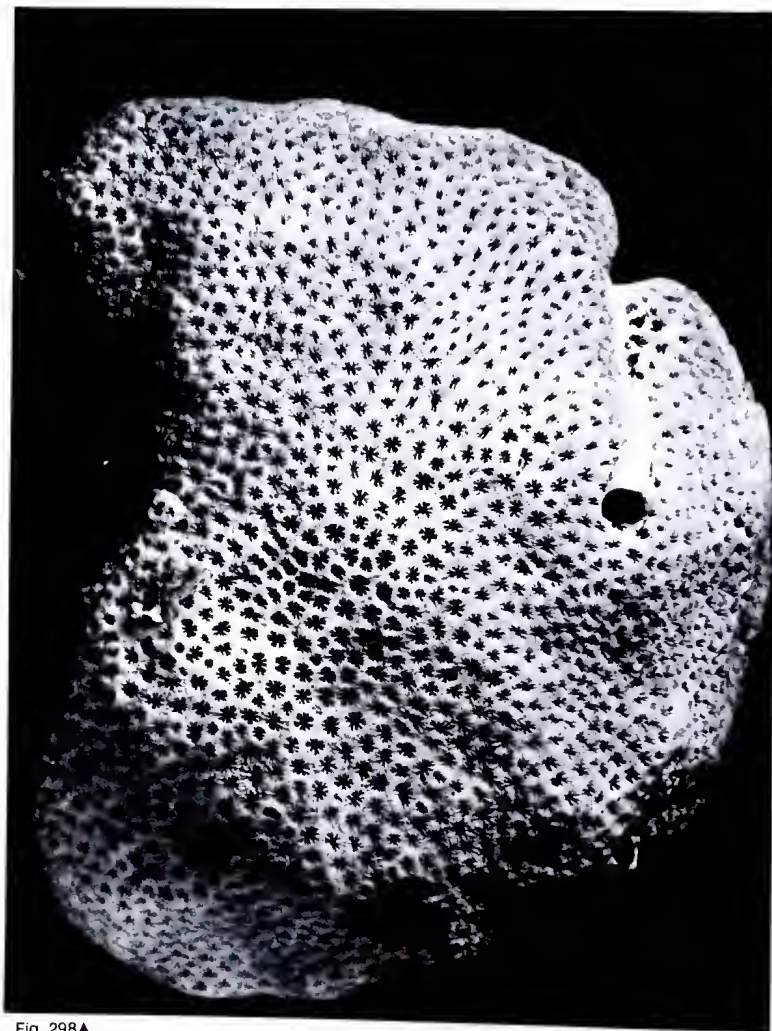


Fig. 298▲

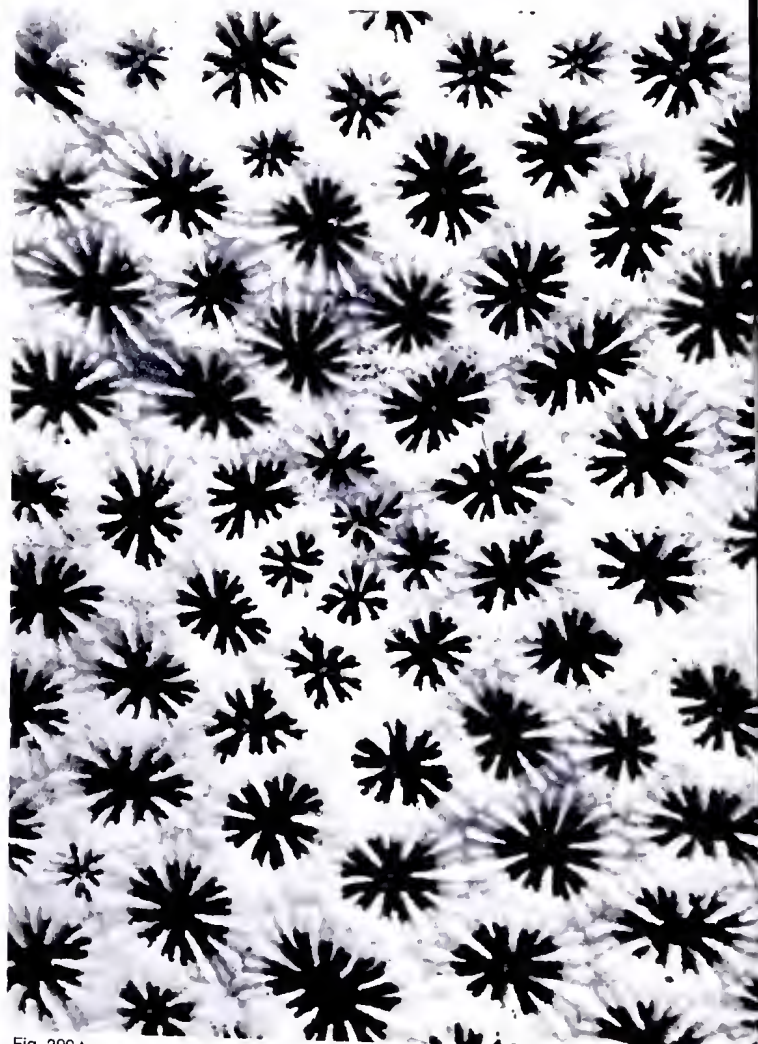


Fig. 299▲

only two cycles. Primary, and sometimes secondary cycle septa may have well developed paliform lobes which are irregular in appearance and are intermixed with, and hardly distinguishable from, the one or more pinnacles of the columellae. The columellae, paliform lobes and septa are all covered with granules. All septa are greatly thickened above the thecae. Costae are usually absent, the coenosteum usually being smooth or finely granulated. In all the specimens of the present series the coenosteum is penetrated by a network of intercalicular grooves and holes, analogous to the 'groove and tubercle' formations of e.g. *Montastrea valenciennesi* (p. 147), without the invasion of the epitheca. Much of the difference between the present series and the holotype of the species is attributable to the absence of these grooves in the latter corallum.

Living colonies are pale cream or yellow with black centres (Fig. 466). They are readily recognisable underwater (hence are much more abundant than is suggested by the number of specimens collected). They frequently occur as coralloliths on sandy reef flats. This species also occurs in a wide variety of biotopes ranging from the front of barrier reefs to protected fringing reefs. There is very little morphological variation over this range.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to Hawaii.

Figs. 300, 301 *Leptastrea* cf. *bottae* from near Yule Entrance, Fig. 300 ($\times 1$), Fig. 301 ($\times 5.0$).

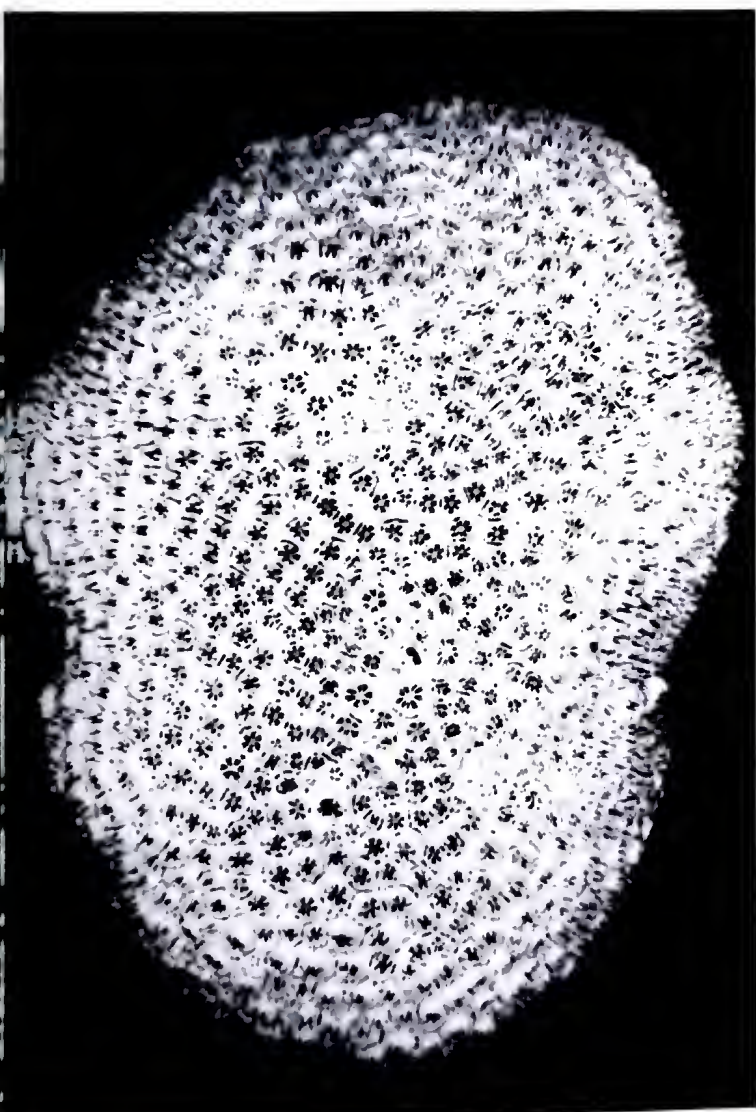


Fig. 301 ▲

Leptastrea purpurea (Dana, 1846)

Synonymy

Astraea purpurea Dana, 1846.

Leptastrea purpurea (Dana); Hoffmeister (1925, 1929); Faustino (1927); Yabe & Sugiyama (1932, 1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Crossland (1948, 1952); Stephenson & Wells (1955); Chevalier (1968, 1975).

Leptastrea ehrenbergana Edwards & Haime, 1849; Edwards & Haime (1857); Quelch (1886); Ortmann (1888); Gardiner (1904) (as *Orbicella (Leptastrea) ehrenbergana*); Crossland (1931, 1952); Chevalier (1968).

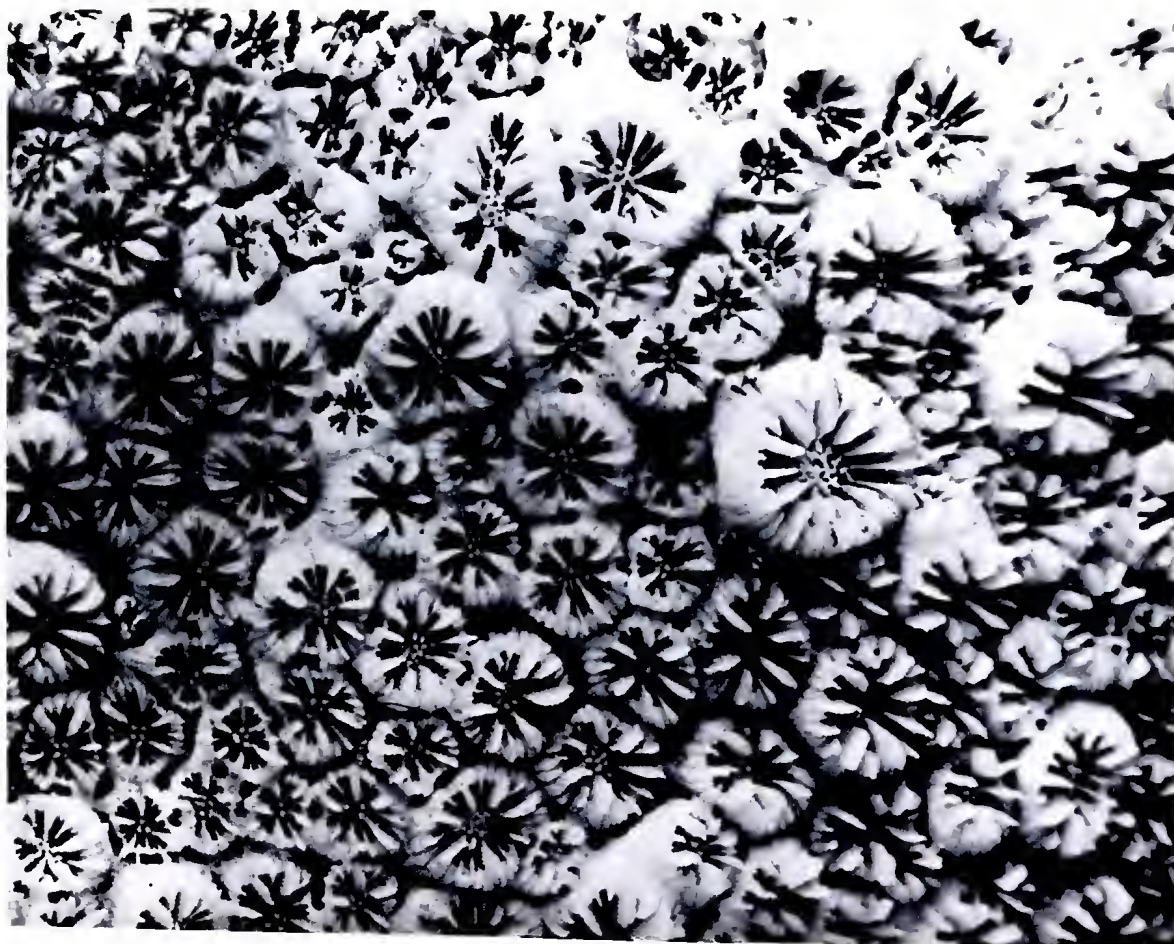
Leptastrea roissyana Edwards & Haime, 1848; Quelch (1886); Matthai (1914, 1923, 1924); Gravely (1927); Crossland (1931); Rosen (1971).

Prionastrea purpurea Edwards & Haime, 1857.

Leptastrea stellulata Verrill, 1867; Studer (1901).

The complex synonymy of this widespread and common species is a direct result of the wide variation in the structure of its calices. The number of nominal species into which it has been divided has been progressively decreased in synonymies of recent authors, although its full range of variation appears to have been recognised in the early work of Vaughan (1918). Indeed, Vaughan considered that 'it is within the range of possibilities that *L. purpurea* and *L. transversa* are variants of one species'. The difficulty of separating these two species was remarked by Scheer & Pillai (1974) and proved to be a problem in the present study, where it was found necessary to make large collections of *Leptastrea* from within uniform biotopes before reliable taxonomic characters for separating them could be determined.

Fig. 302 Variation in calice structure in *Leptastrea* cf. *bottae* from Jewell Reef, collecting station 61 ($\times 5.0$).



The specimens of the present study represent all manner of variations that occur between these two species and the other nominal species which are included in the synonymy. This synonymy is still, however, likely to be incomplete.

Material studied

Yorke Island, Murray Islands (4 specimens), **Sue Island**, reef south of **Yule Entrance**, reef between **Yule Reef** and **Triangle Reef**, **Thursday Island** (2 specimens), **Tijou Reef** (2 specimens), **Bewick Island, Houghton Island, Yonge Reef, Lizard Island** (8 specimens), **Three Isles** (2 specimens), **Hope Island, Low Isles**, (2 specimens), **Palm Islands** (35 specimens), **Magnetic Island** (3 specimens), **Whitsunday Islands** (13 specimens), **Bushy Island-Redbill Reef** (5 specimens), **Pompey Complex, Swain Reefs** (17 specimens).

These localities include collecting stations 2, 7, 9, 12, 13, 17, 18, 29, 30, 32, 33, 34, 35, 36, 37, 40, 41, 42, 43, 54, 55, 56, 57, 58, 60, 67, 69, 75, 77, 79, 80, 81, 84, 85, 86, 90, 91, 93, 96, 97, 98, 99, 100.

Previous records from Eastern Australia

Murray Islands, Mayor (1918), Vaughan (1918); **Low Isles**, (as *Leptastrea*) Stephenson *et al.* (1931), (as *L. roissyana* and *L. ehrenbergana*) Manton (1935), (as *L. purpurea* and *L. ehrenbergana*) Crossland (1952), Stephenson & Wells (1955); **Heron Island**, Salter (1954).

Figs. 303, 304 Holotype of *Leptastrea purpurea*, Fig. 303 ($\times 1.0$), Fig. 304 ($\times 5.0$).

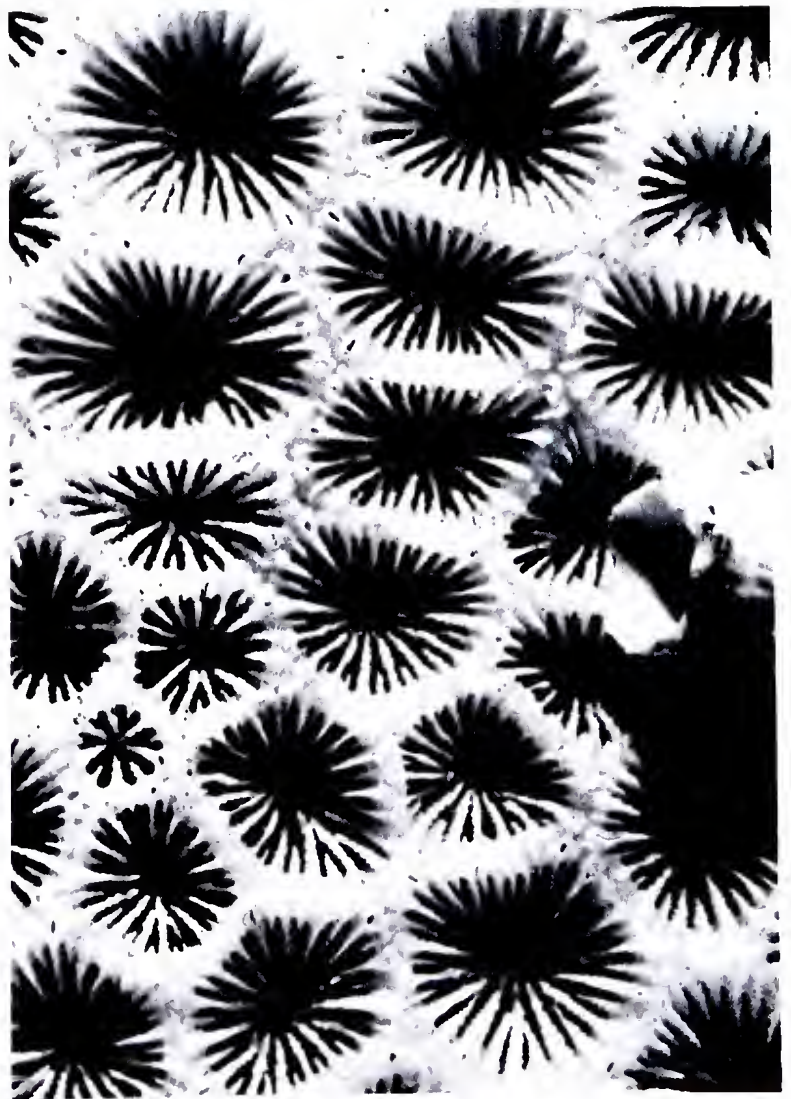


Fig. 304▲

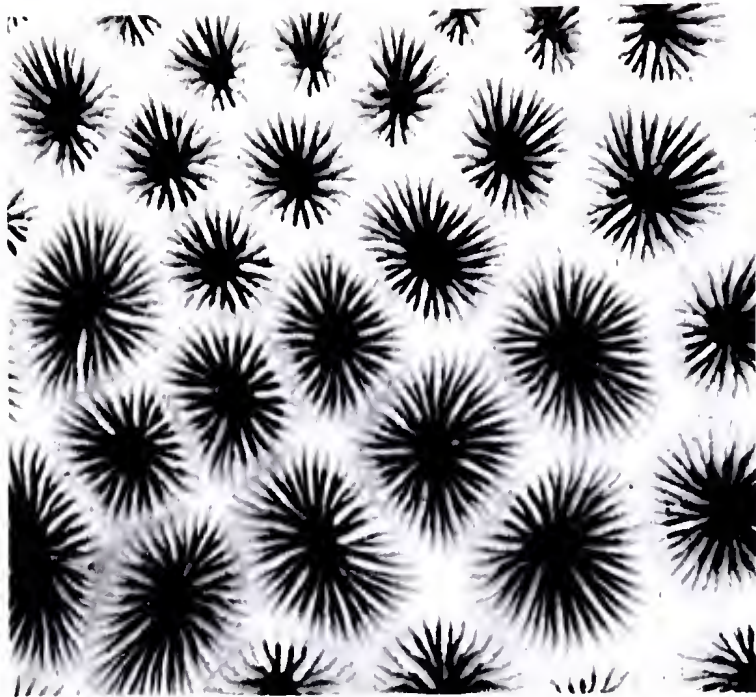


Fig 305▲



Fig 306▲

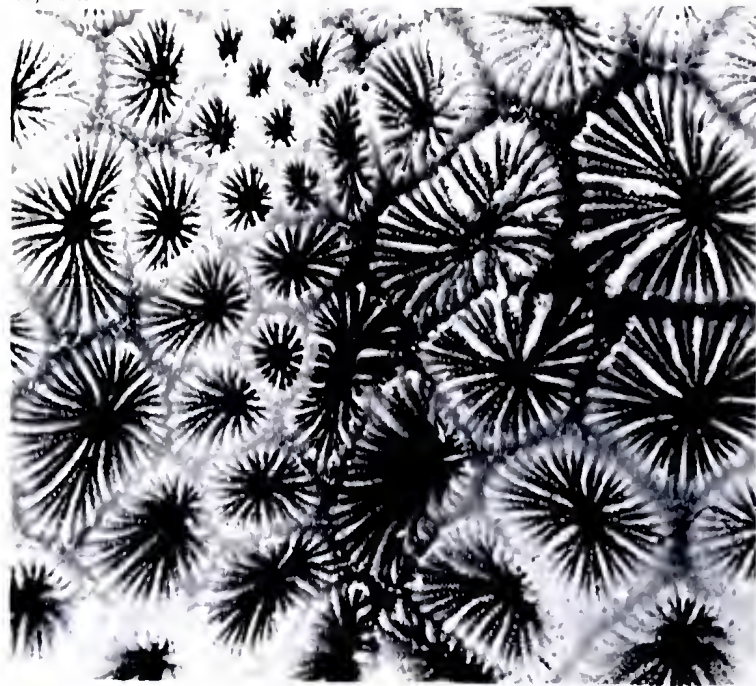


Fig 307▲

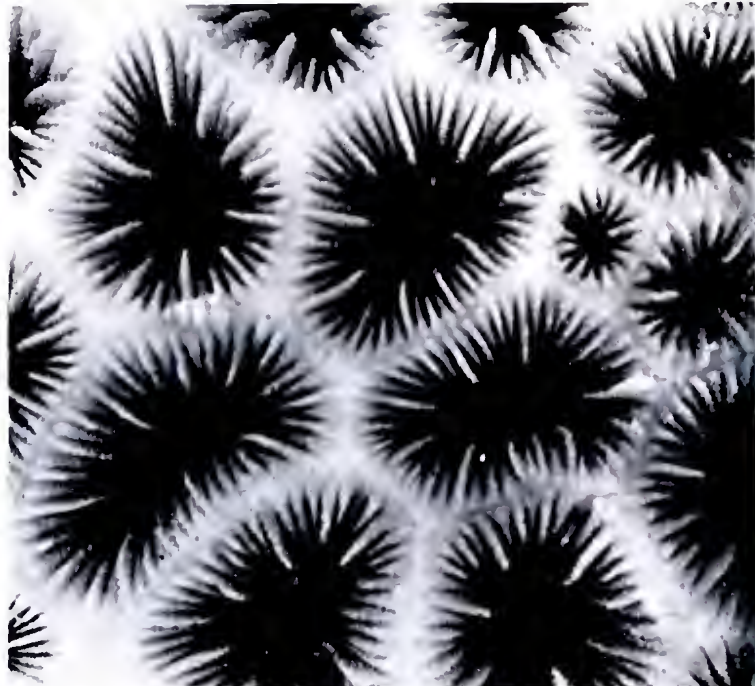


Fig 308▲

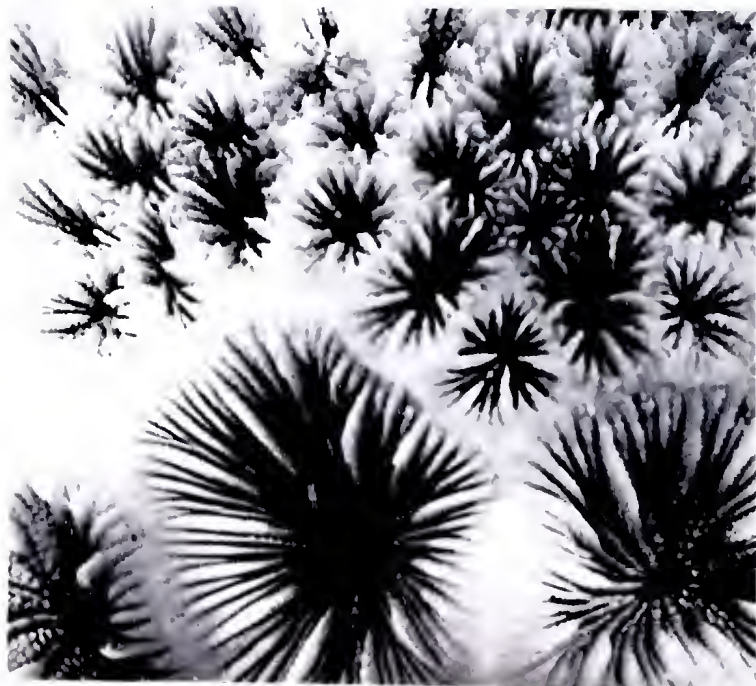


Fig 309▲



Fig 310▲

Characters

Colonies are irregular, encrusting or massive and range in size up to about 1m in diameter. They frequently occur as coralliths up to 15cm across. Colonies are sub-ceroid. Corallites are always discrete and polygonal and are characteristically variable in size (2-11mm in diameter), smaller calices usually occurring in clusters at the base of depressions or around worm or gastropod holes etc. Variations in septal arrangements are illustrated in Figs. 305-310. Four incomplete cycles may be present; those of higher orders frequently fuse with lower ones or else extend only a short distance towards the columella. Different cycles of septa may be quite distinct or impossible to distinguish. As with *L. cf. bottae*, the septa (especially of the primary or secondary cycles) are usually exsert. They may be smooth edged but are usually dentate, the dentations increasing in size toward the calice centre, where they may form inwardly sloping paliform lobes. Their edges are straight or gently curved and usually slope gently towards the columellae. Their sides are usually conspicuously granulated, the granules sometimes being arranged along synapticular rows. There is no apparent correlation between any of these septal characteristics, and they have little association with environmental factors (see below). The columellae are usually similar to those of *L. cf. bottae* in consisting of a few pinnacles intermixed with paliform lobes. Larger calices frequently have prominent columellae of many pinnacles. As with *L. cf. bottae*, the columellae and septa are covered with fine granules. The septa are seldom thickened above the thecae. Costae are usually poorly developed; the coenosteum between adjacent corallites is usually a narrow, smooth strip overshadowed by the exsert septa. If present, the costae are granulated. The thickness of the exotheca is very variable, colonies from very exposed biotopes having thecae which are almost one calice diameter thick. The exotheca is compact; the endotheca is poorly developed. All budding is extratentacular.

Living colonies are usually pale yellow or cream on their upper surface with dark calices. The sides of colonies are usually uniformly dark, although the undersurfaces of coralliths are bleached.

Skeletal variation

Much of the growth form variation of this species is due to its encrusting habit. This variation is reflected in the size and structure of the calices, which may alter enormously between concave, flat and convex growth surfaces. Thus, much of the variation within the species occurs within a single corallum.

Leptastrea purpurea from protected biotopes (Figs. 305-307).

Colonies growing in minimal conditions for the species, especially in turbid water where light penetration is poor, are usually thin and encrusting. Calicular structures tend to be *L. pruinosa*-like, hence the likelihood of confusion in coralla from these biotopes. Inter-calicular grooves are usually well developed and the costae are correspondingly reduced. Septa are usually moderately exsert.

Leptastrea purpurea from exposed biotopes (Figs. 308-310).

Colonies are usually massive. Figs. 308-310 illustrate the range of calice structures normally associated with this species in most exposed reef biotopes. Much of this variation is commonly found within single, large coralla, and even the differences between adjacent calices illustrated in Fig. 309 are not unusual.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to Hawaii.

Figs. 305-310 *Leptastrea purpurea* ($\times 5.0$).

- Fig. 305 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.
Figs. 306, 307 From the Palm Islands.
Figs. 308, 309 From Swain Reefs, collecting station 79.
Fig. 310 From Bushy Island-Redbill Reef, collecting station 80.

Leptastrea transversa Klunzinger, 1879

Synonymy

Leptastrea transversa Klunzinger, 1879; Quelch (1886); Ortmann (1888); Whitelegge (1898); Vaughan (1918); Crossland (1952); Stephenson & Wells (1955); Scheer (1964); Chevalier (1968, 1975); Scheer & Pillai (1974).

As previously noted, *L. transversa* is very similar to *L. purpurea*. Living colonies have the same growth form and similar colour variations. However, series of specimens collected from within one biotope are separable into the two species groups. Even in large, diverse collections they can still be separated on the basis of columella structure and structure of the septa.

Material studied

Murray Islands, reef between **Yule Reef** and **Triangle Reef**, **Houghton Island** (4 specimens), **Jewell Reef**, **Three Isles**, **Hope Island** (2 specimens), **Palm Islands** (9 specimens), **Magnetic Island**, **Whitsunday Islands** (9 specimens), **Bushy Island-**

Figs. 311, 312 Holotype of *Leptastrea transversa*, Fig. 311 ($\times 0.5$), Fig. 312 ($\times 5.0$).

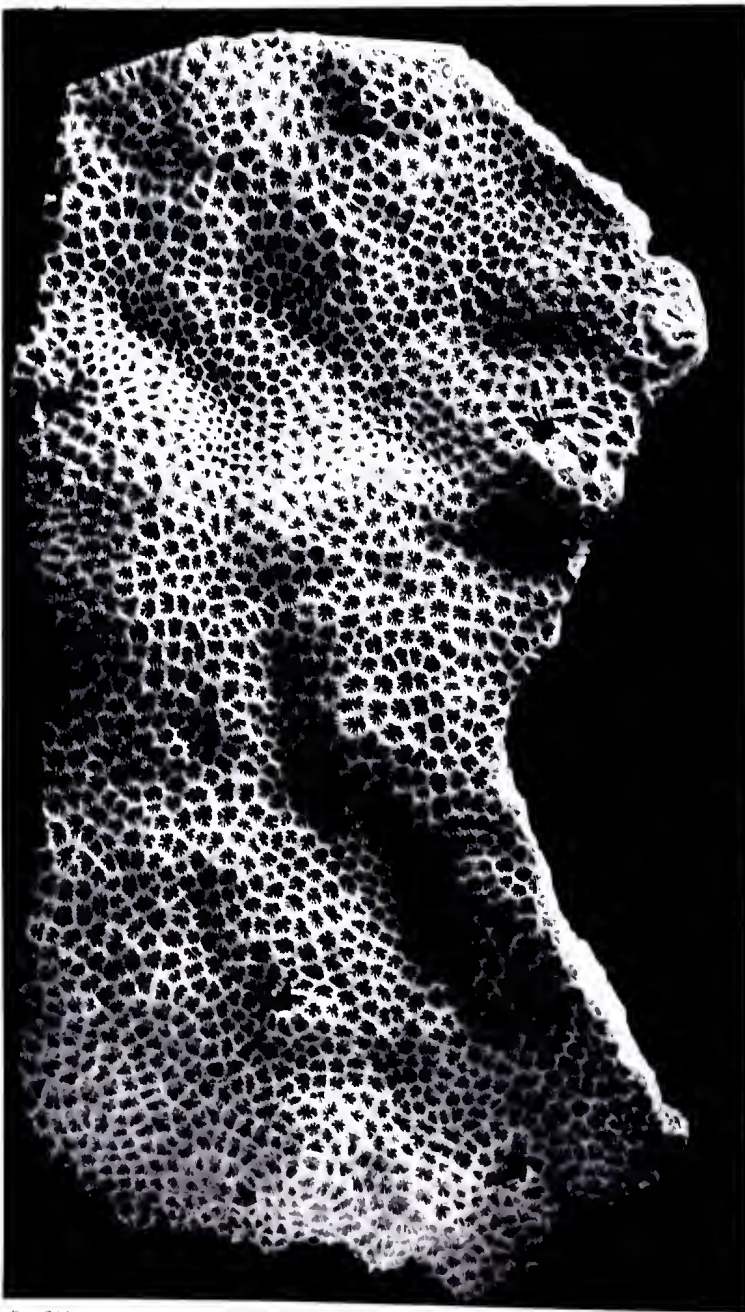


Fig. 311▲



Fig. 312▲

Redbill Reef, Pompey Complex (2 specimens), **Swain Reefs** (10 specimens).

These localities include collecting stations 35, 40, 43, 45, 55, 60, 61, 69, 70, 79, 80, 81, 96, 97, 98, 102, 103.

Previous records from Eastern Australia

Low Isles, Crossland (1952), Stephenson & Wells (1955).

Characters

Colonies are either massive or encrusting. Calices are polygonal, 2-9mm in diameter. They show much less size variation than do those of *L. purpurea*. The septa are characteristically deeply plunging; usually they extend inwards approximately two-thirds of the calice radius before descending vertically or near vertically. The septa are usually strongly dentate near the base of the calice. Up to four orders may be present, very occasionally a fifth. In most coralla, the first two orders are indistinct; they are slightly exsert and sometimes thickened. The first, or more often both, orders reach the columellae. In some coralla where the second order does not reach the columellae, they become thickened on the inner margin, sometimes appearing arrow-shaped as in *Cyphastrea* species. Second order septa are sometimes fused with those of the first order, deep within the calice. The structure of the columella is closer to *L. bewickensis* than *L. purpurea*. The paliform dentations become vertical towards the calice centre where they fuse with each other to form a compact, elongated base, supporting a series of papillae. As with *L. bewickensis*, these papillae are usually aligned lengthwise along the columellae. The columellae sometimes have a more spongy, trabecular nature. Both the septa and columellae are granulated.

The wall, peritheca, costae and intercalicular groove are mostly similar to those of *L. purpurea*. In some colonies, or parts of colonies the intercalicular groove is absent, the septa sometimes being adjoined, sometimes alternate. Budding is always extratentacular. Colonies are usually pale cream, green or yellow, with grey calices (Fig. 468).

Skeletal variation

As with *L. purpurea*, colonies from exposed reef biotopes tend to be mostly massive, those from very protected or turbid biotopes tend to be encrusting. Massive growth forms are associated with a high degree of calcification, especially thickening of the walls, creating small, well separated calices. Such thickening frequently occurs on the sides of rapidly growing colonies whose tops have thin walls and small, frequently dividing corallites.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to Tahiti.

Leptastrea pruinosa Crossland, 1952

Synonymy

Leptastrea pruinosa Crossland, 1952.

Leptastrea cf. *pruinosa* (Crossland); Chevalier (1975).

The type (and only) specimen of this species described by Crossland is 'minute . . . it consists of 6 full-sized calices and 6 small, forming a crust 15mm x 7mm'.

Material studied

Jewell Reef (2 specimens), **Lizard Island** (8 specimens), **MacGillivray Reef** (3 specimens), **Palm Islands** (4 specimens), **Whitsunday Islands** (4 specimens).

These localities include collecting stations 32, 61, 74, 90, 97, 98.

Previous records from Eastern Australia

?**Lizard Island**, Crossland (1952).

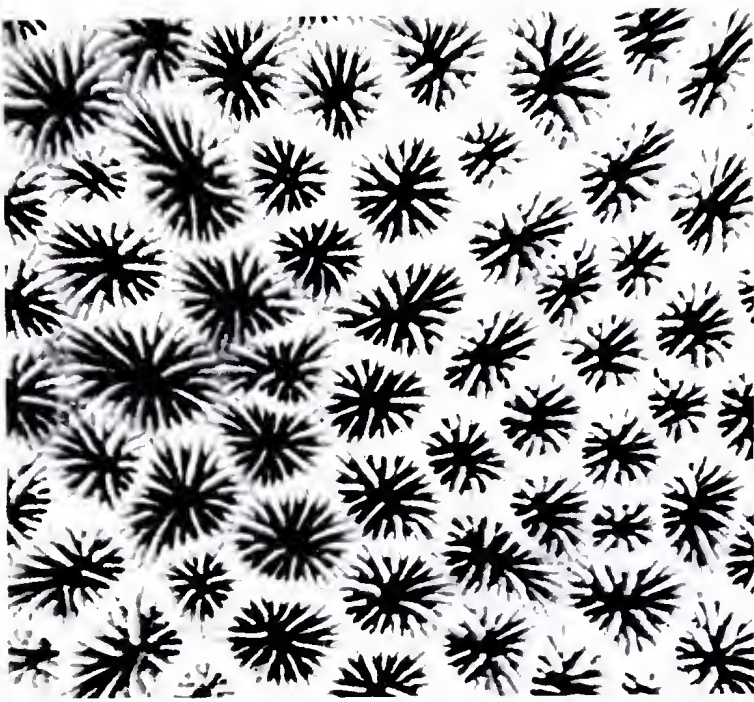


Fig. 313A

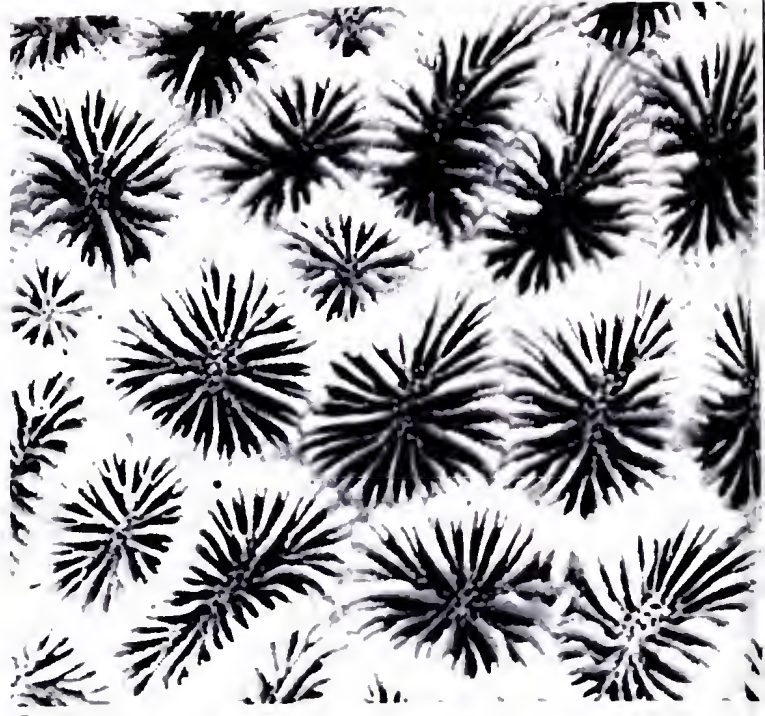


Fig. 314A

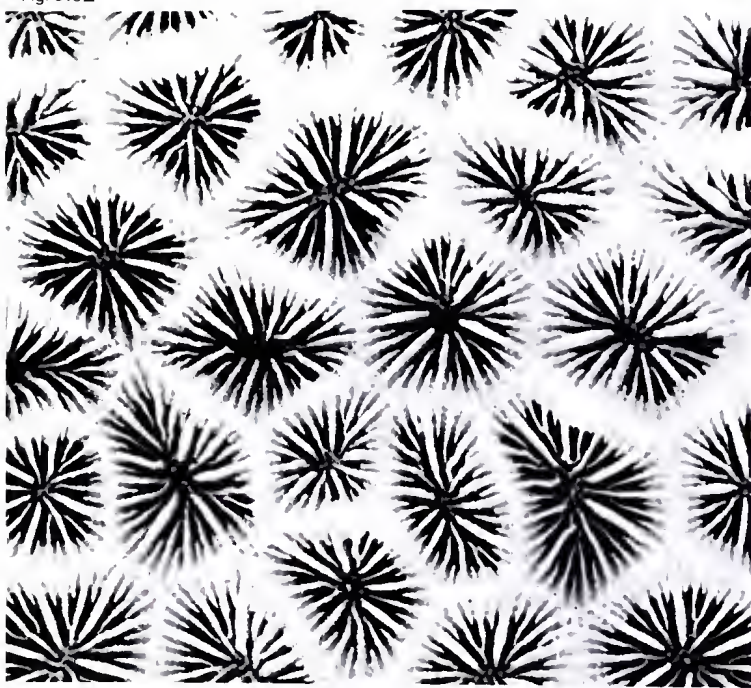


Fig. 315A

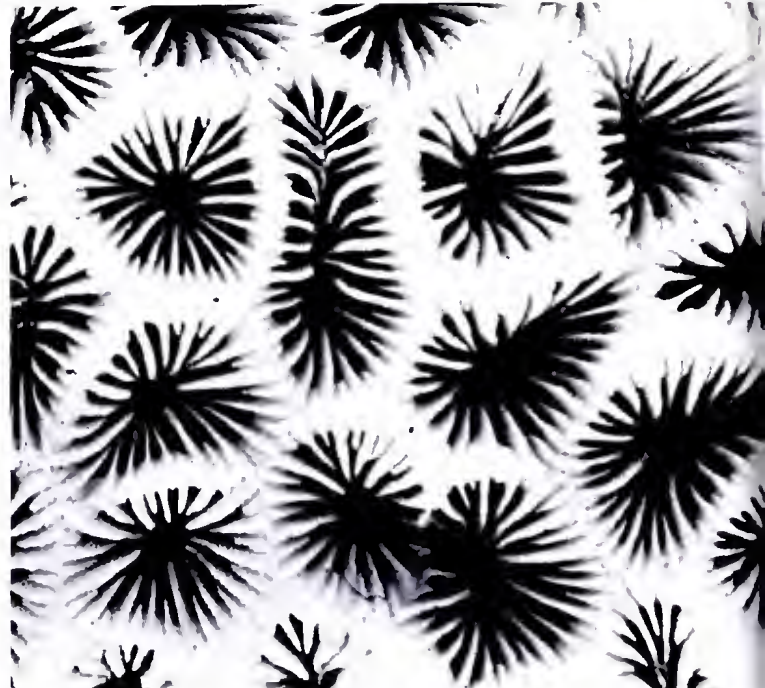


Fig. 316A

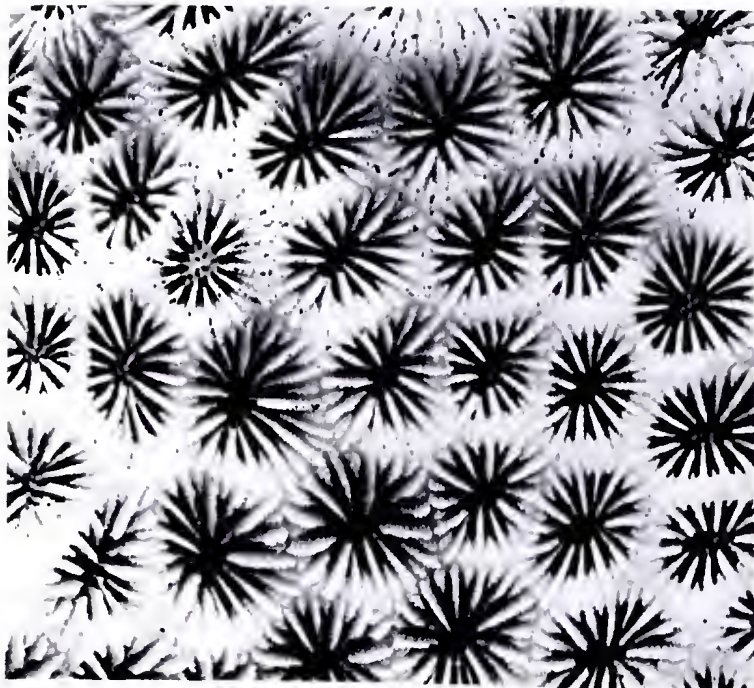


Fig. 317A

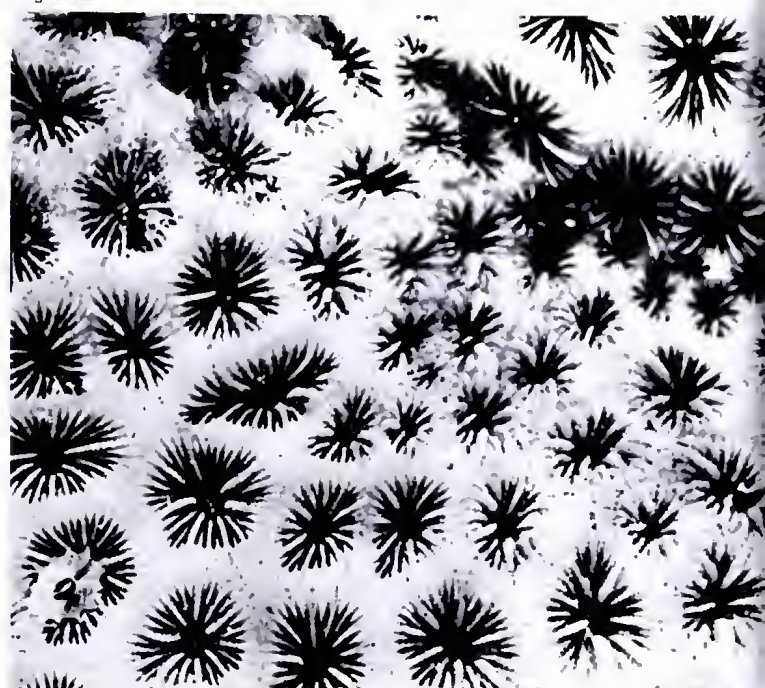


Fig. 318A

Characters and affinities

This species is as difficult to differentiate from *L. purpurea* as the latter is from *L. transversa*. However, it is readily recognised underwater. Polyps are frequently expanded during the day whereas those of *L. purpurea* are usually nocturnal and colour differences are usually striking. Whereas *L. purpurea* is usually creamy-yellow (much the same colour as *L. cf. bottae* except for the black calices in the latter), *L. pruinosa* is usually a dark chocolate brown, normally with a green oral disc. The latter is sometimes a pale green, almost white, sometimes very bright. Occasionally, the stomodaeum is a different colour from the surrounding oral disc. Figures 469-472 illustrate its usual appearance underwater.

Chevalier (1975) assigned four of his specimens to this species on the basis of septal ornamentation and dentation, the formation of pseudosynapticulae from protruding septal granules, the degree of perforation of the septa and lack of intermediates between these coralla and the rest of his *Leptastrea*. This species appears to be far more abundant than *L. transversa* on the Great Barrier Reef and almost as abundant as *L. purpurea*.

Distribution

This species has been recorded only from New Caledonia and the Great Barrier Reef but is probably more widely spread.

Leptastrea bewickensis n.sp.

Four specimens of *Leptastrea* are described here as a new species because they are distinct from all other *Leptastrea* species and also because there is little variation between specimens obtained from three very different biotopes. They thus form a very distinct, if small, species group.

Material studied

Reef between **Yule Reef** and **Triangle Reef** (2 specimens), **Bewick Island, Whitsunday Islands**.

These localities include collecting stations 18, 97.

Previous records from Eastern Australia

Not previously recorded.

Characters

The two colonies from the northern reef flat were both approximately 1cm thick and encrusting; the colony from Bewick Island was more massive, whilst the colony from the Whitsunday Islands was massive, approximately 1m in diameter.

Calices are uniform in size with an overall average diameter range of 2.4mm (on concave surfaces) to 3.2mm. The septa are in three very distinct cycles. Primary septa are symmetrically arranged; they are exsert and very distinctive. Dentations are either absent or occur as horizontal trabecular lobes which unite all primary septa with the columellae. The primary septa have vertical or near vertical inner edges and extend inwards about half the calice radius. The secondary septa extend inwards about half the distance of the primaries and the tertiary cycle extends about half that distance, or are present only as simple ridges. Otherwise, the secondary and tertiary cycles are similar to the primaries. The septa and endothecae are all granulated, the granules sometimes forming neat pseudo-synapticular rows on the septa. The

Figs. 313-318 *Leptastrea transversa* ($\times 5.0$).

- Figs. 313, 315 From Swain Reefs, collecting station 69.
Fig. 314 From Houghton Island, collecting station 40.
Fig. 316 From the Pompey Complex, collecting station 70.
Fig. 317 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 318 From Frigate Cay, Swain Reefs, collecting station 81.

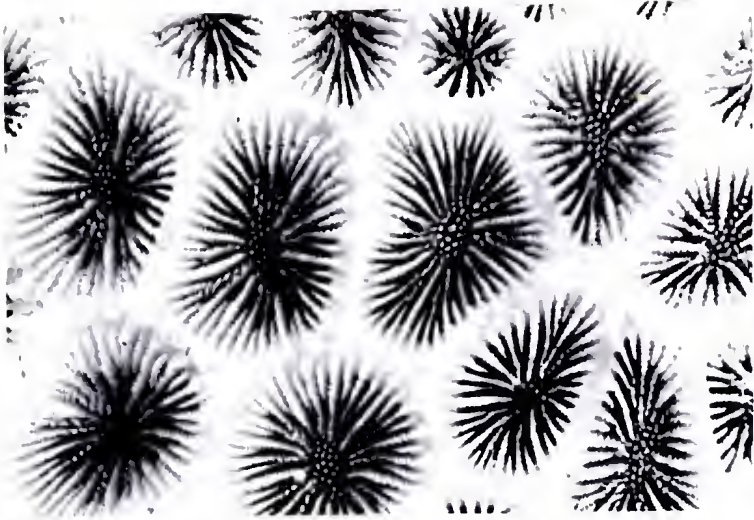


Fig 319▲

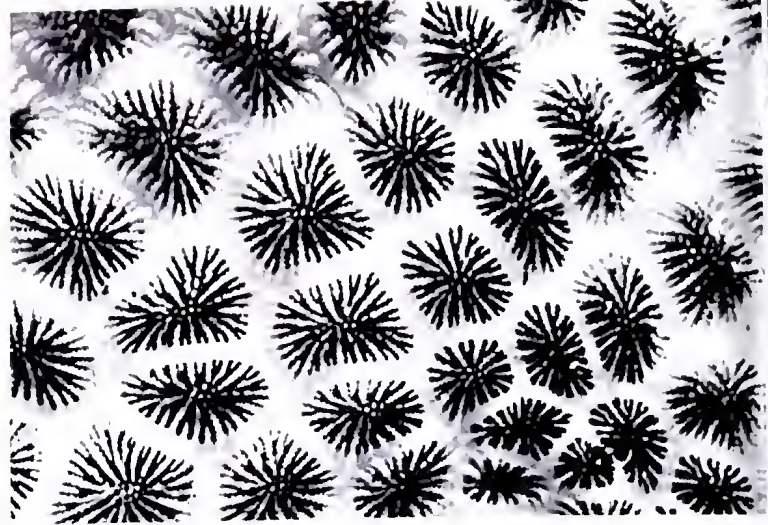


Fig 320▲

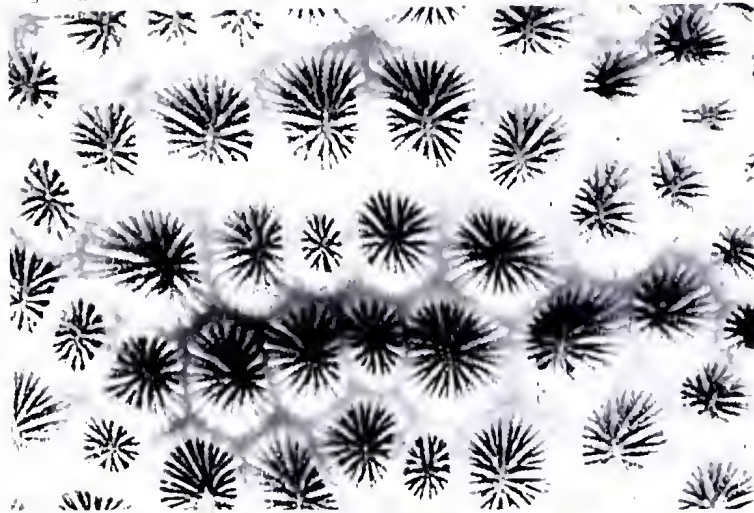


Fig 321▲

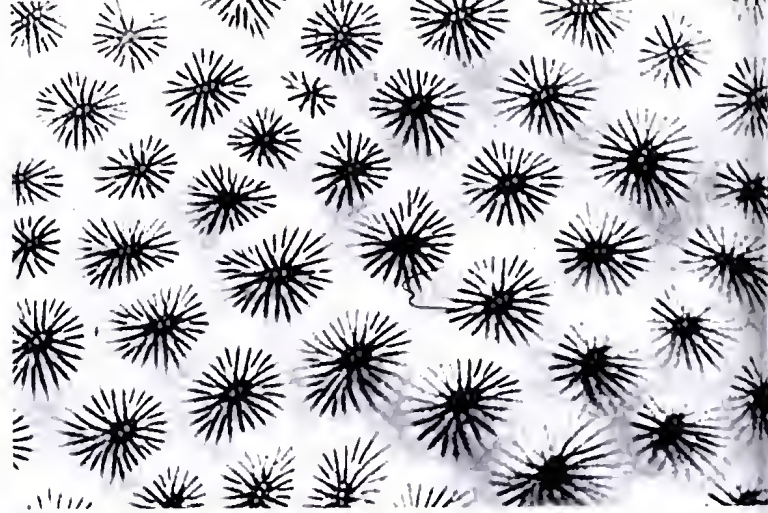


Fig 322▲

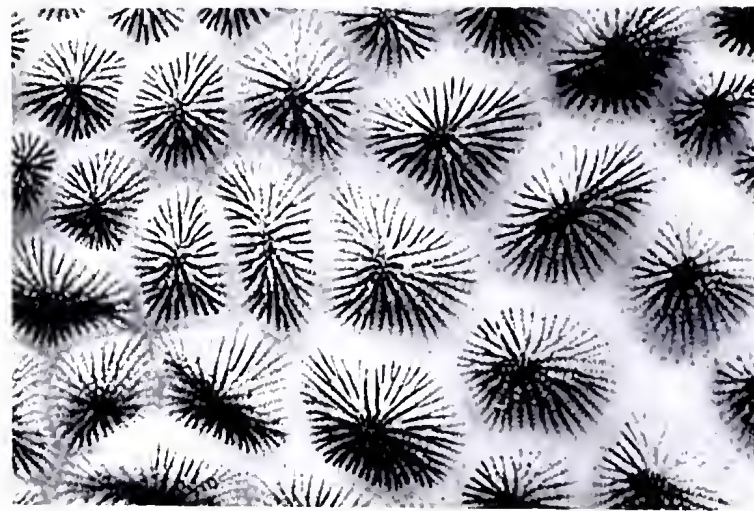


Fig 323▲

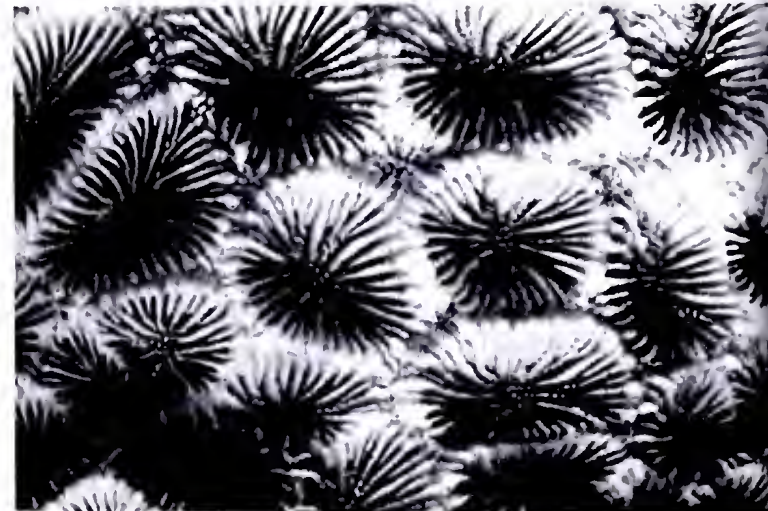


Fig 324▲

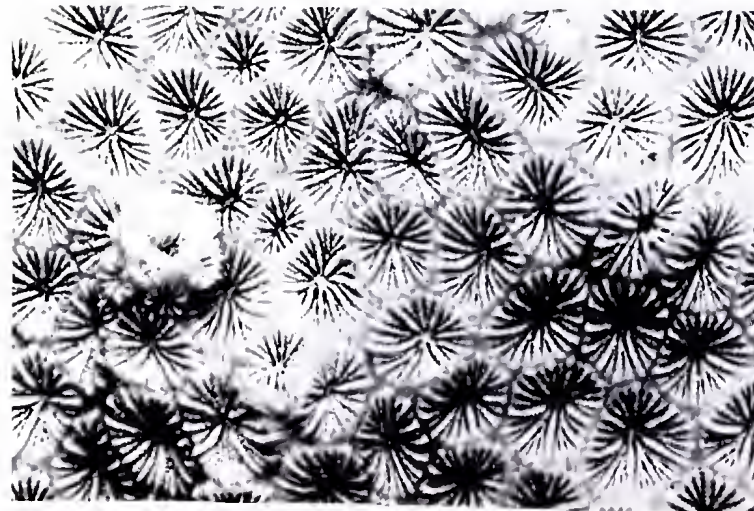


Fig 325▲

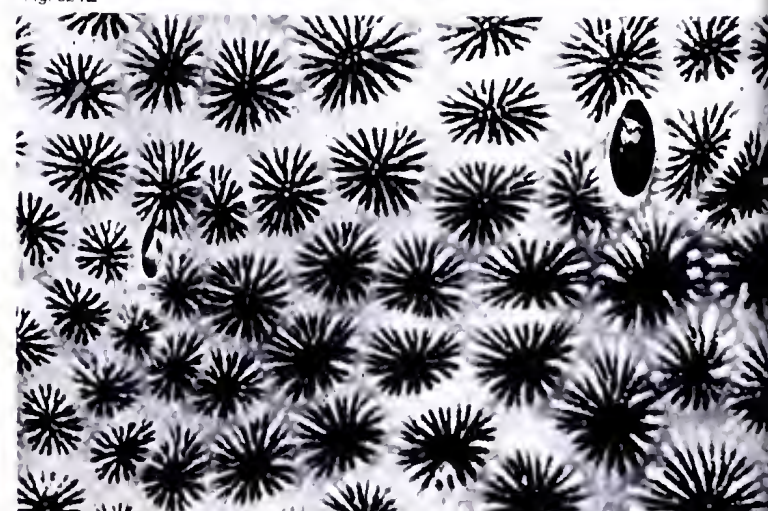


Fig 326▲

columellae are either absent or consist of greatly thickened paliform trabeculae from the primary septa. These are usually fused into a solid, somewhat elongated boss, supporting 1-4 vertical papillae. The exotheca is likewise finely granulated. The intercalicular groove is well defined. Costae are usually short and broad but are sometimes absent. The calices are deep (up to 5.3mm), the thecae are 0.5-1mm thick. The specimens from the barrier reefs were a mottled pale brown and white in colour. The colours of the specimens from Bewick Island and the Whitsunday Islands were not recorded. Budding primarily is extratentacular.

Skeletal variation

The specimen from Bewick Island differs from the others in having slightly thicker walls and better developed calicular structures. The septa and columellae are both better developed, especially the columellae, which are frequently absent from the barrier reef specimens.

Etymology

Named after Bewick Island from where it was first collected.

Holotype

Dimensions: The maximum dimension, including an attached piece of *Porites lobata* is 8.6cm, the minimum dimension 5.6cm.

Locality: Bewick Island, collecting station 18, Great Barrier Reef.

Depth: 5m.

Collector: J. E. N. Veron.

Holotype: British Museum (Natural History) 1977.1.1.5.

Paratypes

Fig. 328 Australian Institute of Marine Science.

Fig. 329 Queensland Museum, Australia.

Distribution

Known only from the Great Barrier Reef.

GENUS *CYPHASTREA* EDWARDS & HAIME, 1848

Generic Synonymy

Cyphastrea Edwards & Haime, 1848.

Solenastraea (*pars.*) Edwards & Haime, 1848.

Type species *Astraea microphthalma* Lamarck, 1816.

Characters of the genus

The genus *Cyphastrea* is one of the most easily recognised of the Faviidae, so, historically, there has been little confusion. The reverse, however, applies to most of the 26 or so nominal species. Of these, only four are valid species of the Great Barrier Reef and the total number of true Indo-Pacific species is probably less than eight.

Figs. 319-326 *Leptastrea pruinosa* ($\times 5.0$).

- Fig. 319 From the intertidal zone, Bushy Island-Redbill Reef, collecting station 86, showing extensive development of the columella and very elongated septal dentations.
- Fig. 320 From Ceteran Bay, Border Island, Whitsunday Islands, collecting station 96.
- Fig. 321 From Swain Reefs, collecting station 77.
- Fig. 322 From Yonge Reef, collecting station 3, showing a heavily calcified corallum from a very exposed biotope.
- Fig. 323 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.
- Figs. 324, 325 From Yorke Island, collecting station 13.
- Fig. 326 From Ceteran Bay, Border Island, Whitsunday Islands, collecting station 96, showing the characteristic appearance of septal dentations in profile.

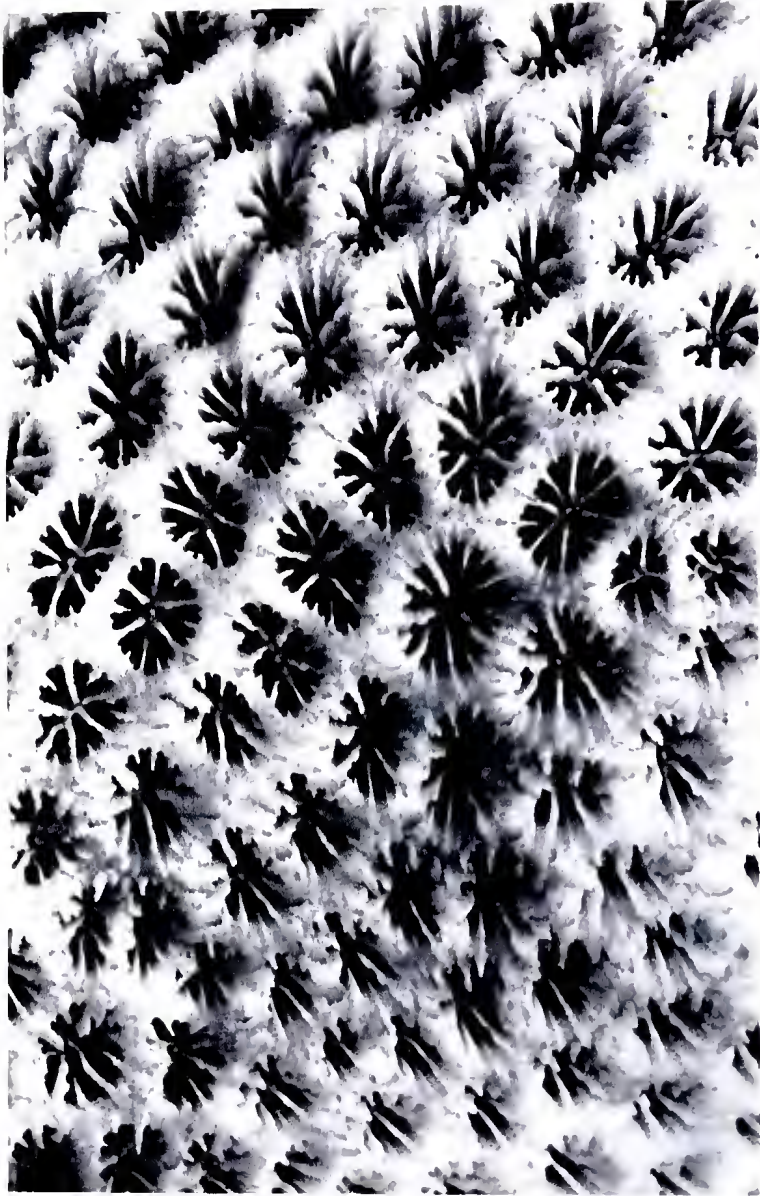


Fig. 327▲



Fig. 328▲



Fig. 329▲

Cyphastrea serailia (Forskål, 1775)

Synonymy

Madrepora serailia Forskål, 1775.

Cyphastrea danai Edwards & Haime, 1857; Ortmann (1888); Whitelegge (1898).

Cyphastrea brueggemanni Quelch, 1886.

Cyphastrea serailia (Forskål); Ortmann (1888); Matthai (1914, 1923, 1924); Vaughan (1917, 1918); Faustino (1927); Gravely (1927); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Crossland (1941, 1952); Wells (1954, 1955b); Nemenzo (1959); Chevalier (1968, 1975); Utinomi (1971).

Cyphastrea suvadivae Gardiner, 1904; Matthai (1914); Yabe, Sugiyama & Eguchi (1936); Crossland (1938).

Cyphastrea conferta Nemenzo, 1959.

Cyphastrea suvadivae is a deep water ecomorph of *C. serailia*. It is lightly calcified with corallites widely separated by a vesicular coenosteum. The single figure of *C. conferta* published by Nemenzo closely resembles *C. serailia*; differences from *C. serailia* noted by Nemenzo are probably the result of the borer attacks which he mentions. Many coralla of the present series are likewise affected.

Chevalier's (1975) synonymy of *C. serailia* incorrectly includes, among others, *C. ocellina*, *C. gardineri*, *C. chalcidicum* and *C. japonica*. The latter two are common and distinct species, while *C. ocellina* is a distinct Hawaiian species and *C. gardineri* is a probable synonym of *C. microphthalma* (see below). There are thus either four or five valid species in Chevalier's six 'varieties' of *C. serailia*.

Material studied

Murray Islands (3 specimens), **Sue Island** (2 specimens); **Thursday Island** (6 specimens), **Great Detached Reef** (3 specimens), **Houghton Island** (2 specimens), **Yonge Reef**, **Jewell Reef**, **Lizard Island** (8 specimens), **Eagle Reef**, **Three Isles** (2 specimens), **Hope Island**, **Low Isles**, **Palm Islands** (57 specimens), **Whitsunday Islands** (6 specimens), **Bushy Island-Redbill Reef** (14 specimens), **Pompey Complex** (13 specimens), **Swain Reefs** (23 specimens), **Solitary Islands** (10 specimens).

These localities include collecting stations 1, 3, 5, 17, 19, 27, 32, 33, 34, 35, 36, 37, 40, 41, 42, 43, 45, 53, 55, 57, 59, 60, 69, 70, 75, 77, 78, 80, 81, 83, 90, 92, 93, 94, 96, 97, 98, 100, 103.

Fig. 327 Holotype of *Leptastrea bewickensis* from Bewick Island, collecting station 18 ($\times 5.0$).

Fig. 328 Paratype of *Leptastrea bewickensis* from near Yule Entrance ($\times 5.0$).

Fig. 329 Paratype of *Leptastrea bewickensis*, different specimen from the same locality as Fig. 328 ($\times 5.0$).

Figs. 330-341 *Cyphastrea serailia* ($\times 7.5$).

Fig. 330 From Pompey Complex, collecting Station 71, showing close similarity with *C. hemprichana*.

Fig. 331 From Iris Point, Orpheus Island, Palm Islands, collecting station 55 (3m).

Fig. 332 From Thursday Island, collecting station 54.

Fig. 333 From Bushy Island-Redbill Reef, collecting station 86.

Fig. 334 From Bullumbooroo Bay, Great Palm Island, collecting station 35.

Fig. 335 From Iris Point, Orpheus Island, Palm Islands, collecting station 55 (22-25m), showing similarity with *C. suvadivae* and *C. maldivensis*.

Figs. 336, 337 From Bullumbooroo Bay, Great Palm Island, collecting station 35. Fig. 337 shows close similarity with *C. regularis*; a hexagonal symmetry can be seen in some corallites.

Fig. 338 From Sue Island, collecting station 17.

Fig. 339 From MacGillivray Reef, collecting station 74.

Fig. 340 From between Orpheus and Fantome Island, Palm Islands, collecting station 60.

Fig. 341 From the Solitary Islands.

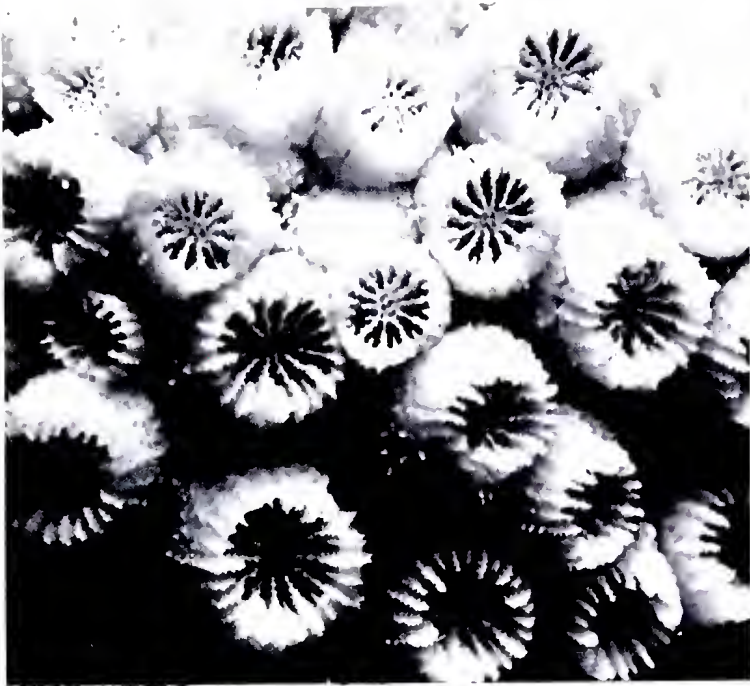


Fig. 330▲

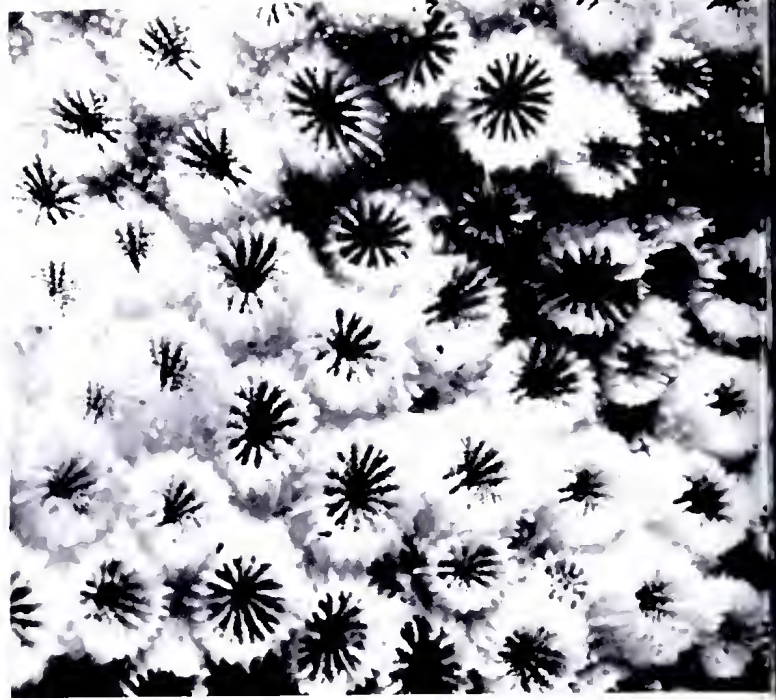


Fig. 331▲



Fig. 334▲

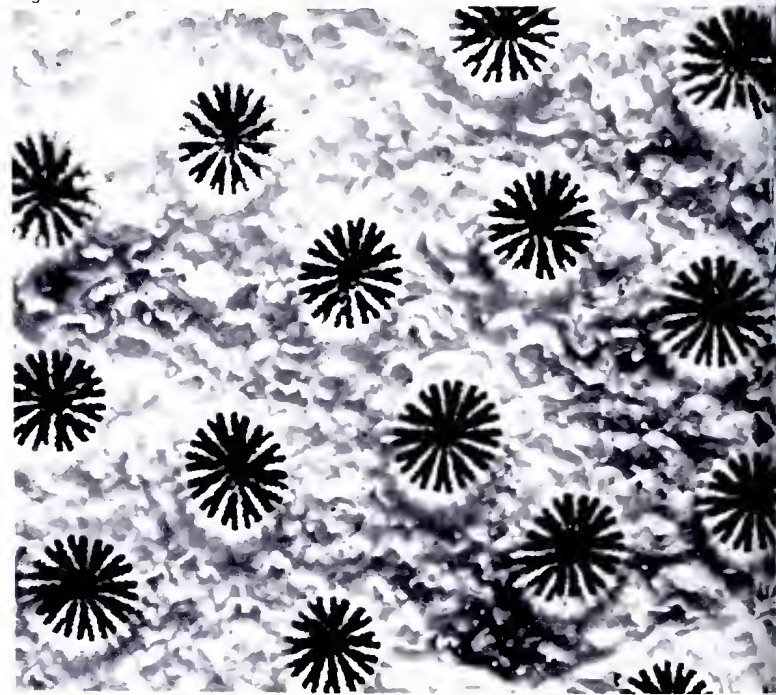


Fig. 335▲

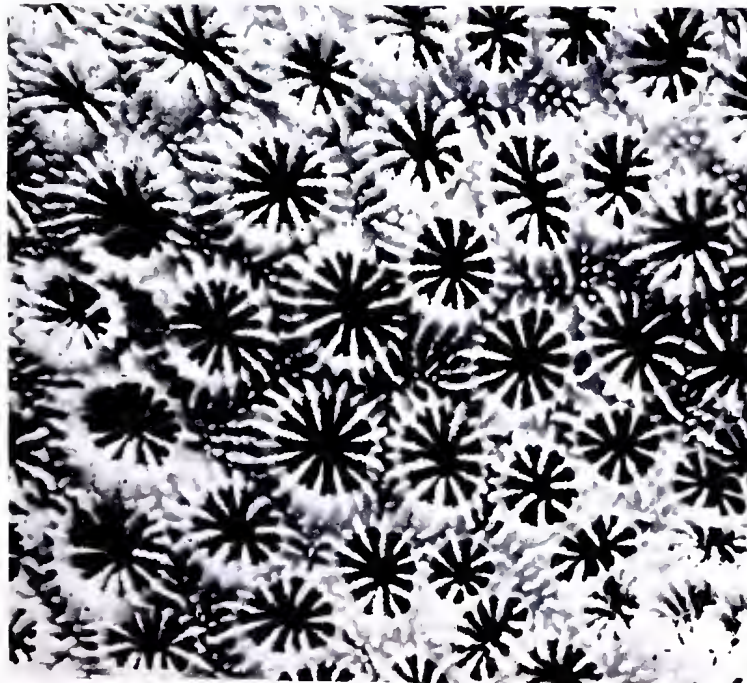


Fig. 338▲

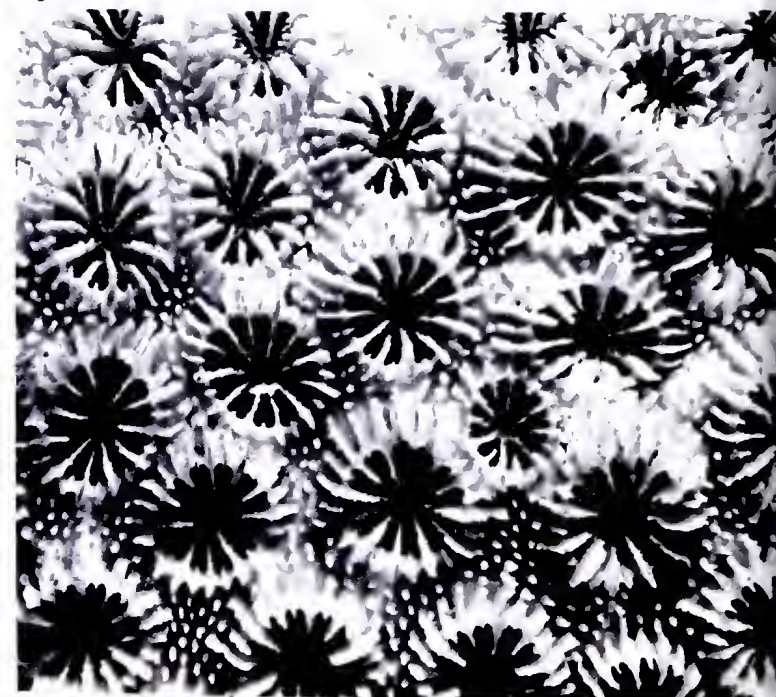
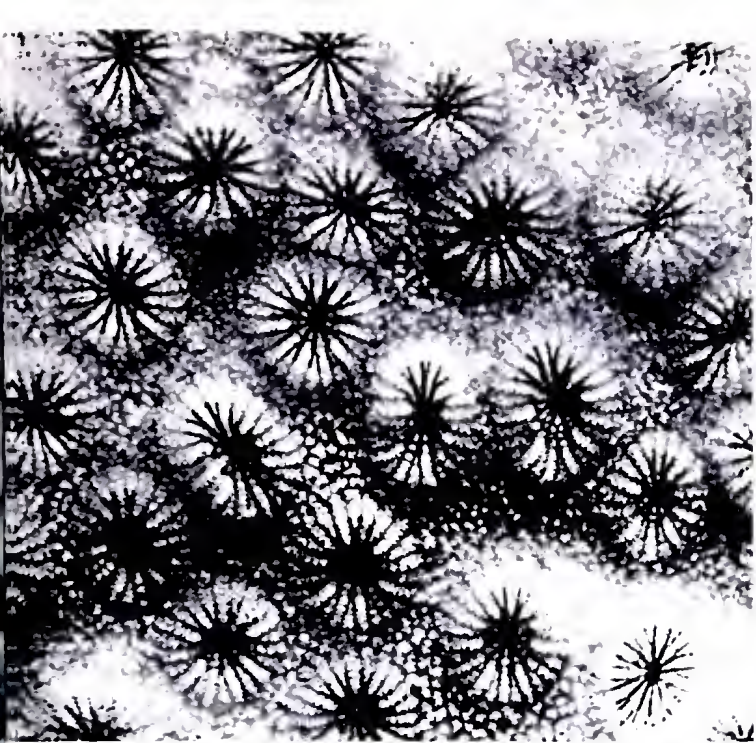


Fig. 339▲



332A

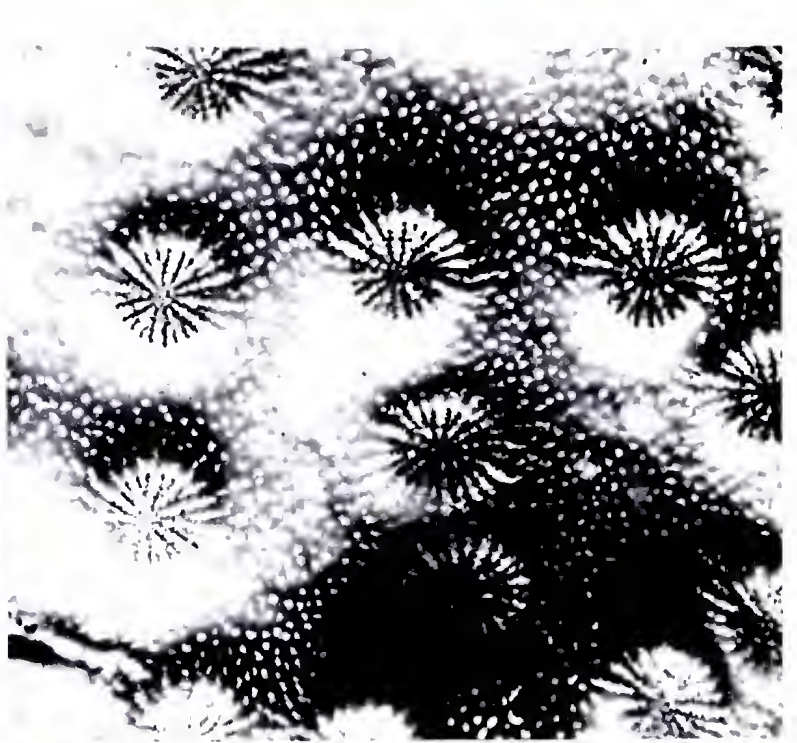
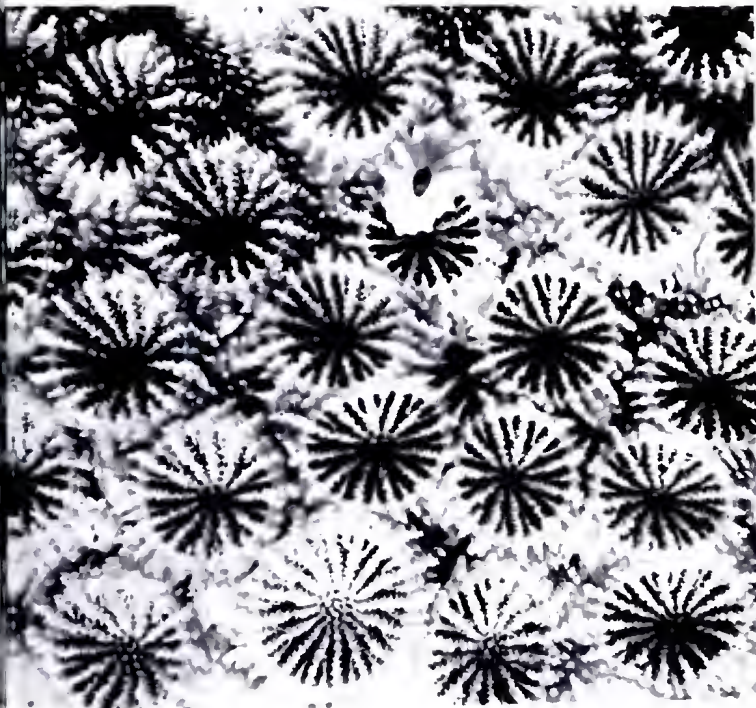


Fig. 333A



336A

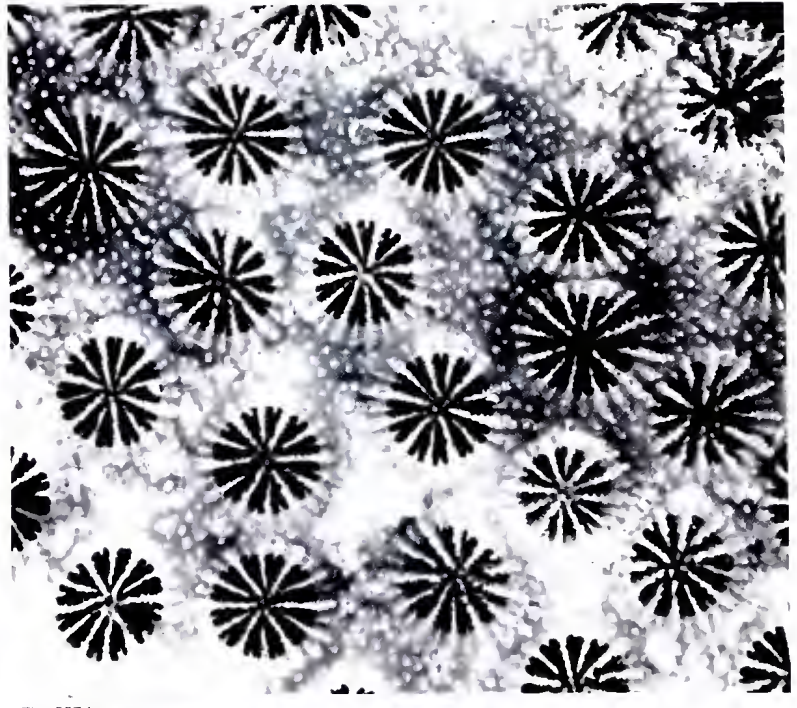
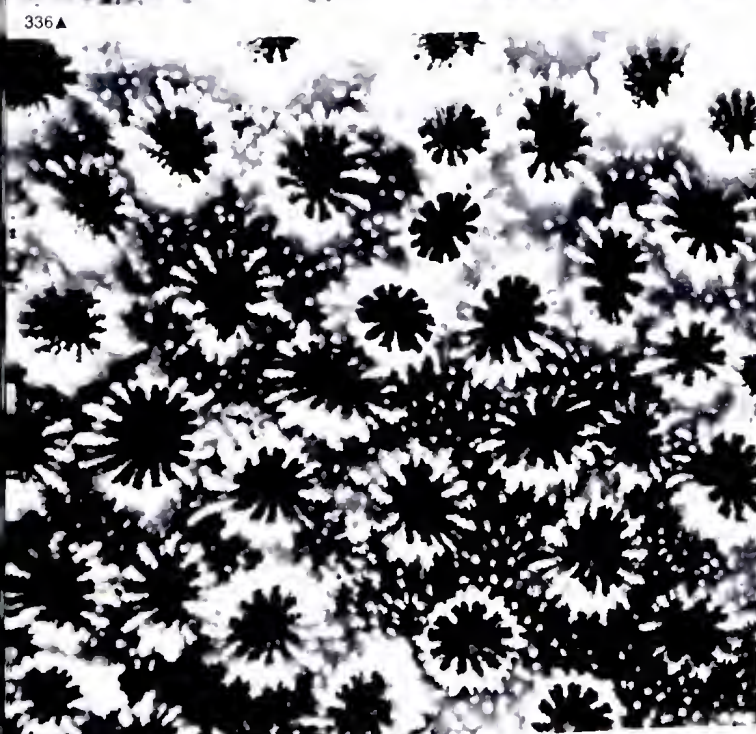


Fig. 337A



340A

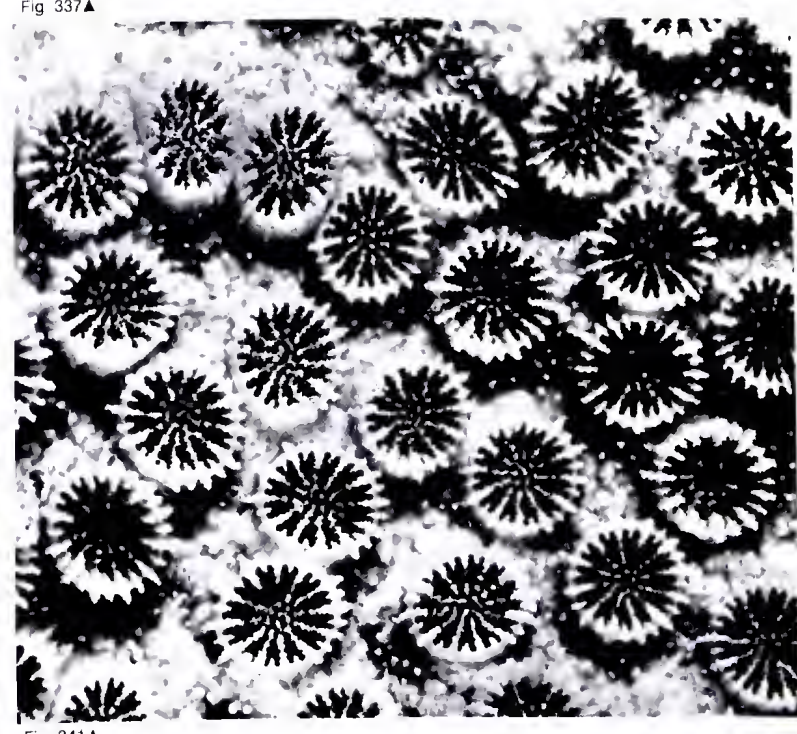


Fig. 341A

Previous records from Eastern Australia

Murray Islands, Vaughan (1918), Mayor (1918); barrier reef NE of **Murray Islands**, Vaughan (1918); **Low Isles**, Stephenson *et al.* (1931), Crossland (1952), Stephenson & Wells (1955); **Heron Island**, Salter (1954); **Moreton Bay**, Wells (1955b); **Solitary Islands**, Veron *et al.* (1974); **Lord Howe Island**, Veron (1974).

Characters

This species is the most abundant and occupies the widest geographical and environmental range of any of the east Australian *Cyphastrea*. Consequently it has by far the greatest diversity of growth forms and the greatest range of calicular structures.

Colonies are usually massive or sub-massive, sometimes encrusting. Corallites are round and very variably exsert, from sub-crioid to about 3mm. Calices of mature corallites are 1.5 to 2.8mm in diameter. Septa are in two very unequal orders of 12 each. First order septa usually cannot be differentiated into two cycles. They may plunge steeply or slope gently to the columellae. They usually have irregular, elongate dentations which point inwards. A paliform crown is usually present, the paliform lobes having a wide variety of shapes which vary from elongated pinnules to thick triangular wedges. Second order (tertiary cycle) septa seldom extend inwards more than half the calice radius. They frequently become attached to the first order septa. All septa are granulated on their margins and sides. The columellae are usually inconspicuous and trabecular. The costae are equal or subequal and are frequently poorly developed. They are heavily ornamented with granulated perithecal spines. The thecae vary greatly in height and thickness; they may be abruptly delineated from the coenosteum or be completely confluent. The coenosteum is often largely composed of dissepimental blisters and is always covered with granulated exothecal spines.

There are no consistent trends in colour variation, except that dark colours are usually, but not necessarily, associated with low light intensities of deep water.

Skeletal variation

The full range of calice structures of this species is illustrated in Figs. 330-341. A few somewhat arbitrary ecomorphs within this range may be distinguished as follows:

Cyphastrea serailia from exposed biotopes (Figs. 330, 331).

As with other *Cyphastrea*, this species is seldom found in areas exposed to strong wave action. Where it does occur on exposed outer slopes, colonies are sub-massive, exhibiting a predominantly horizontal growth component. Coralla are dense with large, rounded corallites having thick vertical thecae. Such coralla often have a conspicuous paliform crown and a heavily ornamented coenosteum.

Cyphastrea serailia from semi-protected biotopes (Figs. 333, 334).

Coralla from a wide variety of semi-protected biotopes have a thin encrusting growth form with widely separated, very exsert corallites. These are usually conical in shape and very irregular in height. Costae are frequently poorly developed and frequently do not extend the full height of the thecae. The extensive coenosteum is frequently blistered as are the edge zones which are frequently wide.

Cyphastrea serailia ecomorph *suvarivae* (Fig. 335).

Coralla from very protected, poorly illuminated biotopes are composed of large amounts of vesicular dissepiments. They thus have a very low density. Corallites have narrow calices and very thin thecae, usually devoid of costae. The coenosteum is very blistered and may be devoid of exothecal spines.

Cyphastrea serailia from sub-temperate biotopes (Fig. 341).

Coralla are thin and encrusting. Corallites have thin, moderately exsert thecae. Septa are characteristically very granulated, the granules of adjacent septa frequently fusing to form

pseudosynapticalae. It is noted, however, that coralla from the Solitary Islands are almost indistinguishable from those of some tropical biotopes.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to the Marshall and Philippine Islands. As previously noted, this species is usually more abundant in the Pacific than *C. microphthalma* but relatively less so in the Western Indian Ocean and Red Sea.

***Cyphastrea chalcidicum* (Forskål, 1775)**

Synonymy

Madrepora chalcidicum Forskål, 1775.

?*Cyphastrea ocellina* (Dana); Nemenzo (1959).

?*Cyphastrea capitata* Studer, 1878.

Cyphastrea chalcidicum (Forskål); Klunzinger (1879); Ortmann (1888, 1892); Gardiner (1899); Matthai (1924, 1923, 1924); Faustino (1927); Crossland (1935, 1941, 1952); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1940); Wells (1954); Stephenson & Wells (1955); Searle (1956); Nemenzo (1959); Utinomi (1965, 1971); Chevalier (1968); Rosen (1971).

In order to stabilise usage of the name *C. chalcidicum* in the absence of any type specimen of the species, the corallum illustrated in Fig. 347 is designated a neotype. The corallum is encrusting and is of irregular shape. Calicular structures characteristic of the species are well developed.

Dimension: The maximum dimension is 19.1cm.

Locality: SW Swain Reefs, collecting station 69.

Depth: 5-14m.

Collectors: J. E. N. Veron and M. Pichon.

Neotype: British Museum (Natural History).

Cyphastrea ocellina was originally considered synonymous with *C. chalcidicum* by Matthai (1914), but Vaughan (1918) and later Nemenzo (1959) upheld its validity. However, neither author gave a strong case for his opinion. Nemenzo's description of *C. ocellina* is very close to the centre of variation of the Great Barrier Reef *C. chalcidicum*, and is quite unlike the Hawaiian species.

Material studied

Barrier reef near **Murray Islands** (3 specimens), **Murray Islands, Great Detached Reef** (2 specimens), **Waining Reef, Palm Islands** (19 specimens), **Bushy Island-Redbill Reef** (11 specimens), **Pompey Complex** (2 specimens), **Swain Reefs** (10 specimens).

These localities include collecting stations 1, 35, 37, 41, 43, 45, 55, 59, 60, 62, 69, 71, 77, 78, 80, 81, 104.

Previous records from Eastern Australia

Low Isles, Yonge (1930), Yonge & Nicholls (1931a, 1931b), Yonge *et al.* (1932), Manton (1935), Crossland (1952), Stephenson & Wells (1955).

Characters

This species is the most readily recognisable of the *Cyphastrea* which have twelve septa of the first order. It is primarily characterised by having very unequal septo-costae, with second order costae being abortive.

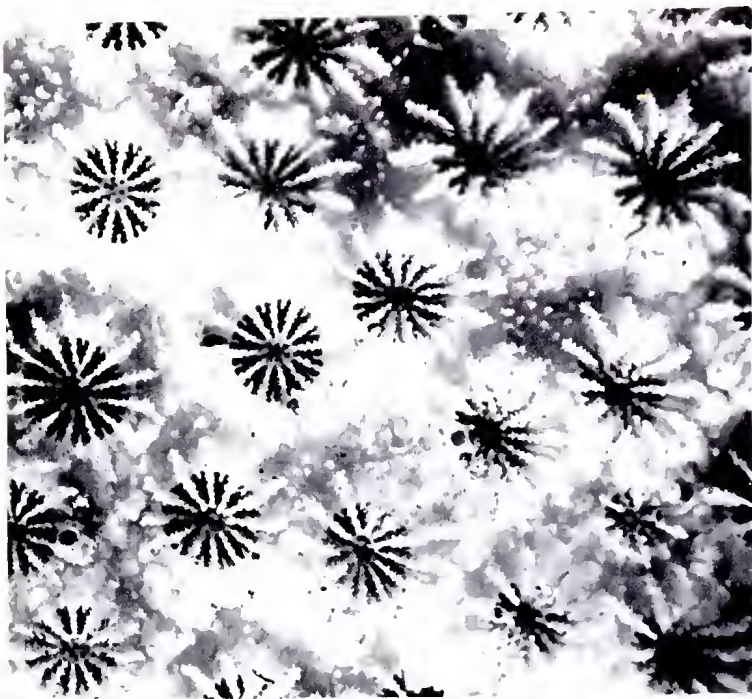


Fig. 342▲

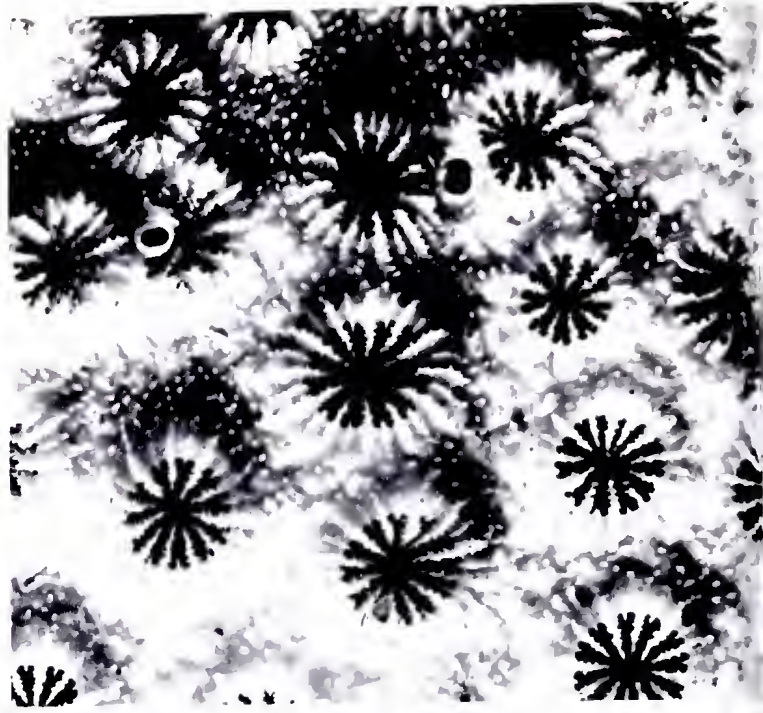


Fig. 343▲

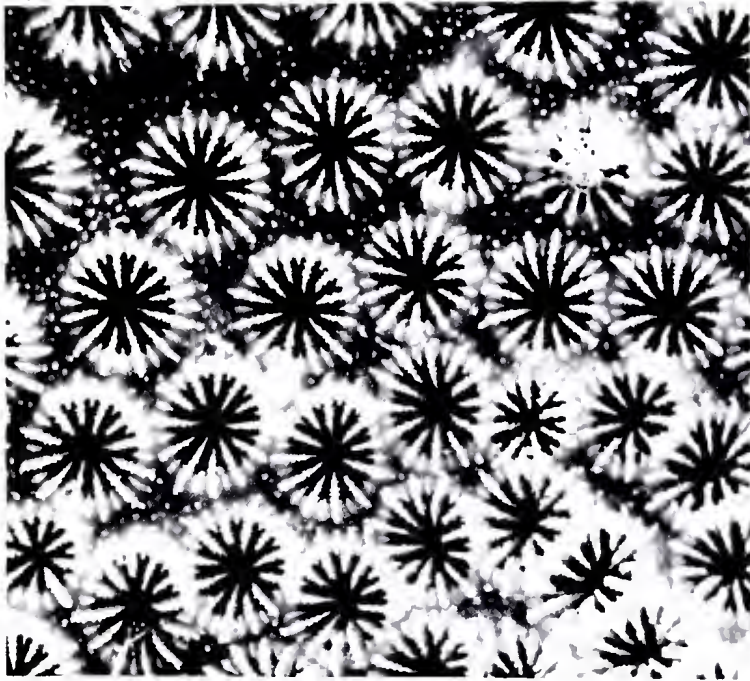


Fig. 344▲

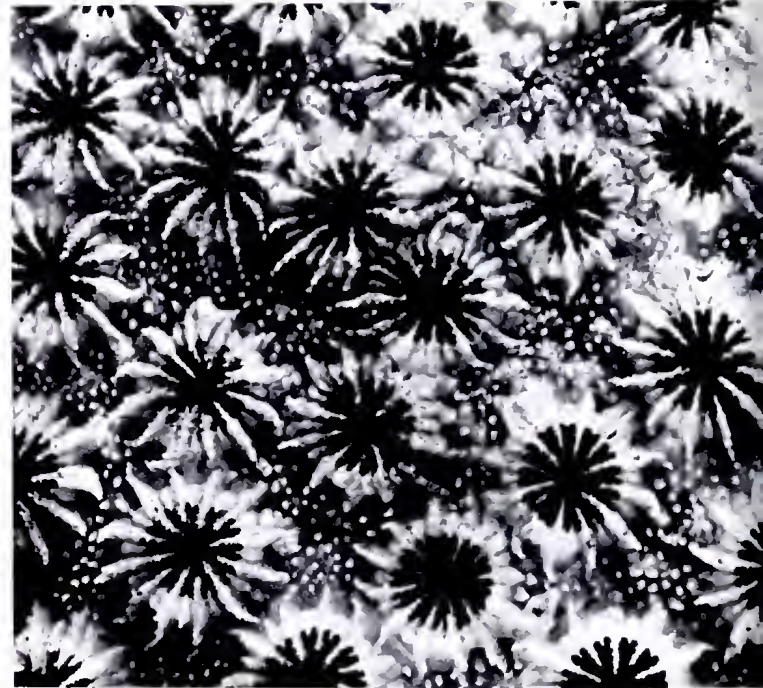


Fig. 345▲

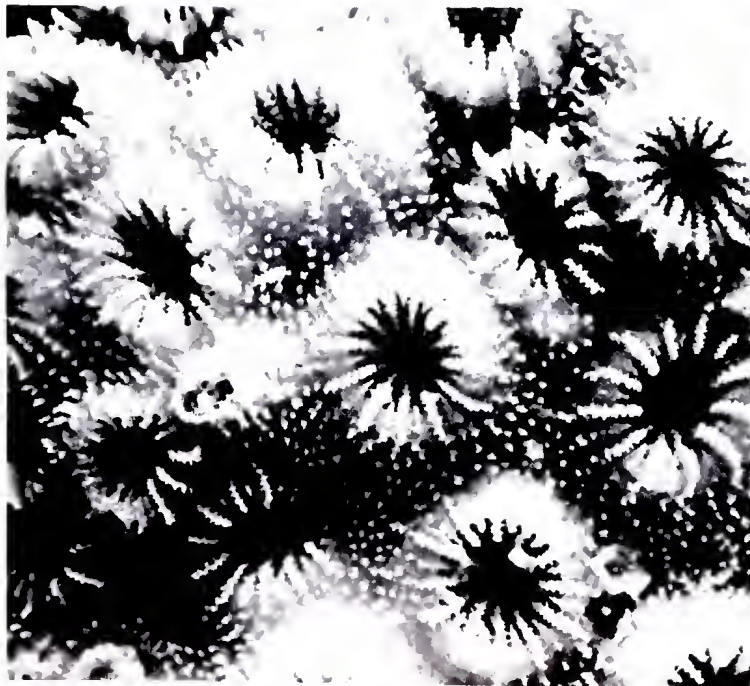


Fig. 346▲



Fig. 347▲

Colonies are encrusting or massive and frequently form coralloliths. Corallites are usually conical in shape and are markedly exsert. Calices are large, averaging 2mm in diameter on convex surfaces but are usually much reduced on concave surfaces. Mature calices have 24 septa in two markedly unequal orders. In some coralla, septa of the first order can be divided into two hexamerous cycles. In such cases, as with *C. japonica*, the primary septa are thicker and more exsert than secondary ones, have no paliform lobe and join the columellae deeper within the calice. However, in most coralla the primary and secondary cycles are indistinguishable. All first order septa have long, irregular dentations which are very granulated. Second order septa are much reduced. The columellae are small, usually consisting of only a few twisted trabeculae.

First order costae are usually well developed, while those of the second order are reduced or absent. This is particularly marked in corallites with exsert thecae. The coenosteum is frequently blistered and is always ornamented with large numbers of granulated exothecal spines.

Living colonies have very variable colours, but the species is nevertheless readily recognisable underwater (Fig. 473).

Figs. 342-347 *Cyphastrea chalcidicum* ($\times 7.5$).

Fig. 342 From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.

Fig. 343 From Juno Bay, Fantome Island, Palm Islands, collecting station 43.

Figs. 344, 345 From Bushy Island-Redbill Reef, collecting station 86.

Fig. 346 From the Palm Islands.

Fig. 347 Neotype from Swain Reefs, collecting station 68.

Fig. 348 *Cyphastrea chalcidicum*, *in situ*, Whitsunday Islands ($\times 1.0$).

Fig. 349 *Cyphastrea chalcidicum* with expanded polyps ($\times 5.0$).



Fig. 349▲

Skeletal variation

Coralla from exposed biotopes are massive or encrusting. Corallites have exsert, thick thecae, usually with thickened, exsert first order septa. The coenosteum is covered with prominent exothecal spines. This species has not been observed in biotopes where wave action is strong. In more protected reef areas the growth form is usually encrusting, with colonies over 1m across being common. They frequently form free-living coralliths which have the variable shapes of the substrates they encrust. Such coralliths are frequently aggregated in depressions in sandy areas, with corallites on their lower surfaces usually being small, thin walled and widely spaced.

Ecomorphs from deep water are thin, encrusting, flake-like colonies which usually have very exsert, widely spaced corallites. First order septo-costae are very prominent, the septa having large, inwardly projecting dentations which are very granulated. The coenosteum is very blistered and the perithecal spines much reduced.

Distribution

Widely distributed throughout the Indo-Pacific.

Cyphastrea microphthalma (Lamarck, 1816)

Synonymy

Astraea microphthalma Lamarck, 1816.

Cyphastrea microphthalma (Lamarck); Edwards & Haime (1849); Tenison-Woods (1878); Quelch (1886); Gardiner (1904); Bedot (1907); Matthai (1914, 1923); Vaughan (1918); Hoffmeister (1925); Faustino (1927); Crossland (1931, 1935, 1941, 1952); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Ma (1937); Eguchi (1938); Umbgrove (1940); Rossi (1954); Wells (1955b); Stephenson & Wells (1955); Nemenzo (1959); Rosen (1971); Utinomi (1971); Scheer & Pillai (1974); Chevalier (1975).

Cyphastrea aspera Quelch, 1886.

?*Cyphastrea gardineri* Matthai, 1914.

Material studied

Murray Islands (3 specimens), **Sue Island** (5 specimens), **Thursday Island, Triangle Reef, Jewell Reef** (2 specimens), **Yonge Reef** (2 specimens), **Lizard Island** (7 specimens), **Three Isles, Hope Island, Palm Islands** (24 specimens), **Whitsunday Islands** (7 specimens), **Bushy Island-Redbill Reef** (4 specimens), **Pompey Complex** (4 specimens), **Swain Reefs** (13 specimens).

These localities include collecting stations 6, 9, 17, 27, 29, 32, 36, 38, 41, 42, 43, 45, 54, 57, 66, 67, 69, 72, 75, 80, 81, 90, 91, 92, 97, 98, 99, 100, 104.

Previous records from Eastern Australia

Low Isles, Crossland (1952), Stephenson & Wells (1955); **?Port Jackson**, (as *C. microphthalma* and *C. muelleri*) Tenison-Woods (1878). Wells (1955b) records this species as a subfossil from **Moreton Bay**.

Characters

Colonies are usually encrusting, rarely sub-massive or massive. They are usually plocoid, with a tendency to become cerioid in many specimens. Calices are 1-2mm in diameter and contain two orders of septa arranged symmetrically. This species is primarily characterised by the presence of ten first order septa in the majority of mature calices. Occasionally, eleven septa are found, although none of the specimens of the present series has twelve first order septa in the majority of calices. This provides a ready criterion for separating *C. microphthalma* from all other *Cyphastrea*. In most coralla, the first order septa are only slightly

exsert, although in some they may be markedly so (Fig. 353). They may have complex, irregular dentations and have well developed paliform lobes. Second order septa are less exsert, and never reach the columellae, which consist of a few twisted trabeculae. All calicular structures are very granulated. The costae are usually equal and support elongated, granulated perithecal spines which extend across the coenosteum, giving an elaborate ornamentation.

Colonies or parts of colonies exposed to good illumination usually have pale, uniform colours; those from turbid biotopes or from shaded positions are usually dark brown or dark green.

Skeletal variation

Like all *Cyphastrea*, this species displays a wide variety of growth forms associated with differing environmental conditions. Coralla from exposed biotopes tend to develop massive growth forms with large, thick-walled, usually closely packed corallites. Those from protected biotopes are encrusting and the corallites thin and widely spaced.

Many coralla of the present series are infested with boring organisms, especially *Lithophaga* and polychaetes. These induce abnormal growth forms. In such cases, corallites are usually irregular in size and shape and frequently have abnormally exsert septa.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to the New Hebrides, Samoa and Tahiti.

Fig. 350 Holotype of *Cyphastrea microphthalmia* ($\times 5.0$).



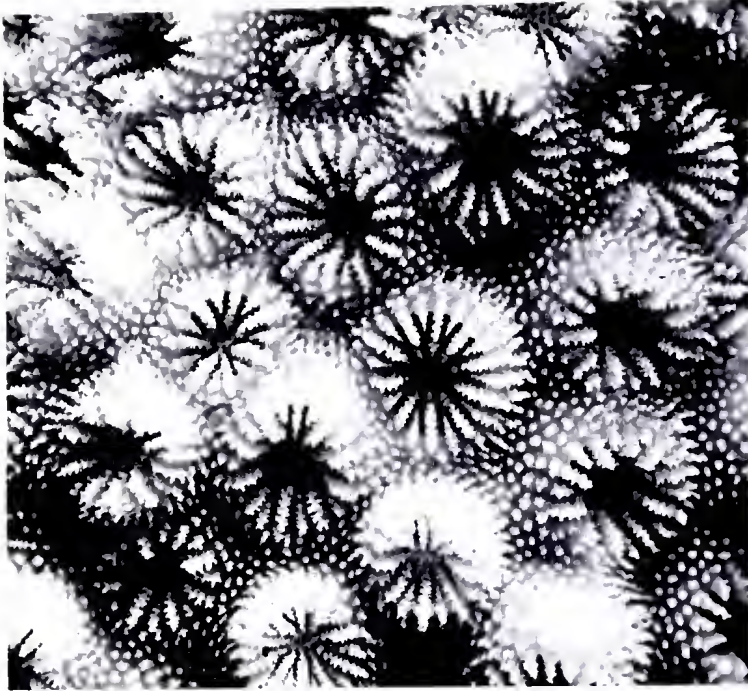


Fig. 351▲

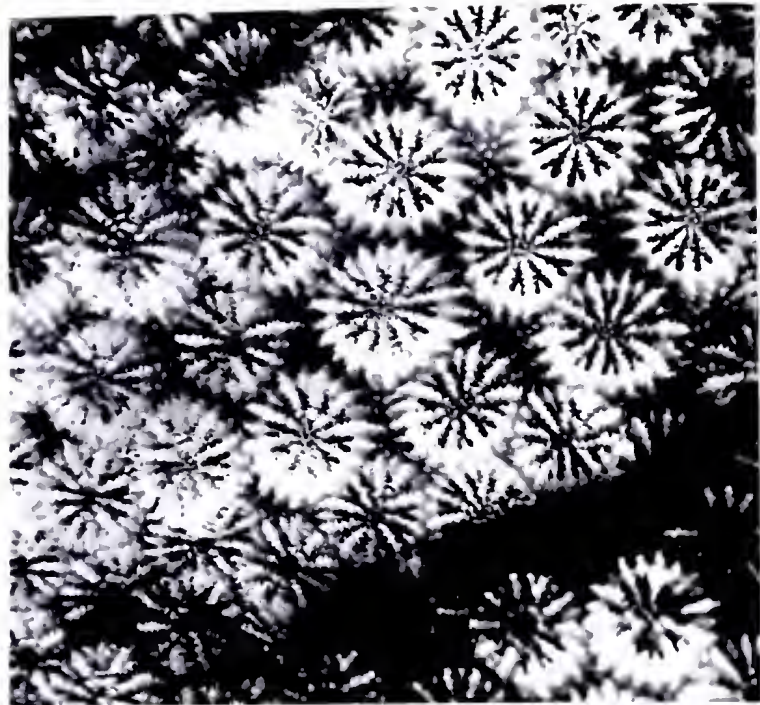


Fig. 352▲

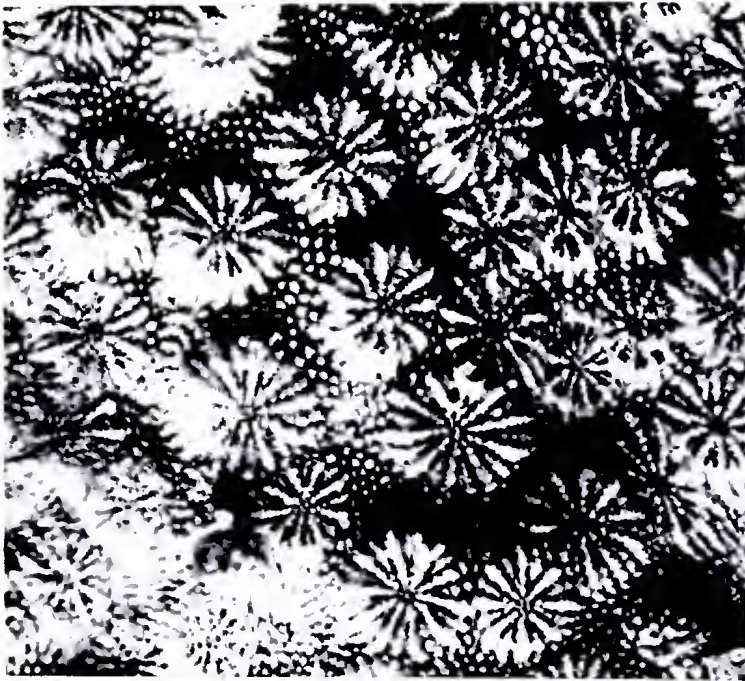


Fig. 353▲



Fig. 354▲

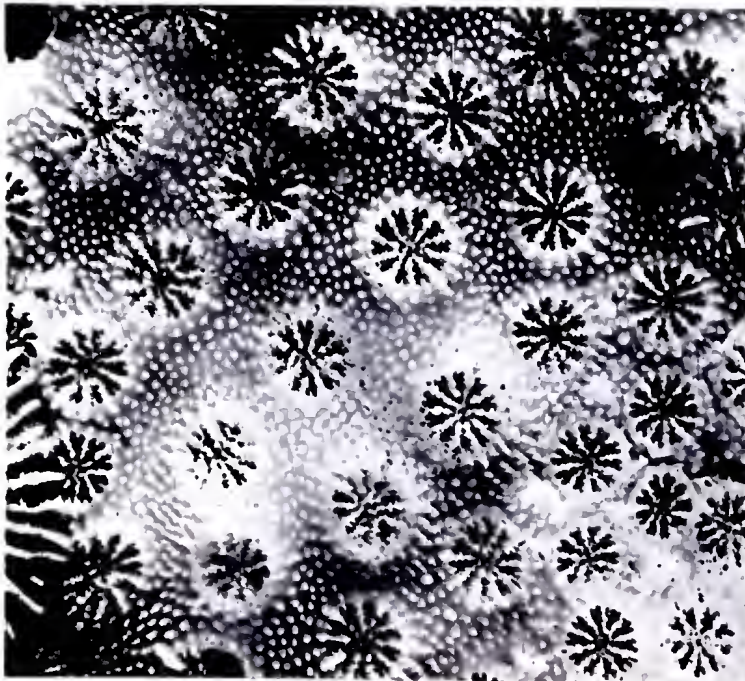


Fig. 355▲

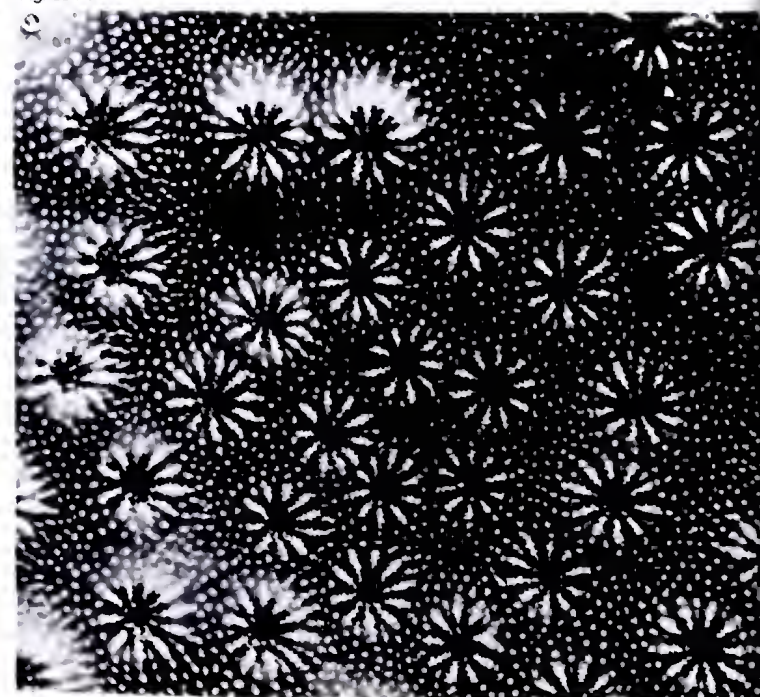


Fig. 356▲

Cyphastrea japonica Yabe & Sugiyama, 1932

Synonymy

Cyphastrea japonica Yabe & Sugiyama, 1932; Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Utinomi (1971).

Material studied

Yorke Island, Murray Islands (2 specimens), **Lizard Island, Palm Islands** (14 specimens), **Whitsunday Islands, Pompey Complex** (2 specimens), **Swain Reefs**.

These localities include collecting stations 11, 13, 29, 30, 35, 37, 41, 42, 45, 57, 60, 69, 75, 91, 102.

Previous records from Eastern Australia

Not previously recorded.

Characters

This species normally has a fruticose growth form, unlike all other *Cyphastrea*. Branches are composed of elongated axial corallites, secondarily thickened by lateral corallites. Axial corallites extend up to 8mm beyond the first lateral corallites and have calices 1-2.5mm in diameter. Most axial and lateral corallites have three cycles of septa arranged in a hexamerous pattern. Occasionally, the primary and secondary cycles are confused and sometimes the tertiary cycle is not developed. The six septa of the primary cycle are thicker and more exsert than the others and usually do not form paliform lobes. They plunge steeply within the calices, usually joining the columellae below the secondary cycle. Septa of the secondary cycle are thinner and have knob-like paliform lobes. The tertiary cycle is little developed, frequently consisting of a ridge running down the endotheca. The columellae consist of one or several styliform processes adjoined by pseudo-synapticulae. All calicular structures and septal margins are very granulated. Three orders of costae are usually present, the first and second equal or subequal, the third reduced. The coenosteum and costae are ornamented with perithecal spines which are frequently very granulated.

Living colonies usually have dull colours, mostly green or brown. Axial corallites are pale or white.

Skeletal variation

The present series includes coralla with an encrusting growth form supporting occasional short branches, sub-massive coralla with short thick branches and coralla with thin anastomosing branches and elongated axial corallites. However, there is no clear correlation between environmental conditions and growth form. Fine, ramose growth forms are usually formed in biotopes protected from strong wave action but where light penetration is good. Thicker branches are usually associated with exposure to wave action and/or currents. Encrusting growth forms are found in deep or turbid water.

Distribution

Previously recorded only from Misaki and Kamae Bay, Japan.

Figs. 351-356 *Cyphastrea microphthalmia* ($\times 7.5$).

- Fig. 351 From SW Swain Reefs, collecting station 69.
- Fig. 352 From Dewar Island, Murray Islands, collecting station 28.
- Fig. 353 From Maude Bay, Magnetic Island, collecting station 84.
- Fig. 354 From One Tree Island.
- Fig. 355 From between Brisk and Falcon Islands, Palm Islands, collecting station 41.
- Fig. 356 From Cateran Bay, Border Island, Whitsunday Islands, collecting station 96.



Fig. 357



Fig. 358

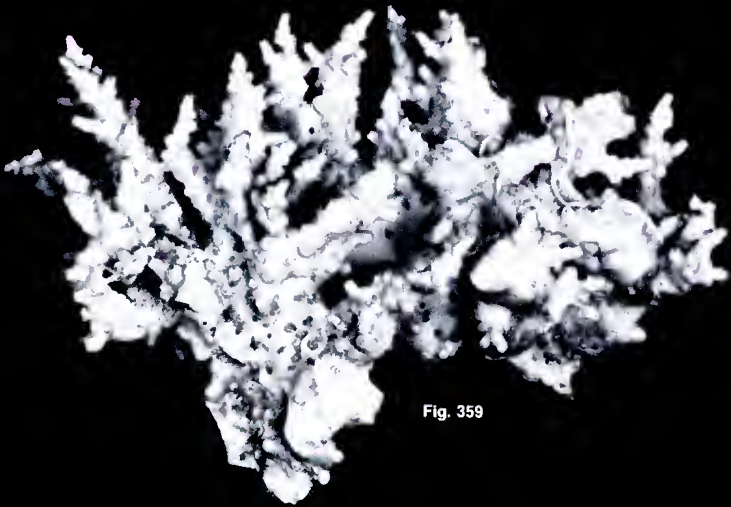


Fig. 359

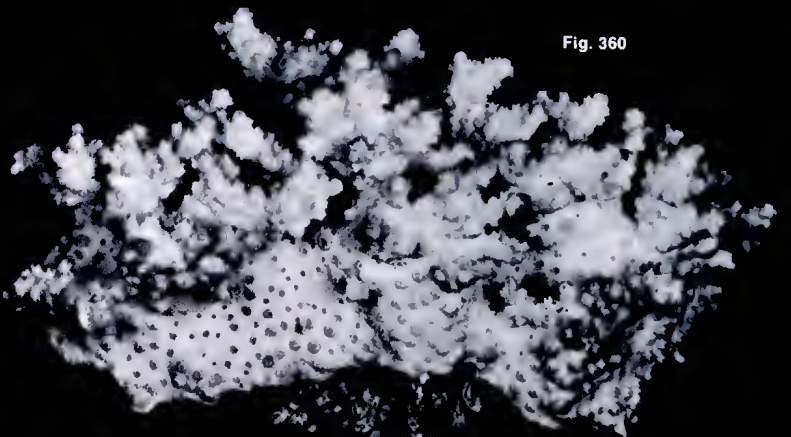


Fig. 360

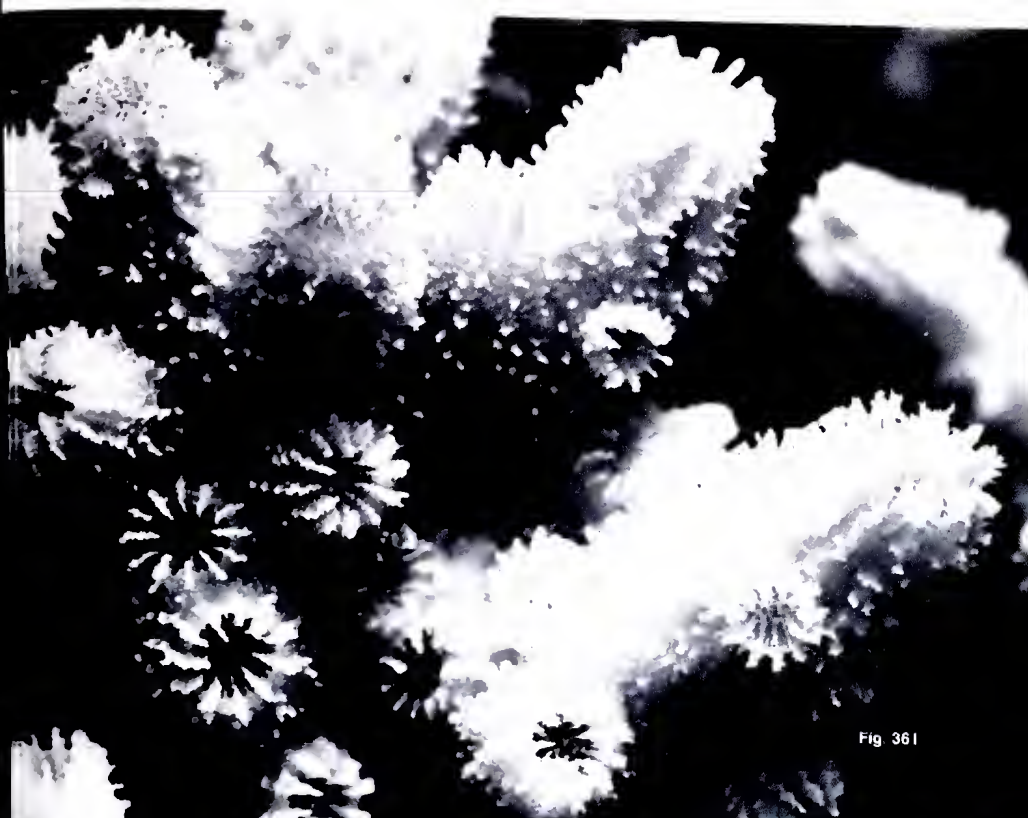


Fig 361



Fig 362

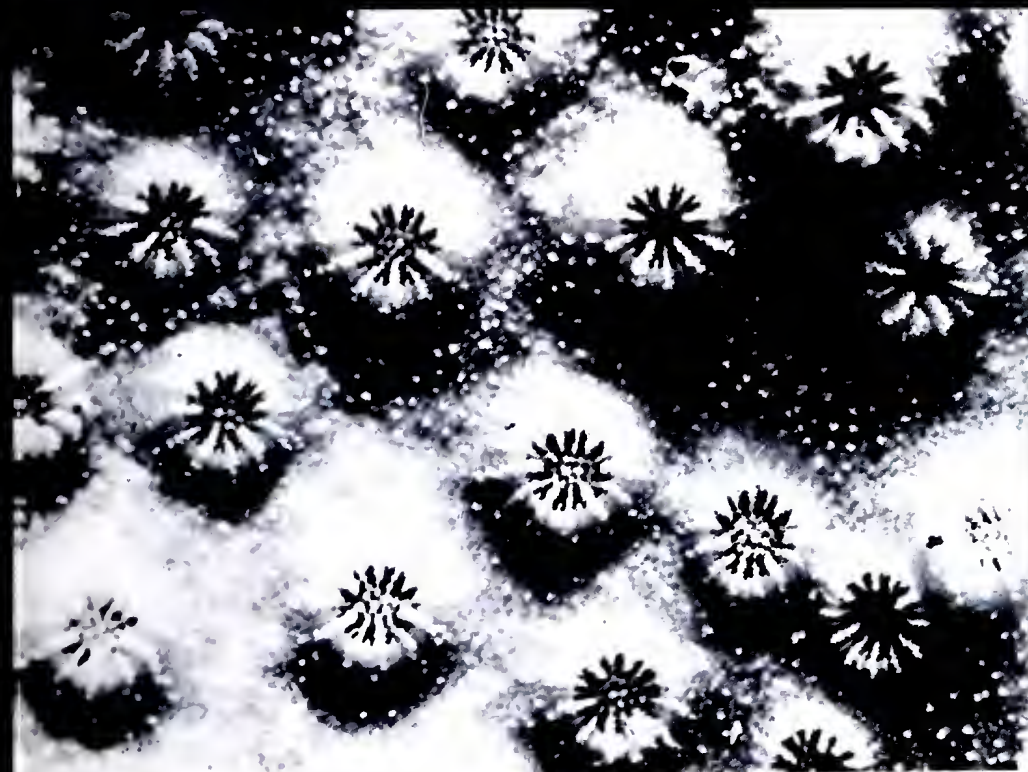


Fig 363



Fig 364

Figs. 361-364 *Cyphastrea japonica*.

- Fig. 361 Dendroid corallites of a corallum from Happy Bay, Long Island, Whitsunday Islands, collecting station 102 ($\times 5.0$).
 Fig. 362 Tip of a branch of the corallum illustrated in Fig. 357 ($\times 5.0$).
 Fig. 363 Flat encrusting part of a corallum, from Bushy Island-Redbill Reef, collecting station 80 ($\times 5.0$).
 Fig. 364 An axial corallite from the corallum illustrated in Fig. 358 ($\times 20.0$).

Figs. 357-360 *Cyphastrea japonica* ($\times 0.5$).

- Fig. 357 From Yorke Island, collecting station 13.
 Fig. 358 From Wyer Island, Murray Islands, collecting station 30.
 Fig. 359 From Lizard Island, collecting station 11.
 Fig. 360 From Elk Cliff, Great Palm Island, collecting station 37.

Synonymy

Echinopora Lamarck, 1816.

Explanaria Lamarck, 1816; (*pars*) Ehrenberg, 1834.

Echinastrea de Blainville, 1830.

Stephanocora Ehrenberg, 1834.

Acanthopora Verrill, 1864.

Acanthelia Wells, 1937.

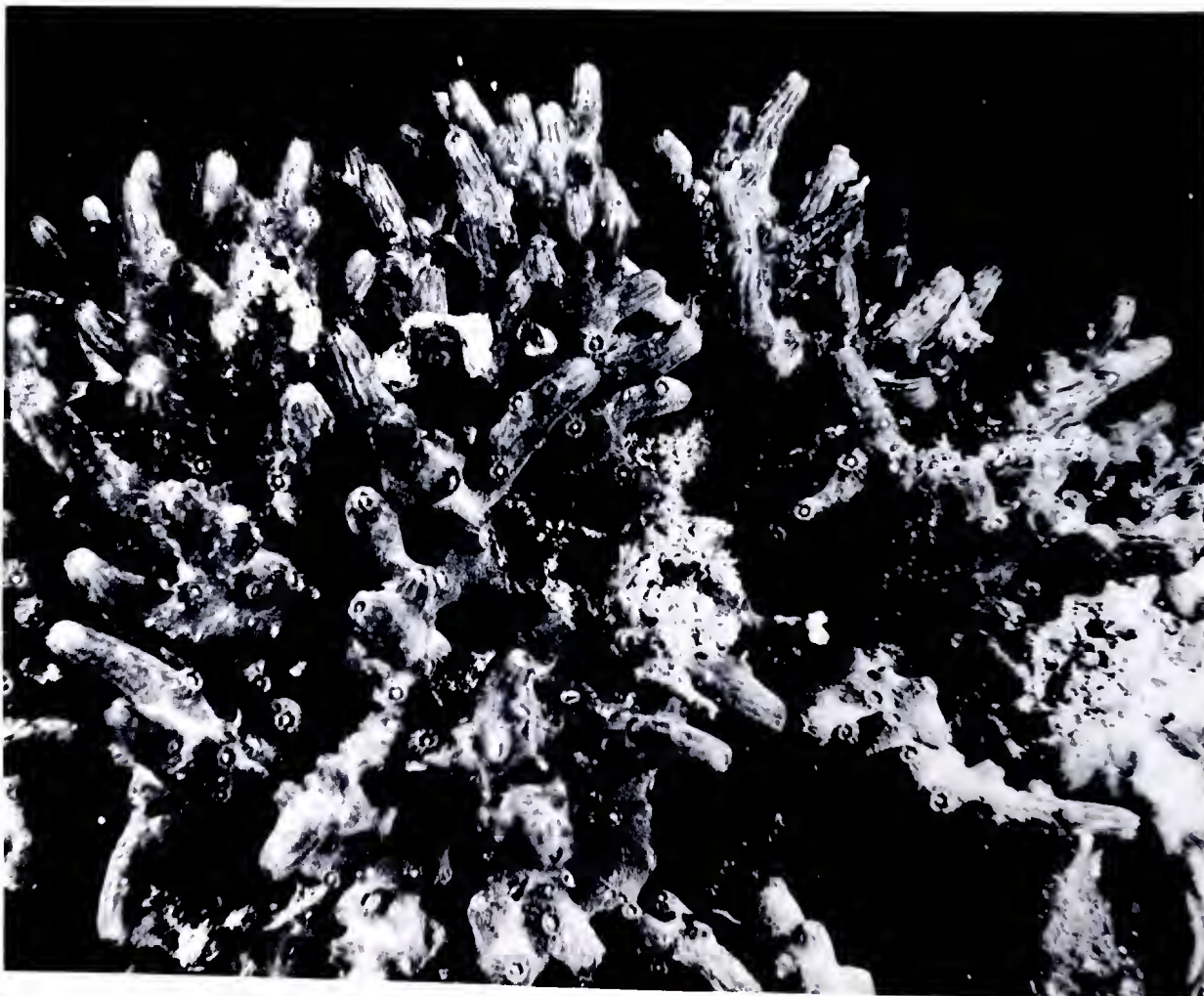
Type species *Echinopora rosularia* Lamarck, 1816 (= *Madrepora lamellosa* Esper, 1897).

Affinities

The genus *Echinopora* clearly belongs in the Faviidae and there are no grounds to justify the family Echinoporidae, proposed by Verrill (1901), in which Yabe, Sugiyama & Eguchi (1936) included *Mycedium* and *Oxyphyllia* (= *Echinophyllia*) and Umbgrove (1939) included *Tridacophyllia* (= *Pectinia*).

Within the so-called Montastreinae, *Echinopora* is most closely related to *Cyphastrea* ('indeed *Echinopora* is almost a *Cyphastrea* enlarged' wrote Crossland in 1952), the major differences between the two genera being the size of the corallites (larger in *Echinopora*), the average growth form (more massive, as a rule, in *Cyphastrea*), and the corallite walls (better developed and imperforate in *Cyphastrea*). The ornamentation of the exotheca (costate or spinulose) is certainly not a good character on which to separate *Echinopora* from closely

Fig. 365 *Cyphastrea japonica*, *in situ* at the Palm Islands ($\times 2.0$).



related genera, since *Echinopora* species can be either spinulose or costate (without spines), as shown by the recent discovery of a glabrous species by Nemenzo (1959), described under the name *Leptastrea mammiformis*. It is precisely the nature of the exotheca, showing well developed costae but no spines, which led Nemenzo, apparently without hesitation, to place his new species in the genus *Leptastrea*, although the latter is subcerioid. Within the genus *Echinopora*, the situation at the species level remained confused until Matthai's (1914) excellent revision, in which many species fell into synonymy. Indeed Matthai's treatment of the genus has been widely adhered to by more recent authors, with the exception of *E. horrida*, which Matthai considered (with doubts) as synonymous with *E. lamellosa*, but which has emerged as a valid, distinct species. It is worth mentioning here that the genera *Acanthopora* Verrill, 1864 and *Acanthelia* Wells, 1937 were proposed for *Echinopora horrida* on the basis of its peculiar, dendroid growth form only, opinions which were not followed by subsequent authors. Since Matthai, the species problems within *Echinopora* have been reappraised by Umbgrove (1939), Crossland (1952) and Chevalier (1975). The difficulties are probably best circumscribed and summarised by Crossland, who writes: 'I believe that the four species *gemmacea*, *lamellosa*, *hirsutissima* and *horrida* are distinct though I am not, in every case, able to separate them with confidence'. This statement received, *a posteriori*, a confirmation from Chevalier, who went a step further when attempting to explain the situation as follows: 'Nous pensons, à titre d'hypothèse, qu'en Mélanésie, l'évolution du genre *Echinopora* a été moins rapide que dans l'Océan Indien, et que les différences entre *E. lamellosa*, *E. gemmacea* et *E. hirsutissima* y sont moins facilement discernables'.

The present authors support Chevalier's hypothesis, which actually applies not only to Melanesia but to the entire south-west Pacific. As a consequence, and in accordance with this hypothesis, the three species of *Echinopora* involved here (*E. lamellosa*, *E. gemmacea* and *E. hirsutissima*) are more distinct in the Indian Ocean (and in the Red Sea) than in the south-west Pacific, but they each display a much greater intraspecific variability.

***Echinopora lamellosa* (Esper, 1795)**

Synonymy

Madrepora lamellosa Esper, 1795.

Echinopora rosularia Lamarck, 1816; Dana (1846); (*pars*) Edwards & Haime (1850, 1857); Studer (1878); Ortmann (1888); Gardiner (1904).

Echinastrea rosularia de Blainville (1830, 1834).

Echinopora undulata Dana, 1846.

Echinopora reflexa Dana, 1846.

Echinopora flexuosa Verrill, 1901.

Echinopora striatula Studer, 1878.

Echinopora elegans Verrill, 1901.

Echinopora concinna Verrill, 1901.

Echinopora lamellosa (Esper); Matthai (1914); Vaughan (1918); Faustino (1927); Boschma (1928); Boschma & Verwey (1930); Thiel (1932); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939); Crossland (1952); Wells (1954); Stephenson & Wells (1955); Nemenzo (1959); Scheer & Pillai (1974); Chevalier (1975).

Material studied

Yorke Island, Sue Island (2 specimens), **North West Reef, Thursday Island, Tjou Reef** (3 specimens), **Yonge Reef, Lizard Island** (9 specimens), **Eagle Reef** (2 specimens), **Low Isles** (6 specimens), **Bowl Reef, Palm Islands** (46 specimens),



Fig. 366



Fig. 368



Fig. 367

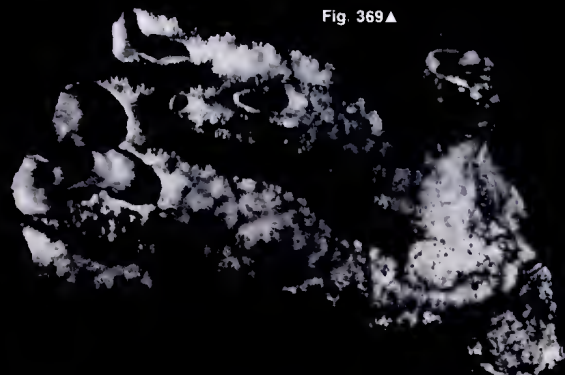


Fig. 369A

Whitsunday Islands, Bushy Island-Redbill Reef (3 specimens), **Pompey Complex** (3 specimens), **Swain Reefs** (3 specimens).

These localities include collecting stations 2, 9, 10, 13, 14, 17, 19, 32, 34, 35, 36, 37, 38, 41, 42, 43, 45, 51, 54, 55, 56, 57, 59, 69, 71, 73, 76, 90, 91, 92, 100, 101, 103.

Previous records from Eastern Australia

Low Isles and vicinity, Yonge (1930), Stephenson *et al.* (1931), Manton (1935), Crossland (1952), Stephenson & Wells (1955); **Heron Island**, Salter (1954).

Characters

Colonies are laminar, foliate or cyathiform, rarely encrusting. Laminar or foliate colonies expand horizontally or vertically. The margins of lamina are entire or in large lobes. Hollow, knob-like protuberances may develop from the central part of some colonies. These are up to 30cm high and may be funnel-shaped. The type of budding described by Boschma (1928) and Boschma & Verwey (1930) is frequently observed on the lower face of subhorizontal colonies, leading to the existence of a second layer of calices. Larger laminar or cyathiform colonies are generally entirely bifacial (i.e. with corallites on both sides), with a number of smaller lamina growing in a vertical plane, at right angles to the principal ones.

Corallites are circular, cylindrical or markedly conical, equal or subequal in height. Septa are in three or four cycles, the fourth being generally rudimentary when present. The first two cycles reach the columella. Septa of the primary cycle are usually markedly exsert above the theca. Sometimes they are divided into two or three equal or unequal lobes, which can eventually take the appearance of echinulated dentations. The margins of the septa bear small granules or dentations, slightly more developed on the inner and lower part, where they may become sub-horizontal. The septal sides are ornamented with numerous, slightly elongated or lamellar granulations, arranged according to the direction of the septal trabeculae. Secondary cycle septa have a structure similar to the primary cycle. In some instances they are equally well developed but are usually slightly smaller. A ring of paliform lobes is generally present in front of the first two cycles of septa, bearing granules similar to those of the septa on their margin and lateral sides. These paliform lobes can be as tall as the principal septal lobes, but may be reduced to vertically projecting spiniform processes. Paliform lobes are connected to the septa by the fusion of subhorizontal dentations, leaving between them a vertical row of pores. The columellae are well developed, spongy and composed of the distal part of subvertical or slightly inclined trabeculae, horizontally connected by transverse thickenings and intermingled at the periphery with the free margin of the lower septal dentations. Costae are variably developed, equal or subequal, generally more distinct towards the upper margin. They bear one to three well developed spines which are themselves ornamented, particularly at their tips, with granules similar to those observed on the upper and inner septal margins. The exotheca is compact, composed of fused costae which are sometimes hardly distinguishable except in the peripheral area of the colony where they become laminar. These exothecal costae bear numerous, well developed spines, close to each other and arranged in regular, parallel rows except close to the corallites, where their disposition becomes confused. These exothecal spines have the same structure as the costal spines, and there is often a remarkable continuity, and uniformity of aspect between exothecal spines, costal spines and septal lobes.

Living colonies (Figs. 474, 475) are amber, pale brown or green in colour with darker brown or green oral discs. The margins of the colonies are lighter in colour.

Figs. 366-369 *Echinopora lamellosa*.

- Fig. 366 From the Swain Reefs, showing a flat uni-facial corallum with numerous small corallites ($\times 0.75$).
Fig. 367 From Bowl Reef, collecting station 10, a piece of a thick flat bi-facial corallum with large, widely spaced corallites ($\times 1.5$).
Fig. 368 From the Swain Reefs, collecting station 69 ($\times 1.0$).
Fig. 369 From Yorke Island, collecting station 13, showing the characteristic foliate growth form ($\times 1.0$).



Fig. 370▲

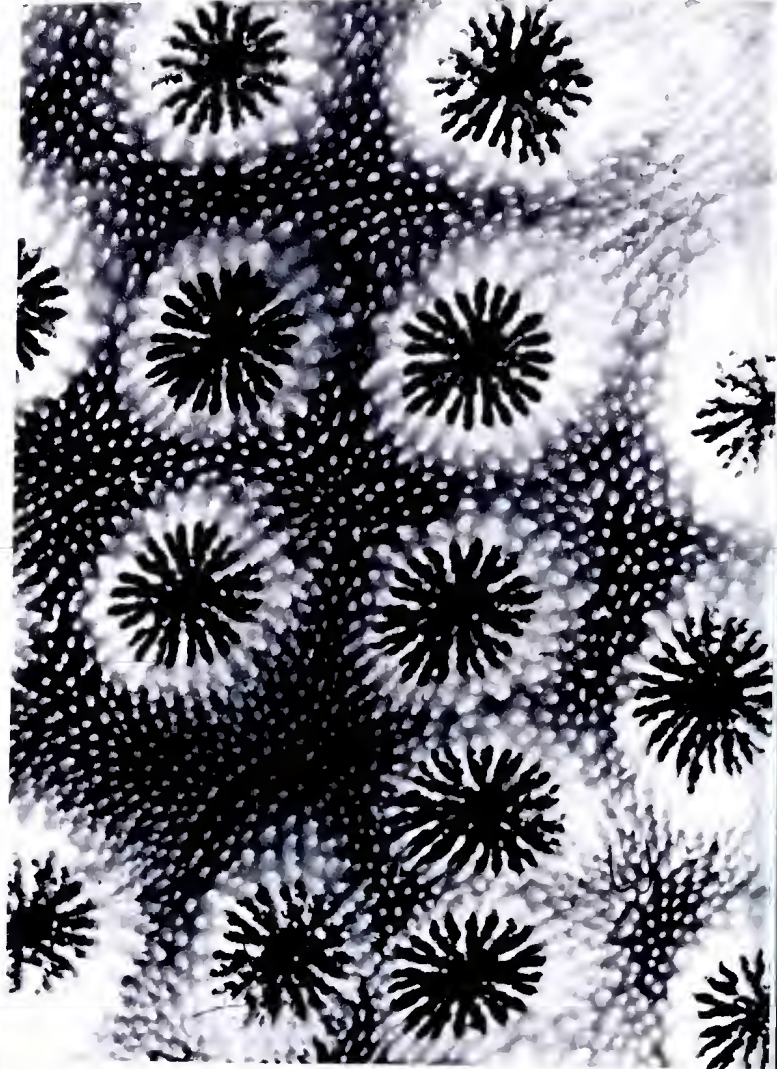


Fig. 371▲

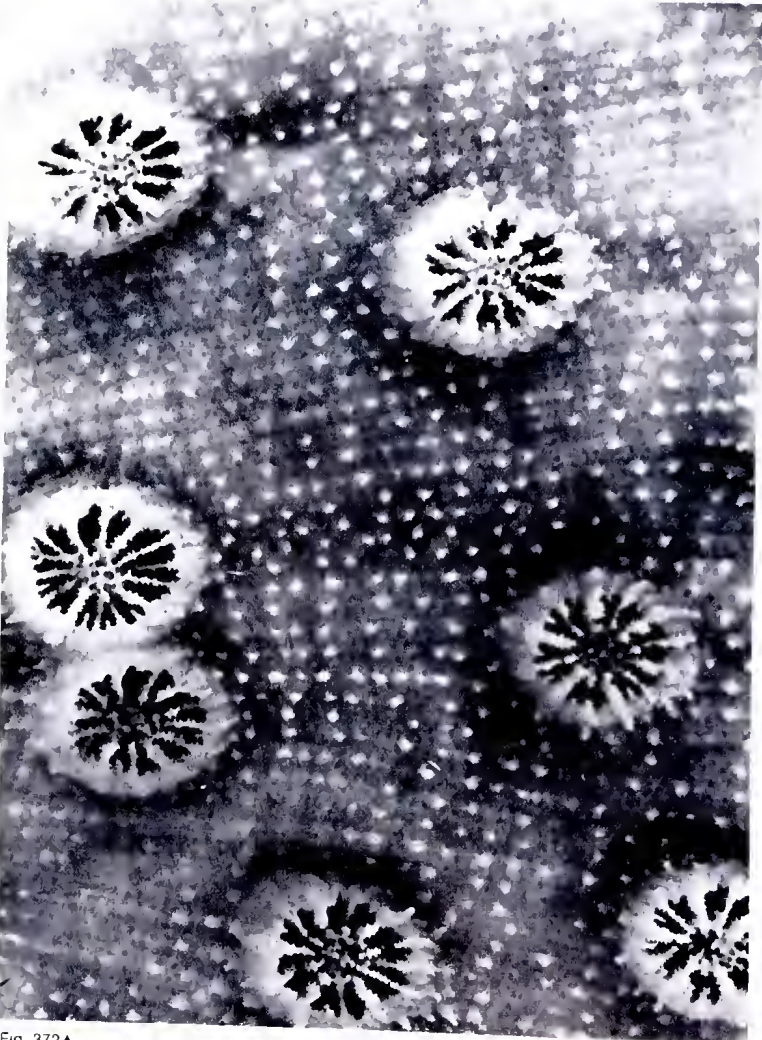


Fig. 372▲



Fig. 373▲

Skeletal variation

Echinopora lamellosa displays a wide range of intraspecific variations. In addition to the above-mentioned variations in growth forms and colony shapes, there is wide variation in the development of the septa and paliform lobes, and in their ornamentation. In particular, spines may be more or less developed, and more or less granular or echinulate. Sometimes they are very prominently and strongly ornamented, tending towards *E. hirsutissima*, the validity of which remains doubtful (see below).

However, the general structure of the corallites and exothecal characters, particularly within the one colony, remains remarkably regular, and the uniform distribution of costal spines (remaining always comparatively well developed and close together) are characteristic of the species.

Distribution

Widespread in the Indo-Pacific, from the Red Sea and south-west Indian Ocean to Japan, Bonin Island, Marshall Islands and Samoa.

Echinopora gemmacea (Lamarck, 1816)

Synonymy

Explanaria gemmacea Lamarck, 1816.

Echinastrea gemmacea (Lamarck); de Blainville (1830, 1834).

Figs. 370-373 *Echinopora lamellosa* ($\times 5.0$).

Fig. 370 From Bullumbooroo Bay, Great Palm Island, collecting station 35.

Fig. 371 Same corallum as Fig. 366.

Figs. 372, 373 Same corallum as Fig. 368, showing slightly hirsute spines arranged in regular rows; Fig. 373 showing incomplete fusion between adjacent exothecal costae giving rows of pits.

Fig. 374 *Echinopora lamellosa* from the Pompey Complex, collecting station 71, showing both laminar and foliate growth forms.



Stephanocora hemprichii Ehrenberg, 1834.

Explanaria hemprichii Ehrenberg, 1834.

Echinopora gemmacea (Lamarek); Edwards & Haime, 1849; Edwards & Haime (1857); Matthai (1914); Thiel (1932); Umbgrove (1939); Crossland (1941); Rossi (1954); Scheer (1967); Chevalier (1975).

Echinopora rousseaui Edwards & Haime, 1849.

Echinopora solidior Edwards & Haime, 1849; Edwards & Haime (1857).

Echinopora chrenbergi Edwards & Haime, 1849; Edwards & Haime (1857); Klunzinger (1879); Gravier (1911).

?*Echinopora hemprichii* Edwards & Haime, 1857.

?*Orbicella mammillosa* Klunzinger, 1879.

Echinopora fruticulosa Klunzinger, 1879; Gravier (1911).

Echinopora concamerata Klunzinger, 1879.

Echinopora carduus Klunzinger, 1879.

Material studied

Sue Island (2 specimens), **Great Detached Reef, Tijou Reef** (4 specimens), **Bewick Island, Yonge Reef, Lizard Island, Eagle Reef, Low Isles, Palm Islands** (6 specimens), **Bushy Island-Redbill Reef** (3 specimens), **Swain Reefs** (2 specimens).

These localities include collecting stations 1, 2, 9, 17, 18, 19, 34, 36, 51, 55, 56, 60, 73, 77, 80, 81.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are lamellar, rarely thick or encrusting, sometimes with ramose and subdendroid proliferations. Corallites are up to 5mm in diameter, circular or slightly elongated. They are cylindrical and superficial or conical and protruding. Conical corallites are sometimes inclined on the general surface of the corallum. Marginal corallites are slightly smaller and inclined towards the periphery of the corallum. Septa are in three cycles, with occasional rudiments of a fourth abortive and incomplete cycle. Septa of the primary cycle are very exsert and thick near the wall, thinning rapidly towards the centre. Septa of the secondary cycle are well developed. They reach the columellae, but are less exsert than those of the primary cycle. The tertiary cycle is reduced to narrow lamellae in most cases. Septa of the primary cycle have a prominent upper lobe (sometimes divided into two parts) which is markedly exsert above the thecae. Ornamentation of the upper margin of septal lobes is composed only of small inconspicuous dentations. The free inner septal margin is subvertical and bears a few dentations which are subvertical on the upper margin, and which become increasingly inclined deeper in the corallites. Paliform lobes are not well developed, contrary to the situation found in *E. lamellosa*.

Septal sides have numerous echinulated granules arranged in rows towards the septal margin, where they sometimes fuse into short lamellae. Septa of the secondary cycle also have an upper lobe, but this does not extend above the tips of the first costal spines. The inner septal margin bears dentations, the lower of which fuse with the columellae, leaving between

Figs. 375-377 *Echinopora gemmacea* ($\times 0.75$).

Fig. 375 From Fantome Island, Palm Islands, collecting station 34.

Fig. 376 From Sue Island, collecting station 17.

Fig. 377 From Bushy Island-Redbill Reef, collecting station 73.



Fig. 375



Fig. 376

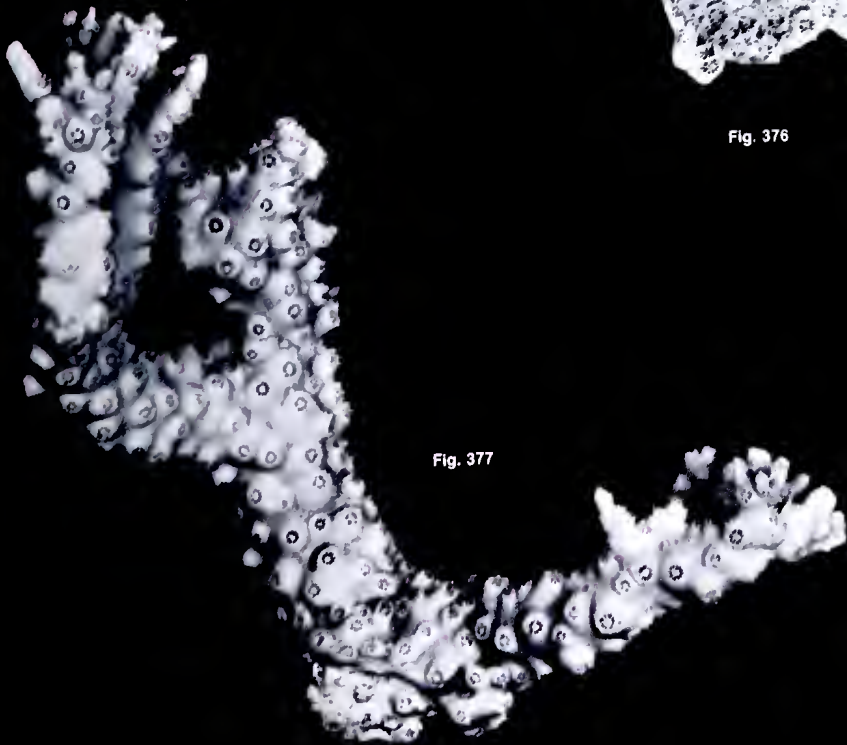


Fig. 377

them a number of large pores. The columellae are well developed and spongiöse. They are composed of subvertical trabeculae with flattened, twisted tips towards the centre and of septal dentations at the periphery. The columella processes are close to each other, and the whole axial organ has a dense, although porous appearance. Costae are present, fused together, equal or unequal. In the latter case, those corresponding to primary septa are higher and thicker than those of the secondary cycle. When the corallites are inclined on the general surface

Figs. 378-381 *Echinopora gemmacea* ($\times 5.0$).

Fig. 378 Holotype of *Echinopora gemmacea*.

Fig. 379 Same corallum as Fig. 377.

Fig. 380 From Fantome Island, Palm Islands, collecting station 34.

Fig. 381 From Elk Cliff, Great Palm Island, collecting station 37, showing incomplete fusion between adjacent exothecal costae giving rows of pits.

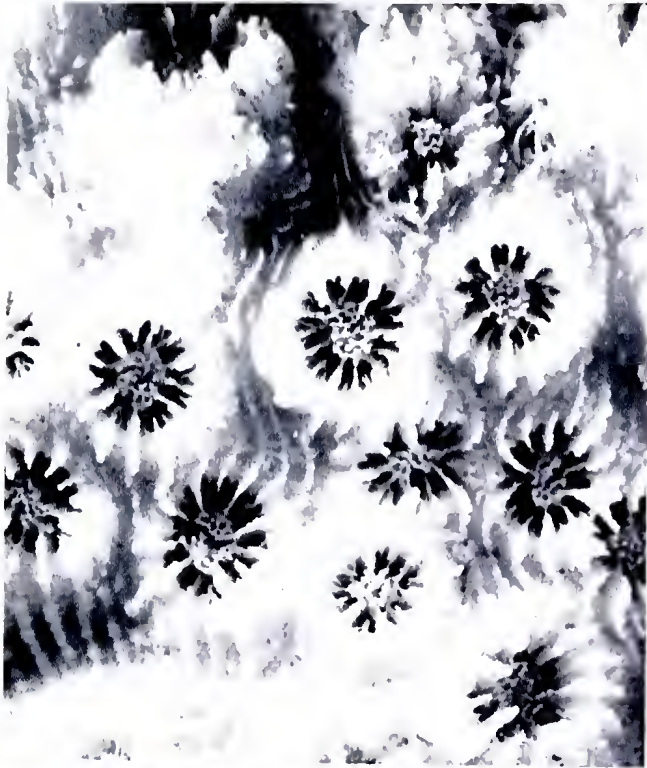


Fig 378▲

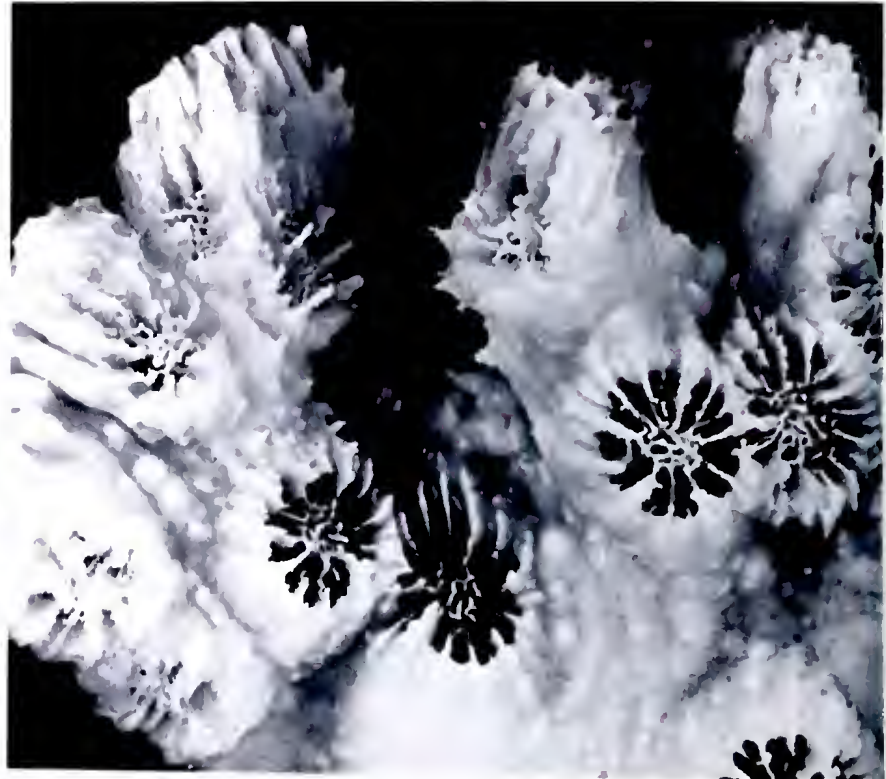


Fig 379▲

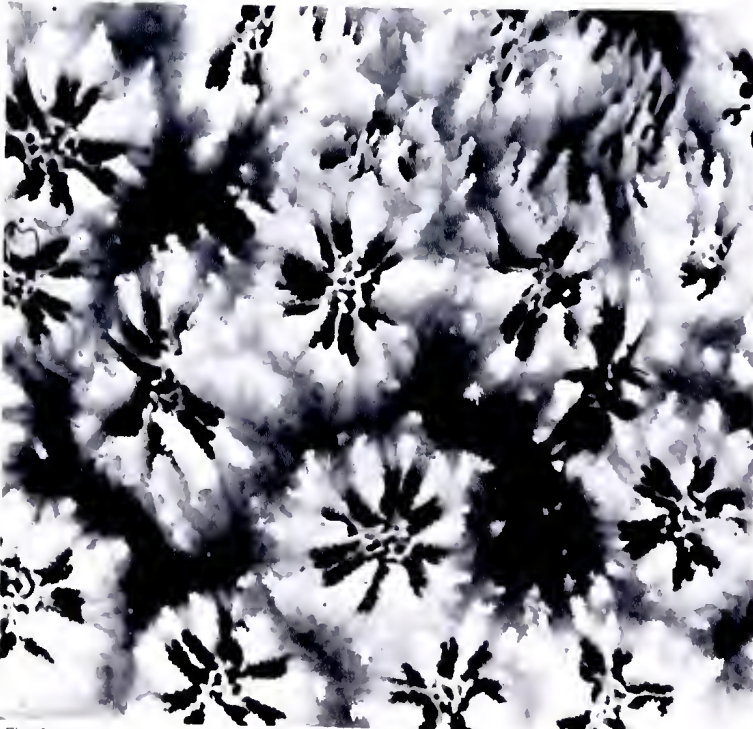


Fig 380▲



Fig 381▲

of the corallum, costae tend to be better developed on the upper side of the corallites. Costae bear 1-4 well developed spines with thick bases and granules or echinulations at their tips. The exotheca is mostly compact, with only a few vesicular exothecal dissepiments present. The exotheca is thus mainly composed of fused exothecal costae. They are generally high, lamellar and very conspicuous towards the margin of the corallum. Fusion between the exothecal costae is usually incomplete and intercostal grooves show regular lines of small depressions. On their summit the costae bear irregularly spaced, well developed spines or dentations with a structure similar to those of the calicular costae.

Skeletal variation

Most of the coralla in the present series are lamellar, but a few of them have upward proliferations giving them a somewhat branching aspect. However, they never reach the typically fruticose growth form common in the Red Sea. None of these colonies has the characteristic dendroid growth form of *E. horrida*. Corallites tend to be close together, although they are further apart in some specimens with protuberant conical and often slightly inclined corallites. There is comparatively little intraspecific variation in the calicular structures, although the number and development of septa may differ slightly from one corallite to another, and from one colony to another. The number and development of costal and exothecal dentations or spines is also variable, being less developed in specimens with protuberant corallites. At the same time, the exothecal spines tend to fuse into short ridges, but never to the degree observed in some *E. gemmacea* of the Red Sea and western Indian Ocean.

Affinities

Chevalier (1975) pointed out the difficulty of identifying *E. gemmacea* from the south-west Pacific (French Melanesia) by comparison with the holotype from the Indian Ocean. The present series as a whole is fairly similar to Chevalier's; both show comparatively little intraspecific variation. They come close to the types of *E. concamerata* and *E. carduus* (both

Fig. 382 *Echinopora gemmacea* from the Swain Reefs, collecting station 67.



E. gemmacea), although they show some differences with the actual holotype of *E. gemmacea*. Thus there is less difference between *E. gemmacea* and *E. lamellosa* in the western Pacific, than between the same two species in the Indian Ocean and the Red Sea. Western Indian Ocean *E. gemmacea* is a much more distinct species with a much wider range of intraspecific variations, and it is considerably more common in the Red Sea and western Indian Ocean than in the western Pacific. These observations tend to support the hypothesis that evolution of *E. gemmacea* is more advanced in the Red Sea and western Indian Ocean than in the western Pacific.

A number of species of *Echinopora*, previously considered as distinct, have been put into synonymy with *E. gemmacea* by Matthai (1914) and Chevalier (1975). After studying the descriptions and figures and, whenever possible, re-examining type material, the present authors reached the same conclusions. However, the relationships of *Orbicella mammillosa* Klunzinger and *E. gemmacea* remain unsolved. Von Marenzeller (1907) and Matthai (1914) considered both *Orbicella mammillosa* and *O. forskalana* Edwards & Haime to be synonyms of *E. gemmacea*, a standpoint recently quoted by Scheer (1967), but not re-examined since Matthai. *Orbicella mammillosa* Klunzinger has been identified as *Plesiastrea mammillosa* by Loya & Slobodkin (1971) and as *Echinopora mammillosa* by Wells (Tel Aviv University Collections). A few specimens of this series have been examined by the present authors, who conclude only that synonymy with *E. gemmacea* is a possibility.

Distribution

Widely distributed in the Indo-Pacific, including the Red Sea, the Gulf of Aden, East Africa, Madagascar, the Mascarene Islands, the Seychelles Islands, Java, Celebes, the Great Barrier Reef and New Caledonia.

***Echinopora hirsutissima* Edwards & Haime, 1849**

Synonymy

Echinopora hirsutissima Edwards & Haime, 1849, Edwards & Haime, (1857); Matthai (1914); Wells (1961); Chevalier (1975).

Echinopora helli Rousseau, 1854; Edwards & Haime (1857).

Echinopora solidior Gardiner, 1904; *non* Edwards & Haime (1849).

Echinopora tertia Gardiner, 1904.

Material studied

Yorke Island, Palm Islands.

These localities include collecting stations 13, 36.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are laminar, explanate or contorted in vertically rising, hollow projections without apertures at the top. Corallites are superficial or only slightly protruding, and sometimes inclined on the general surface of the corallum. Septa are in three cycles with a fourth rudimentary and very incomplete cycle present in some corallites.

Septa of the primary cycle are comparatively thick, very exsert, hirsute and reach the columella. The upper margin is divided in two or three distinct, very prominent lobes, covered with granules. The inner septal margin bears vertical or inclined dentations which are separated from the rest of the septa by a series of pores. The outer septal lobe is often flattened in a direction perpendicular to the radial direction. It is sometimes concave towards the corallite centres or even divided into two elements. In some instances, this flattened or divided lobe appears to replace the first costal spine (or costal dentation). The septal sides are covered

with granules. Septa of the secondary cycles are less developed and usually less exsert, but nevertheless reach the columellae. The internal part of the septa is distinctly perforate, being composed of a series of inclined or even subhorizontal dentations, the extremities of which join the inner, vertical paliform lobe. Costae are well developed, equal or sub-equal and bear 2-5 well developed spines, ornamented with granules or echinulations. The upper costal spines are often club-shaped, with an inflated tip, or are sometimes divided incompletely or completely into two parts. In the latter instances, the spines tend to be arranged in two rows along the calicular costae. The columellae are well developed, spongy and composed of some vertical trabeculae and the inner free extremities of the septal dentations which are intricately anastomosed. The exotheca is compact. Exothecal costae are well developed, equal or sub-equal. They bear numerous tall spines close together, with abundant granulations or echinulations.

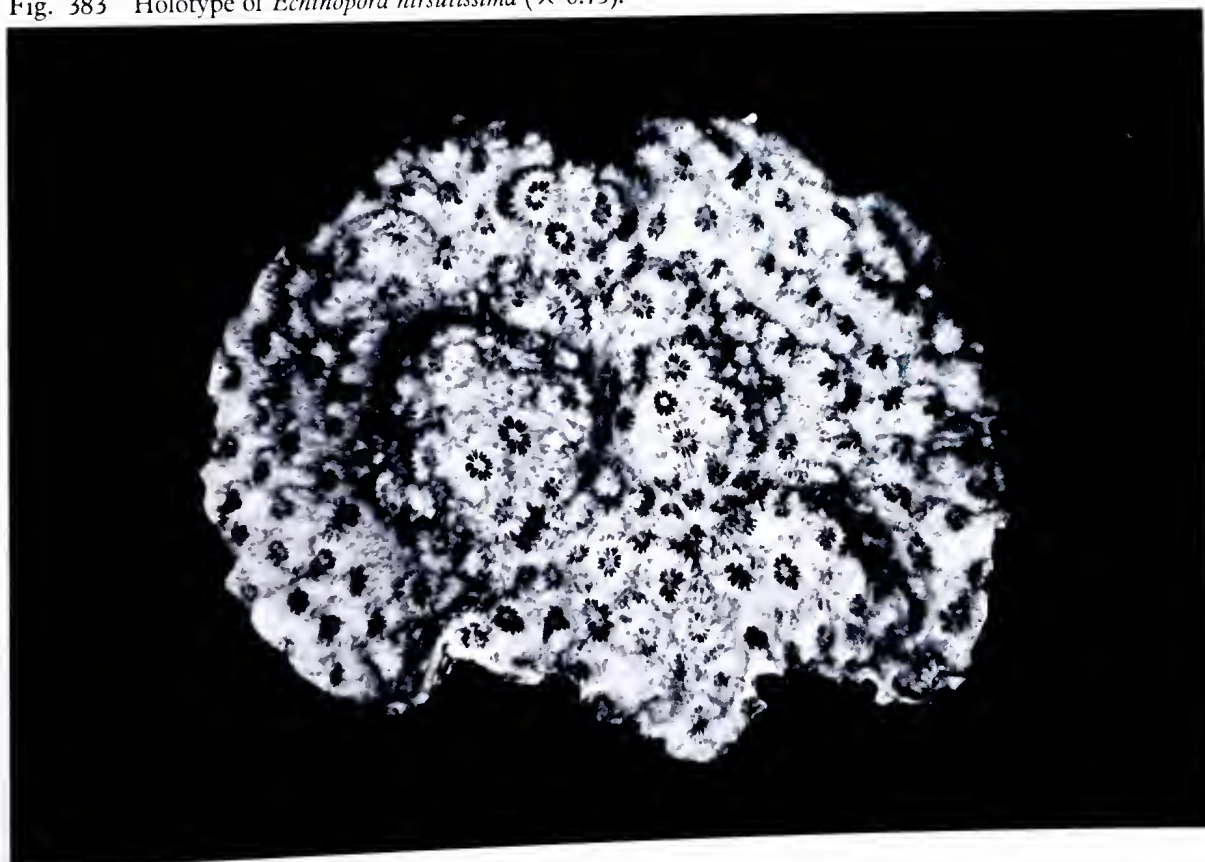
Affinities

The status of the present series of two specimens is uncertain and nothing can therefore be said of the intraspecific variability, which Chevalier (1975) suspected to be important. Our specimens, like Chevalier's, have characteristics in common with *Echinopora lamellosa*, although a comparison of the holotypes of *E. hirsutissima* and *E. gemmacea* suggests closer affinity between these two species. Chevalier even suggested that *E. hirsutissima* could be synonymous with *E. gemmacea*, but so far, there is no convincing proof. The present authors support Chevalier's view that differences between *E. lamellosa*, *E. hirsutissima* and *E. gemmacea* are less conspicuous in the western Pacific than in the Indian Ocean.

Distribution

Widely distributed in the Indo-Pacific from the Red Sea to New Caledonia including the Maldive and Seychelles Islands, Chagos, the Mascarene Islands, India, Ceylon and the Great Barrier Reef.

Fig. 383 Holotype of *Echinopora hirsutissima* ($\times 0.75$).



Echinopora horrida Dana, 1846

Synonymy

Echinopora horrida Dana, 1846; Brüggemann (1878); Studer (1881); Ortmann (1888); Faustino (1927); Umbgrove (1939); Crossland (1952); Nemenzo (1959); Chevalier (1975).

Acanthopora horrida (Dana); Verrill (1864).

Acanthelia horrida (Dana); Wells (1937).

Material studied

Yorke Island (3 specimens), **Murray Islands, Sue Island** (2 specimens), **Tijou Reef, Lizard Island** (4 specimens), **Eagle Reef, Hope Island, Palm Islands** (9 specimens), **Whitsunday Islands, Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex** (3 specimens), **Swain Reefs** (3 specimens).

These localities include collecting stations 6, 7, 11, 13, 17, 19, 34, 42, 45, 55, 57, 60, 71, 73, 75, 80, 81, 97, 100, 105.

Figs. 384, 385 *Echinopora hirsutissima* ($\times 0.75$).

Fig. 384 From Yorke Island, collecting station 13.

Fig. 385 From Electra Head, Great Palm Island, collecting station 36.

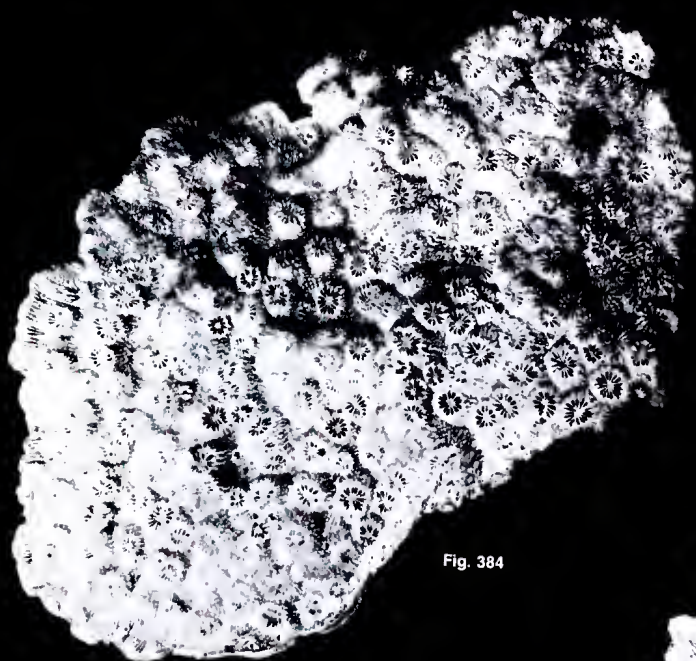


Fig. 384



Fig. 385

Previous records from Eastern Australia

Low Isles and vicinity, Crossland (1952); Heron Island, Salter (1954).

Characters

Colonies are branching, dendroid, sometimes with a flat expanded laminar base, with dimensions up to 20 x 15cm. Branches are up to 40mm in diameter, regularly decreasing towards the extremity, which is an acute or flattened expansion of exothecal costae. A few specimens have thick, solid, almost cylindrical branches, with comparatively blunt tips.

Corallites are circular, up to 4mm in diameter, cylindrical or with the shape of a truncated cone more or less protruding from the branches. Septa are generally in three cycles, the first two reaching the columella. Primary cycle septa are very exsert above the thecae, with septa being very thick at the periphery, decreasing rapidly in thickness from the thecae towards the centre of the corallites. Septa of the secondary cycle are less exsert and the upper lobe does not extend horizontally as far as those of the primary cycle. Secondary septa reach the columella deeper in the corallites. The tertiary cycle of septa is less developed, with a free inner margin. Some rudiments of a fourth cycle, always incomplete, are occasionally present.

The upper margin of the septa of the primary cycle expands to a tall prominent lobe, which may be divided into two to three smaller lobes. The free margin of these lobes bears

Figs. 386, 387 *Echinopora hirsutissima* ($\times 5.0$).

Fig. 386 Same corallum as Fig. 385.

Fig. 387 Same corallum as Fig. 384.

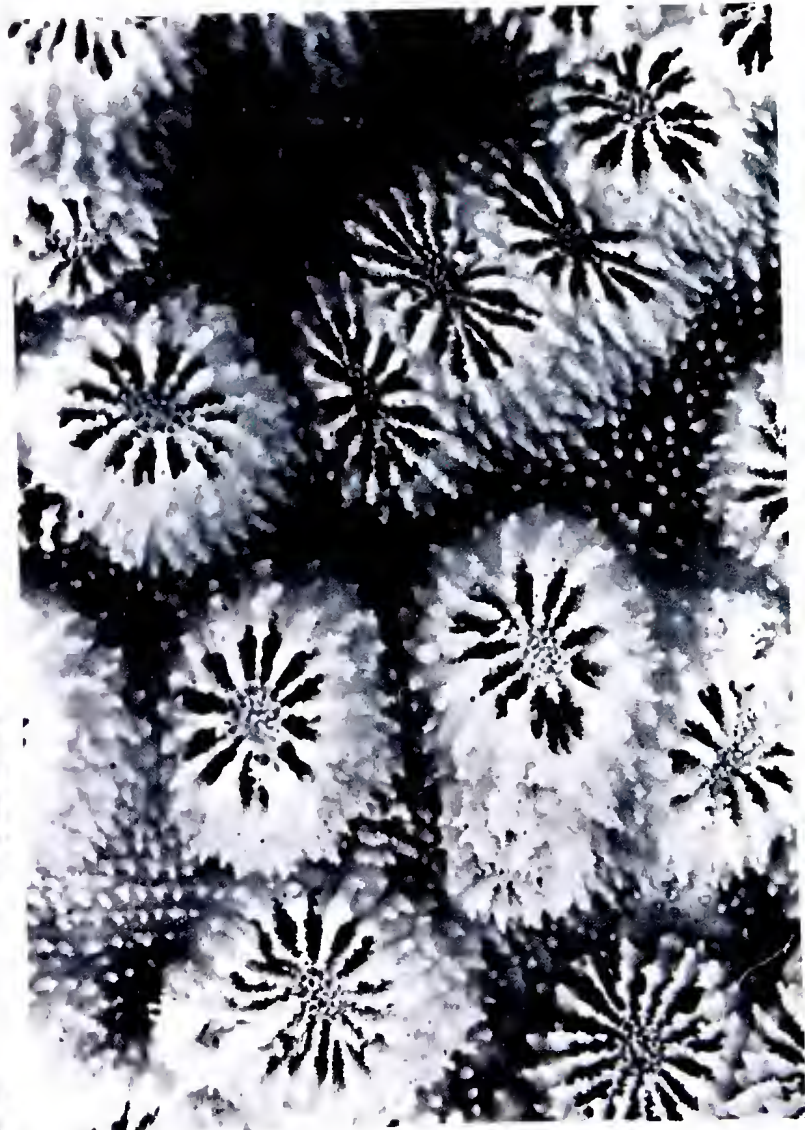


Fig. 387▲

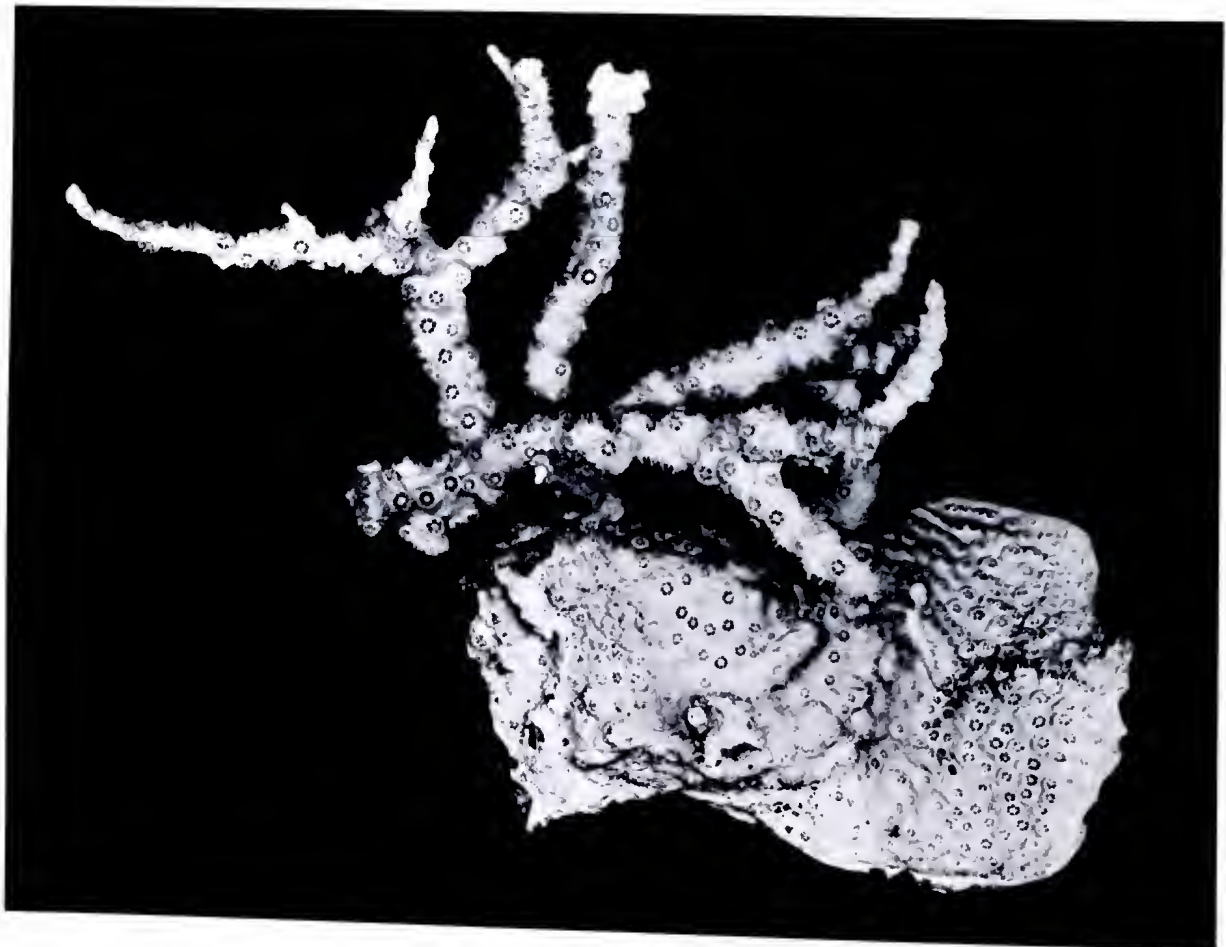
small granules or echinulations. The inner margin frequently has a subvertical or slightly inclined paliform dentation, which is separated from the inner and lower part of the septa by a series of vertically arranged pores. The septal sides have numerous small granules, sometimes fusing together and arranged in trabecular rows. Septa of the secondary cycle are thinner and much less exsert than those of the primary cycle. Their inner margins may bear a few paliform dentations, the lower ones merging with the columella. The columellae are spongy, well developed and are composed of the free extremities of vertical trabeculae, connected by horizontal elements. Towards the periphery, these trabeculae are inclined in a clockwise direction, and mix with the lower long dentations of the inner septal margin. The structure of the columellae is very similar to that of *Echinopora mammiformis* although generally more compact. Costae are well developed. They alternate slightly in size (those corresponding with the primary cycle being better developed), and increase in size towards the base of the corallites. They often bear up to four tall spines with terminal echinulations. The exotheca is compact or with only very few vesicular exothecal dissepiments. Exothecal costae are present and well developed, but are sometimes discontinuous or sinuose. They more or less follow the general direction of the branches except when close to the corallites and in areas where they are crowded. The exothecal costae appear to be incompletely fused and, in intercostal grooves, they show a series of conspicuous, regularly arranged, small depressions. Costae bear well developed spines, equal or unequal, often with an inflated base and terminal echinulations or granules.

Living colonies (Fig. 476) are pale to dark brown, rarely brown-green.

Skeletal variation

Although the colony shape is always dendroid (with a possible flat, laminar base), some variations are observed in the average diameter of the branches and branchlets, in the tapering

Fig. 388 *Echinopora horrida* from Frigate Cay, collecting station 81, showing both ramose and laminar growth forms ($\times 0.5$).



Figs. 389-391 *Echinopora horrida*.

Figs. 389, 390 From Frigate Cay, collecting station 81, showing exothecal ornamentation ($\times 5.0$).
Fig. 391 From Sue Island, collecting station 17 ($\times 6.25$).

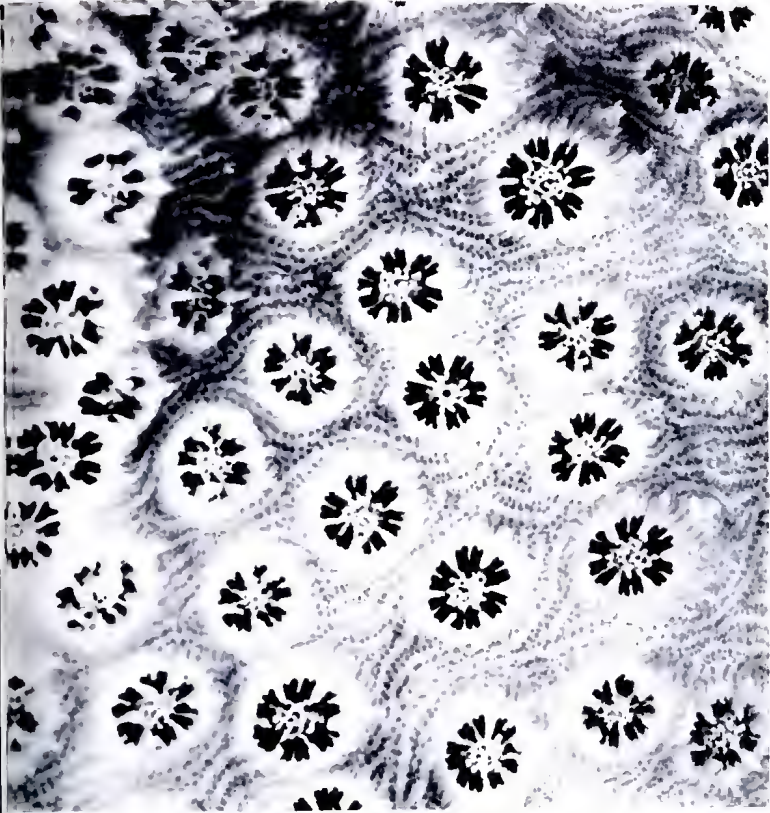


Fig. 389▲



Fig. 390▲

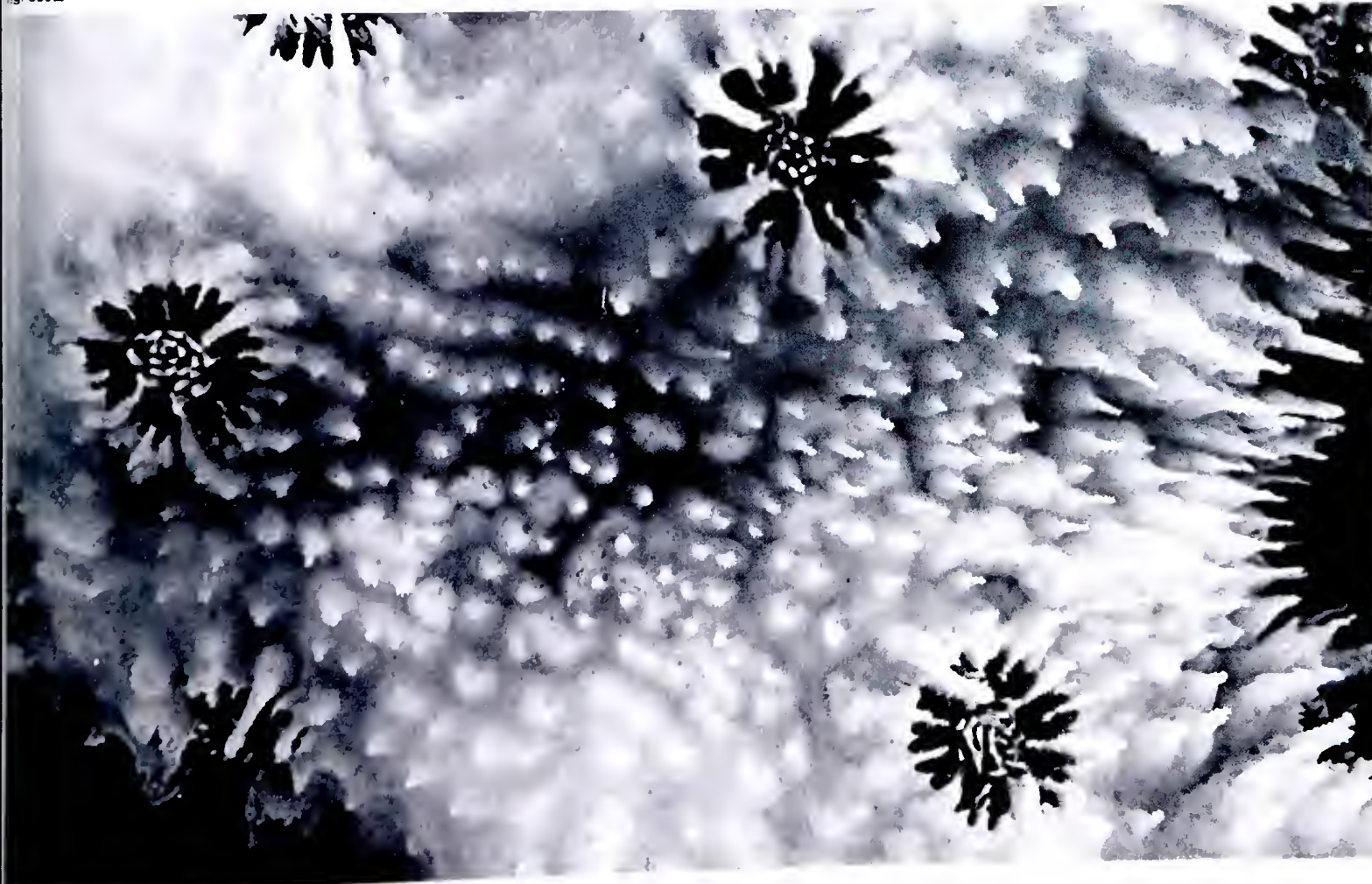


Fig. 391▲

of the tips (ranging from very acute to blunt) and in the degree to which branches anastomose.

The corallites may be superficial, with only the septal lobes of the primary cycle prominent or, on the contrary, they may be protuberant, in which case they usually take the shape of a truncated cone. The most variable character lies in the ornamentation of the exothecal costae. In some instances, they bear only a very few, small, irregularly distributed blunt spines. In other specimens, the exothecal spines are very tall, close together and regularly spaced, tending to be arranged in rows, along the branches (this pattern being that of the longitudinal exothecal costae themselves). On the horizontal laminar bases, the exothecal costae are well developed, with few spines, giving the exotheca a rather smooth appearance.

Affinities

By its growth form, *E. horrida* is similar to *E. mammiformis*, this resemblance being increased in the more glabrous specimens of *E. horrida*. However, even in that case, the two species can be separated without difficulty. Both species have in common the clockwise rotation of the trabecular elements of the columella, this characteristic being more obvious in *E. mammiformis*. The two species differ in some other characters of the calicular structure and of the exotheca. In particular, the series of small depressions between adjacent costae are constant in *E. horrida* and never found in *E. mammiformis*.

The affinities of *E. horrida* with *E. gemmacea* have been discussed by several authors. In particular, Vaughan (1918), Umbgrove (1939), Crossland (1952) and Chevalier (1975) have considered that the two species are different, despite a possible subdendroid, fruticose aspect of some colonies of *E. gemmacea* (particularly those from the Red Sea). Chevalier (1975) pointed out other distinctive characters: the tips of branches are composed of fused exothecal costae in *E. horrida* and the exothecal costae irregularly thickened and sinuous. The discovery of specimens of *E. horrida* with a well developed laminar base is not a character sufficient to reopen the discussion: calicular structure and exothecal characters (including branch tips) are different enough to justify maintaining the two species as separate, despite a superficial similarity of growth form in some instances.

Distribution

The present known distribution includes Singapore, Indonesia, New Guinea, the Philippines, the Great Barrier Reef, New Caledonia and Fiji.

***Echinopora mammiformis* (Nemenzo, 1959)**

Synonymy

?*Oculina fasciculata* Saville-Kent, 1900.

Leptastrea mammiformis Nemenzo, 1959.

Echinopora glabra Chevalier, 1975.

Material studied

Yorke Island (3 specimens), **Yonge Reef** (2 specimens), **Lizard Island** (9 specimens), **Bowl Reef**, **Palm Islands** (8 specimens), **Whitsunday Islands** (2 specimens), **Bushy Island-Redbill Reef** (3 specimens), **Pompey Complex** (7 specimens).

These localities include collecting stations 9, 10, 13, 32, 33, 35, 38, 41, 45, 57, 59, 71, 75, 80, 97, 99, 100.

Figs. 392-396 *Echinopora mammiformis*

Figs. 392, 395 From the Pompey Complex, collecting station 91, ($\times 0.8$ and $\times 0.35$ respectively).

Fig. 393 From the Swain Reefs, collecting station 79 ($\times 0.5$).

Fig. 394 From Iris Point, Orpheus Island, Palm Islands, collecting station 55 ($\times 0.8$).

Fig. 396 From the Pompey Complex, collecting station 75 ($\times 0.6$).

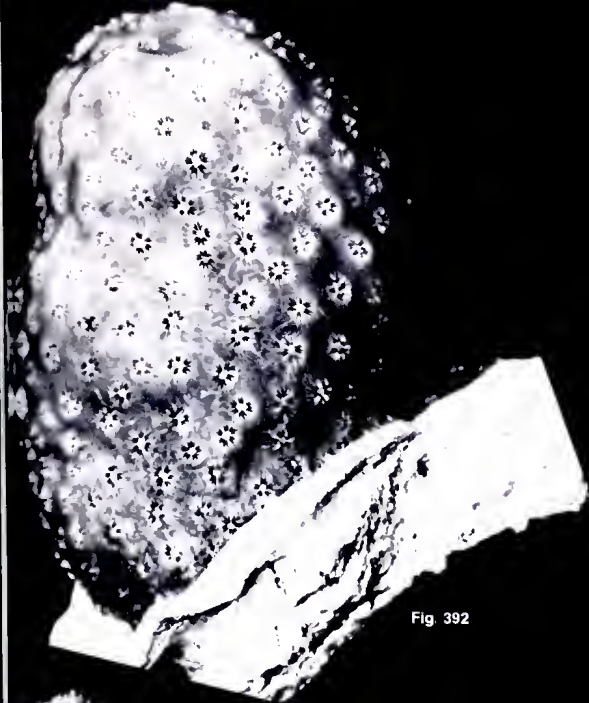


Fig. 392



Fig. 393



Fig. 394



Fig. 395

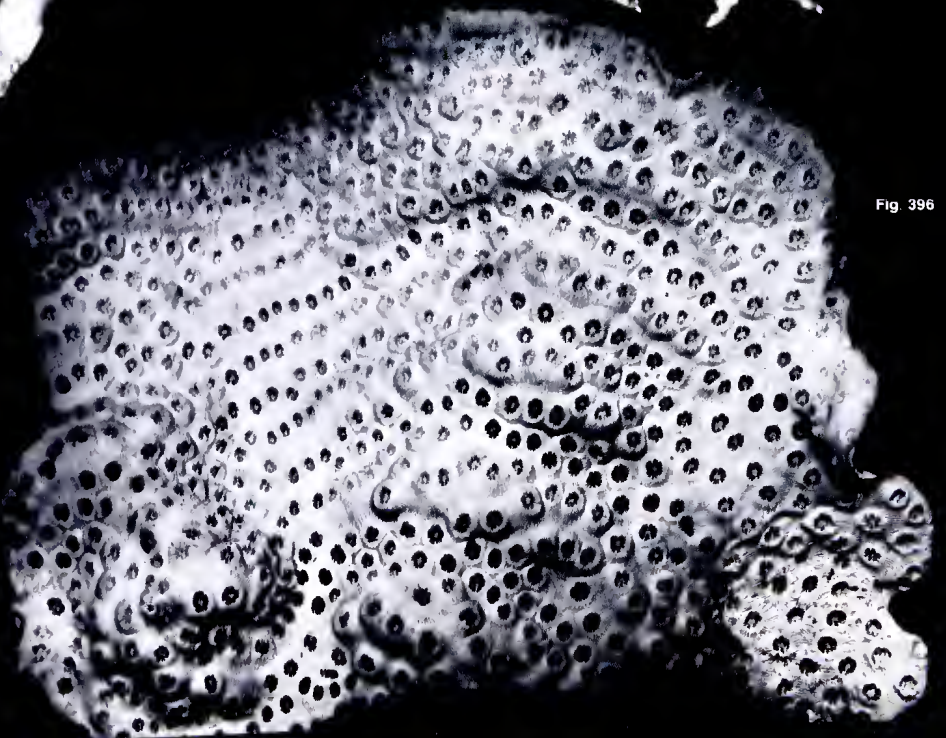


Fig. 396

Previous records from Eastern Australia

Not previously recorded.

Characters

Growth form is massive, hemispherical, explanate (lamellar or foliate), cyathiform or branching. In explanate or cyathiform colonies, the corallites tend to be arranged in rows parallel with the free margin. Most often, colonies are in large plates or cups from the centre of which arises a dense network of branches, up to 50cm high. Corallites are 'mammiform', with the shape of a truncated cone, more or less protruding, sometimes slightly inclined outwards close to the margins of the colony. Average diameter is 3-4mm. Younger corallites are almost cylindrical. Septa are thin, in three or four cycles. The tertiary cycle is sometimes incomplete, the fourth appears only as vertical ridges on the wall in the corallite cavity. Primary septa have an exsert upper margin. In coralla with superficial, non-protuberant corallites, only the septa of the primary cycle are prominent and reach the columellae. In coralla with very mammiform corallites, especially in well developed cones, all septa of the secondary cycle and some of the tertiary cycle are almost as developed as those of the primary cycle, with prominent upper margins extending to the columellae. The upper and inner margins of the septa are smooth, or have very small blunt dentations. Deeper in the corallites, the septal margin bears a few long, slender, subhorizontal paliform dentations. Still deeper, these dentations tend to fuse with a well developed columellar centre. As noted by both Nemenzo (1959) and Chevalier (1975), these horizontal trabecular expansions are often irregularly directed away from the radial direction, generally in a clockwise direction, around the centre of the columellae. The septal sides are granular, the small granules arranged in rows following a trabecular direction, or sometimes fused together in a series of small ridges. The columellae are lax, spongiose and well developed. They are composed of a series of vertical trabeculae with a long free upper part and a slightly swollen tip, surrounded by, and fusing with, the subhorizontal, obliquely directed, long and twisted dentations of the lower inner septal margin.

Costae are well developed, thick, triangular and laminar. Those corresponding to the primary septa are almost glabrous or with small, rounded, exceptionally acute dentations. Other costae are swollen towards the base of the protuberances, slightly lower than principal ones and bearing numerous blunt granules. Costae extend over the whole exotheca, sometimes partitioning the surface of the corallum into polygonal areas, the centre of which is occupied by a mammiform corallite. Vesicular dissepiments sometimes partly cover the costae.

Skeletal variation

Echinopora mammiformis is a well defined species, showing comparatively little intraspecific variability, except for the growth form, which falls into three broad categories: massive, explanate and branching. Two types of branching colonies can be recognised. (1) those with very thick branches (up to 5cm in diameter at the base), decreasing rapidly and regularly in diameter. Branchlets are few in number, tapering, but with blunt tips. (2) Those with thin branches, sometimes showing a typically dendroid growth form, with an approximately uniform diameter except towards the tips, which become flattened, lacinate or palmate.

Some variations have also been observed in the degree of protuberance of the corallites, massive or thick-branched colonies generally having a smooth surface with mammillae hardly developed and shallow, superficial corallites. Furthermore, massive or thick-branched colonies have less developed, equal or subequal costae, a character which also contributes to the smooth appearance of the corallum. In other types of growth forms, with protruding corallites, the above-mentioned partitioning of the corallum surface is well defined and costae tend to be more developed. They sometimes alternate regularly in shape, lamellar or triangular costae corresponding to primary septa, and slightly lower, rounded ones corresponding to secondaries.

Affinities

The specimens of the present series correspond perfectly with both descriptions of *Leptastrea mammiformis* Nemenzo (1959) and *Echinopora glabra* Chevalier (1975), which are obviously identical. Nemenzo did not discuss the affinities of his new species and its inclusion within the genus *Leptastrea* arises from excessive importance given to growth form and to the spinose or non-spinose exotheca, as generic characters. Undoubtedly, *L. mammiformis* Nemenzo belongs to the genus *Echinopora* but, as mentioned by Chevalier, the species is markedly different from all other species of the genus, particularly because of its well developed costae, without prominent dentations.

Distribution

Recorded only from the Great Barrier Reef, New Caledonia and the Philippines.

GENUS MOSELEYA QUELCH, 1884

Generic synonymy

Moseleya Quelch, 1884.

Figs. 397-399 *Echinopora mammiformis* ($\times 5.0$).

Fig. 397 Same corallum as Fig. 396, showing protuberant corallites with well marked, alternating costae.

Fig. 398 Same corallum as Fig. 392, showing costae covered with granules.

Fig. 399 From the Palm Islands, showing the spiral structure of the columellae.



Fig. 397▲



Fig. 398▲



Fig. 399▲

Type species *Moseleya latistellata* Quelch, 1884.

Characters of the genus

This is a monospecific genus, hence its characters are those of *M. latistellata*.

***Moseleya latistellata* Quelch, 1884**

Synonymy

Moseleya latistellata Quelch, 1884; Bernard (1904); Vaughan & Wells (1943).

Material studied

Thursday Island (6 specimens), **Palm Islands** (34 specimens), **Magnetic Island** (6 specimens), **Whitsunday Islands** (12 specimens).

These localities include collecting stations 34, 36, 41, 43, 45, 46, 53, 54, 55, 58, 59, 85, 90, 96, 97, 98, 102.

Previous records from Eastern Australia

Islands of the **Torres Strait**, Quelch (1884), Pace (1901), Totton (1952); 8 records south to the **Northumberland Islands**, Wells (1955a).

Fig. 400 *Moseleya latistellata* from between Brisk and Falcon Islands, Palm Islands, collecting station 41, showing the large central calice ($\times 0.7$).

Fig. 401 Extratentacular budding at the circumference of a large *Moseleya* colony ($\times 2.5$).



Fig. 400



Fig. 401

Characters

Several distinguishing characters make this species readily recognisable. All but very large colonies have a large central calice (Fig. 400) (up to 3.5cm in diameter) surrounded by smaller calices which are 4, 5, or 6 sided, and which, in the present series, are produced by extratentacular budding at the colony perimeter (Fig. 401). Most septa have an inner series of large paliform lobes, which are regularly exsert and dentate. Usually two to ten septa are thicker than the others and have more prominent paliform lobes.

This species is usually found in turbid water, frequently on muddy substrates. Colonies are frequently unattached to any substrate other than a small shell or similar object to which the primary polyp was originally attached. It also occurs in muddy areas exposed at low tides. It has not been recorded from localities exposed to strong wave action or currents.

Living colonies are pale to deep browns and greens in colour. Polyps are very light sensitive and are usually seen fully extended only on dark nights.

Skeletal variation

Most of the variation of this species is attributable to stages of development. The species commonly occurs as single corallites (Fig. 402) or as very small colonies (Fig. 403). Maximum colony size is approximately 25cm.

Septal structures, especially development of the paliform lobes, is the main source of variation in mature colonies (Figs. 404, 405).

Affinities

This species is one of the most isolated of the Faviidae. Superficially, *Moseleya* most closely resembles *Favites*. However, the budding and growth pattern of a central corallite are unlike any species of that genus. Septa most closely resemble *Trachyphyllia*. There is a remarkable similarity between *M. latistellata* and *Acanthastrea hillae*, which is described in Part III of the present series.

Figs. 402, 403 Juvenile coralla of *Moseleya latistellata* from the Palm Islands ($\times 2.5$).

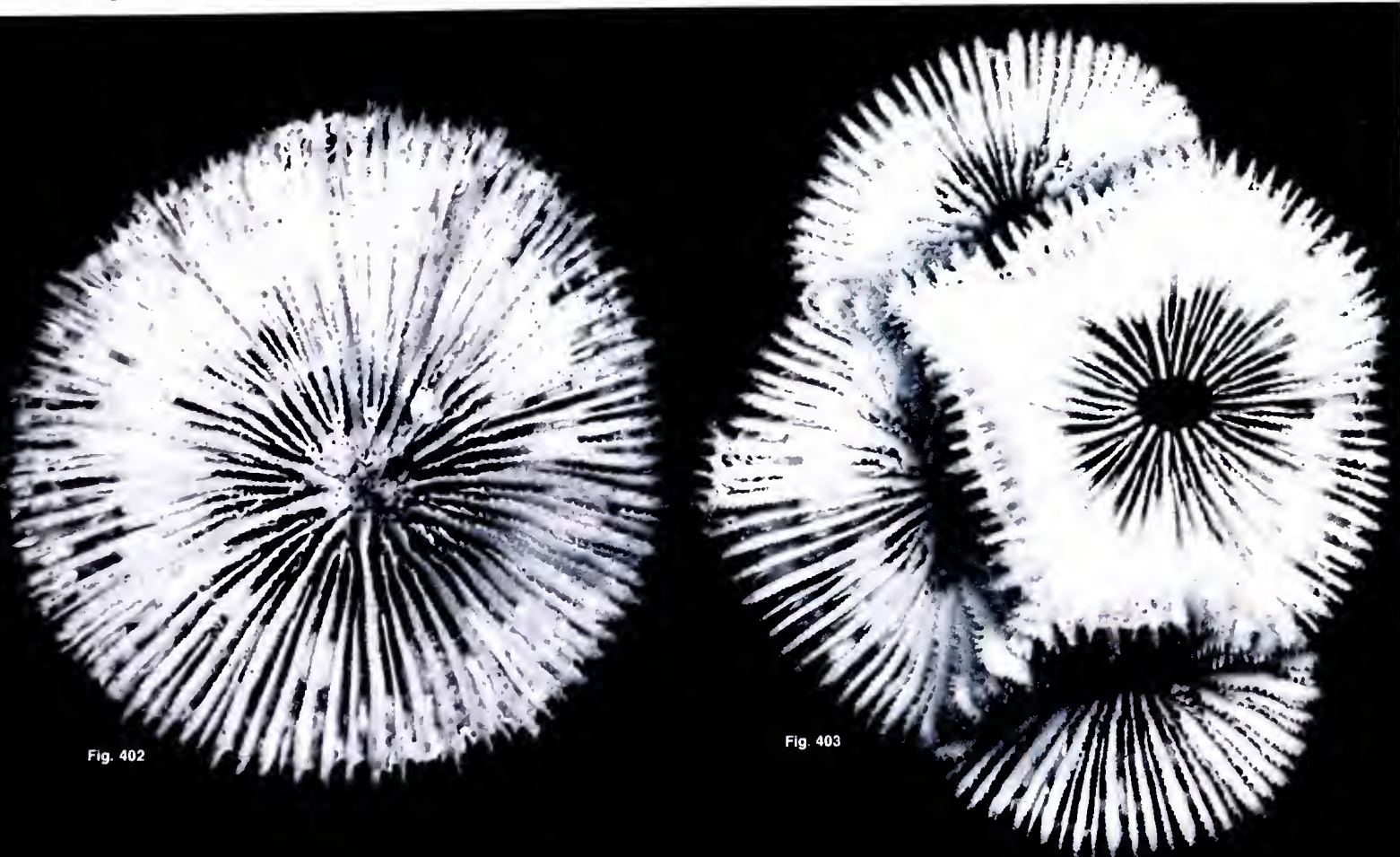


Fig. 402

Fig. 403

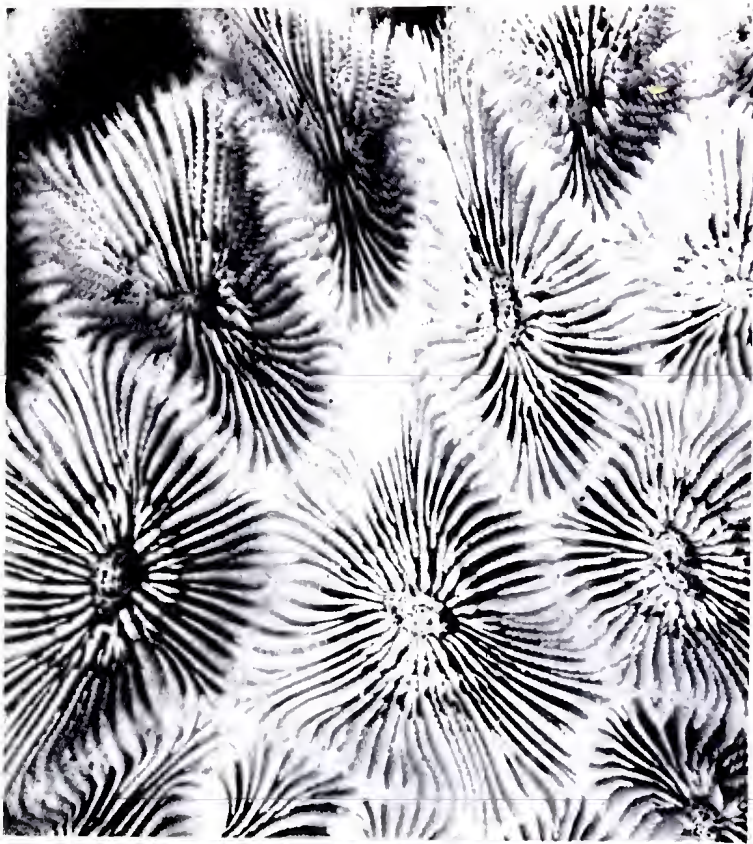


Fig. 404▲

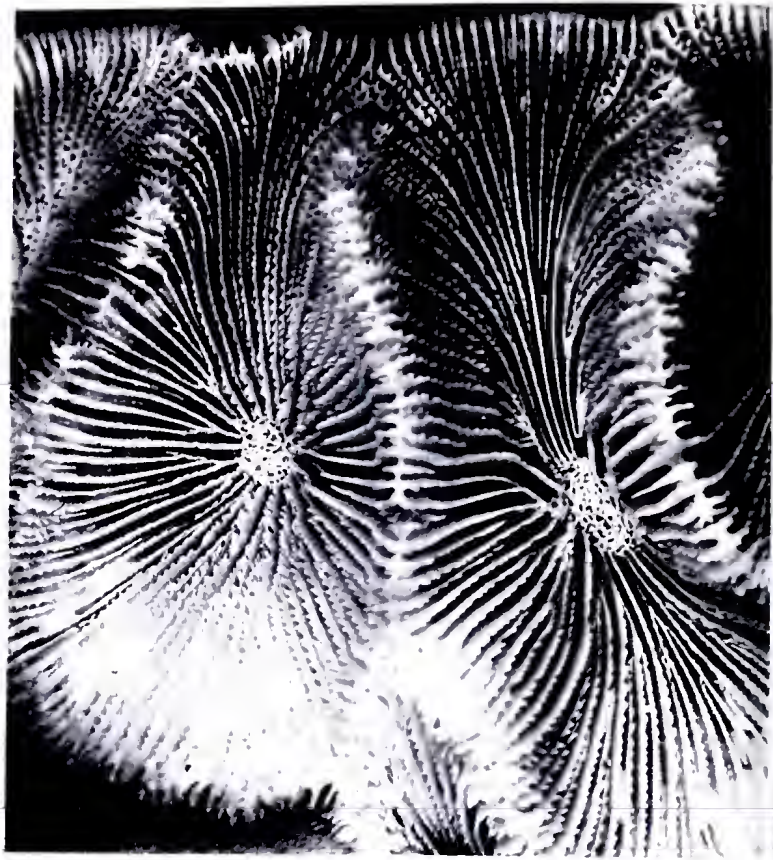


Fig. 405▲

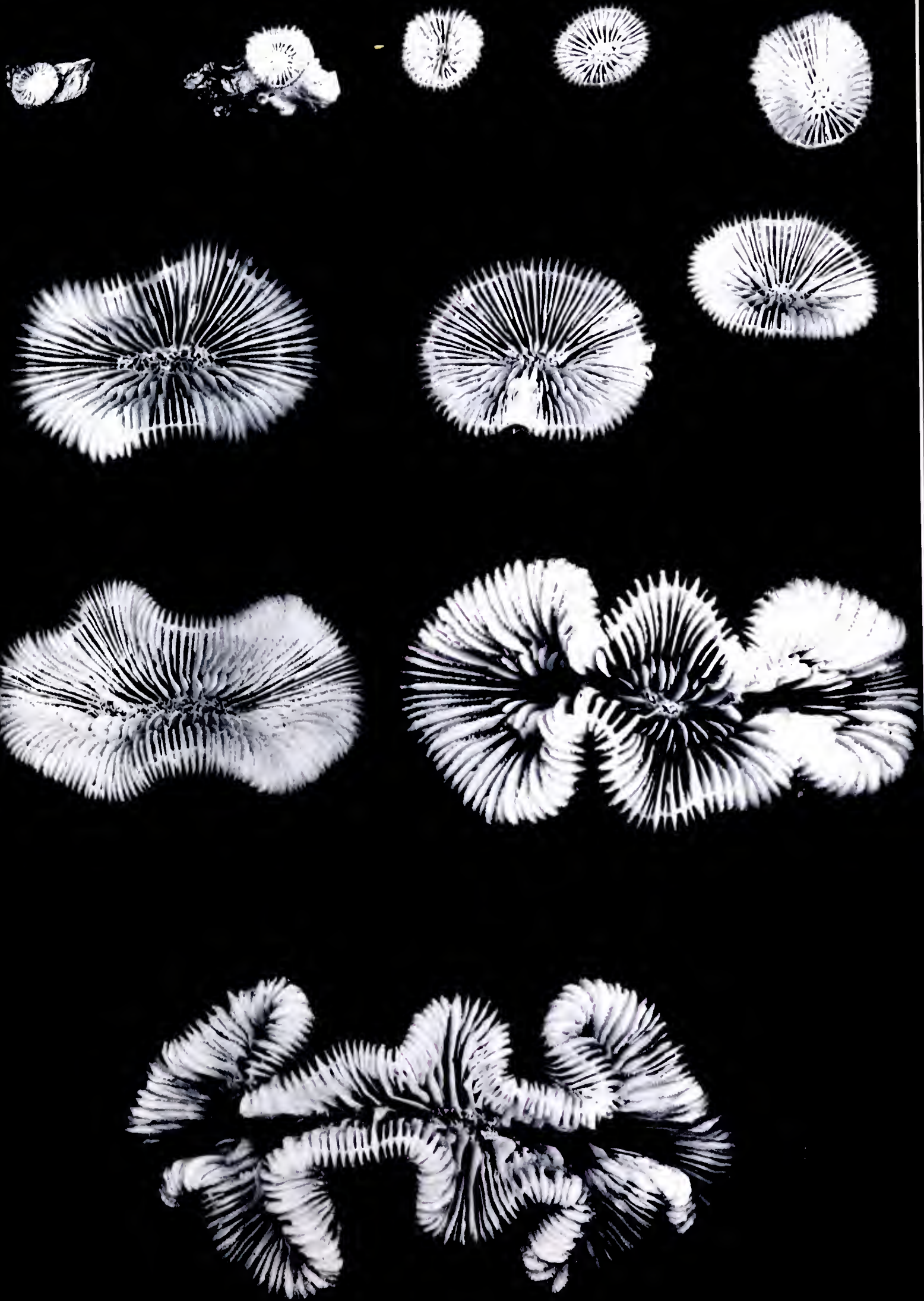
Figs. 404, 405 Variation in calicular structures of *Moseleya latistellata* ($\times 2.5$). Fig. 404 from Dido Rock, Palm Islands, collecting station 58, Fig. 405 from Thursday Island.

Fig. 406 *Moseleya latistellata*, *in situ* at the Palm Islands with polyps retracted ($\times 2.5$).



Distribution

Restricted to north western Australia, Torres Strait, eastern Papua New Guinea, the Great Barrier Reef and the Philippines.



IV

Family Trachyphylliidae Verrill, 1901

The Subfamily Trachyphylliinae Wells, 1956, was separated from the rest of the Faviidae and raised to the rank of a Family by Chevalier (1975) on the grounds that it has two major distinctive characters:

- (1) Two diverging systems of simple trabeculae, the inner one forming prominent lobes.
- (2) Septo-costal margin with small, closely situated, subequal dentations.

This treatment, which is followed here, excludes *Moseleya*, previously placed by Wells in his Trachyphylliinae. Indeed, Chevalier (1975) pointed out that *Moseleya* has strong affinities with *Favites*, an opinion which we share, although the differences in budding characters should be stressed.

As it stands now, the Family Trachyphylliidae includes only two living genera, *Trachyphyllia* and *Callogyra*, both of them from the Indo-Pacific. The former only is present in eastern Australia, the latter being restricted, as far as is known, to the Indo-Malayan archipelago.

GENUS *TRACHYPHYLLIA* EDWARDS & HAIME, 1848

Generic synonymy

Trachyphyllia Edwards & Haime, 1848.

Turbinolia Audouin, 1826 (*pars*).

Manicina Dana, 1846 (*pars*).

Antillia Duncan, 1876 (*pars*) and others.

Antillophyllia Vaughan, 1932.

Type species *Turbinolia geoffroyi* Audouin, 1826.

Characters of the genus (after Vaughan & Wells, 1943, partly altered)

Colonies are usually free-living, colonial and flabello-meandroid, resulting from intramural budding. Series are short and laterally free. The walls appear to be primarily parathecal (below) and primarily septothecal (above). The columella is trabecular; centres are linked.

***Trachyphyllia geoffroyi* (Audouin, 1826)**

Synonymy (partly after Matthai, 1928 and Crossland, 1952).

Turbinolia geoffroyi Audouin, 1826.

Trachyphyllia amarantum (Dana); Edwards & Haime (1848, 1857); Verrill (1864); Harrison & Poole (1909); Matthai (1924); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936).

Trachyphyllia geoffroyi (Audouin); Haeckel (1875); Ortmann (1892); Matthai (1928); Vaughan & Wells (1943); Crossland (1952); Scarle (1956); Utinomi (1965).

Trachyphyllia amarantus (Müller); Studer (1881); Bedot (1907); Folkesson (1919); Faustino (1927); Yabe & Sugiyama (1932, 1935).

?*Trachyphyllia lindahi* Nemenzo, 1971.

Matthai (1928) and Crossland (1952) also add several species of *Antillia* (*lonsdaleia*, *lonsdalei*, *geoffroyi*, *constricta* and *sinuata*) to the synonymy of this genus, which consequently appears to be monospecific.

Material studied

Many hundreds of specimens have been dredged or collected throughout the Great Barrier Reef. Specific localities include: **Thursday Island, Eagle Reef, Lizard Island, Palm Islands, Magnetic Island, Whitsunday Islands** and **Heron Island**.

These localities include collecting stations 20, 24, 25, 43, 45, 46, 53, 55, 90.

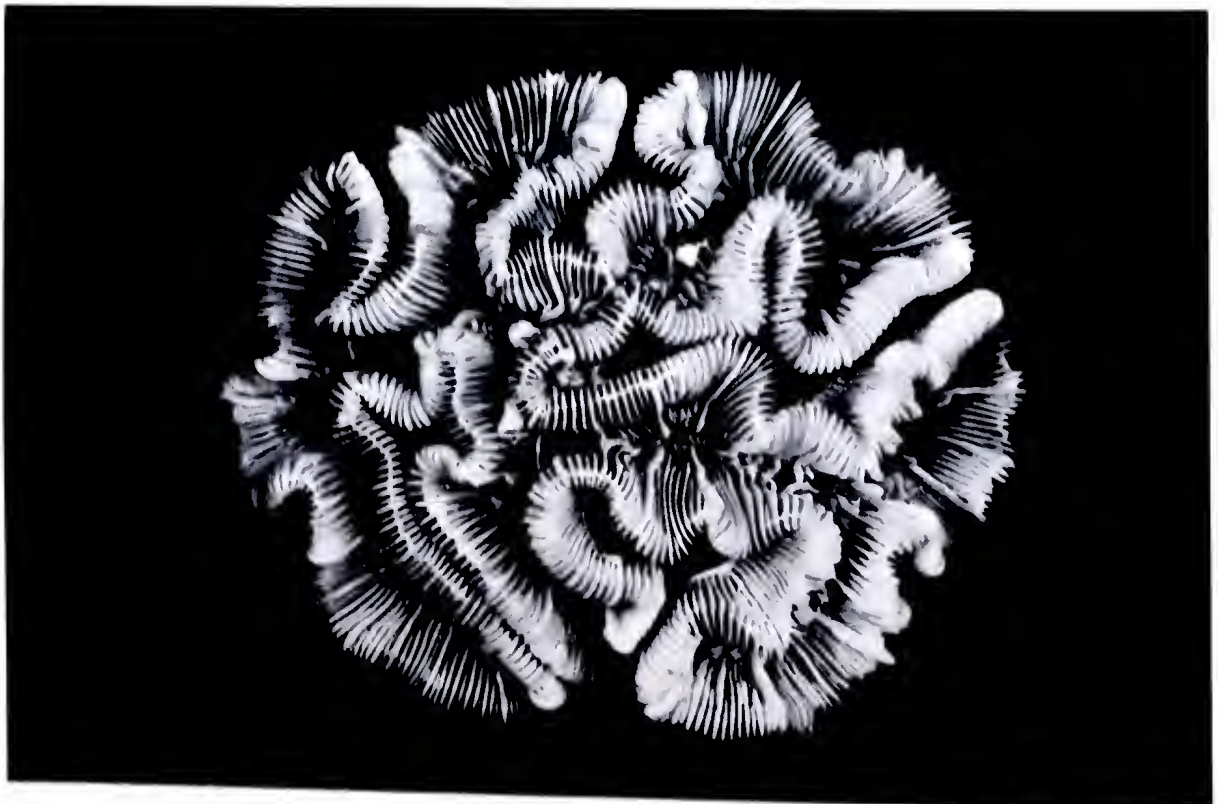
Previous records from Eastern Australia

Near **Lizard Island**, Yonge (1930), Crossland (1952), Goreau & Yonge (1968); nine localities south to **Bushy Island-Redbill Reef**, Wells (1955a).

Characters

Figures 407 & 408 illustrate the principal growth stages of the species. Colonies seldom reach the size and complexity of that of Fig. 408 which is similar to those illustrated by Matthai (1928) (Plate XXIII, Figs. 1, 5), and Faustino (1927) (Plate 38, Figs. 1, 2). Larger colonies appear to be restricted to sheltered reef areas where there is some water turbulence. Smaller colonies are often very common in sheltered areas such as collecting stations 24 and 46. At Lizard Island (e.g. collecting station 24), they are found on flat, soft sand along with other free-living corals, *Heteropsammia* cf. *michelini* Edwards & Haime, *Cycloseris cyclolites* (Lamarck) (see Goreau & Yonge, 1968) and, less frequently *Diaseris distorta* (Michelin) (in sandy areas) and *Heterocyathus acquiricostatus* Edwards & Haime (in soft muddy areas). At the Palm Islands (e.g. collecting station 46), they are most commonly found on flat, soft mud

Fig. 408 A large colony of *Trachyphyllia geoffroyi* from the N end of Nara Inlet, Hook Island, Whitsunday Islands ($\times 0.8$).



along with *Moseleya*, *Euphyllia* and *Catalaphyllia*. They have not been found in coarse sand or in any area exposed to marked currents, as has been observed in Madagascar (Pichon, 1974).

Living colonies (Figs. 411-413) are almost always brightly coloured, various mixtures of reds, blues and greens being the most common. The polyp is large and fleshy, and, unless disturbed, always has the mantle extended. The upper surface consists of a large oral disc surrounded by a single circle of tentacles which are normally only extended at night or in other conditions of low light intensity. Outside the tentacles is a large prominent peritentacular mantle which is used to clear the colony of foreign objects. Comparison of the living polyps of *Moseleya* and *Trachyphyllia* strongly supports the present contention that these genera are not closely related.

Early growth stages of *Trachyphyllia* are readily distinguishable from those of other genera by: 1. the presence of fine dentations on the septa; 2. the presence of well developed paliform lobes, and 3. the presence of well developed columellae.

Larger colonies, which are free living, become laterally constricted in one diameter and develop separate mouths either side of the constriction. Subsequent mouths develop with subsequent constrictions. The height of the epitheca is very variable (Figs. 409, 410), probably reflecting the height of the colony above the substrate and hence the nature of the substrate.

Distribution

Widely distributed from the Red Sea to the Philippine Islands and Eastern Australia.

Figs. 409, 410 Variation in the height of the epitheca in two *Trachyphyllia geoffroyi* from Lizard Island ($\times 2.0$).

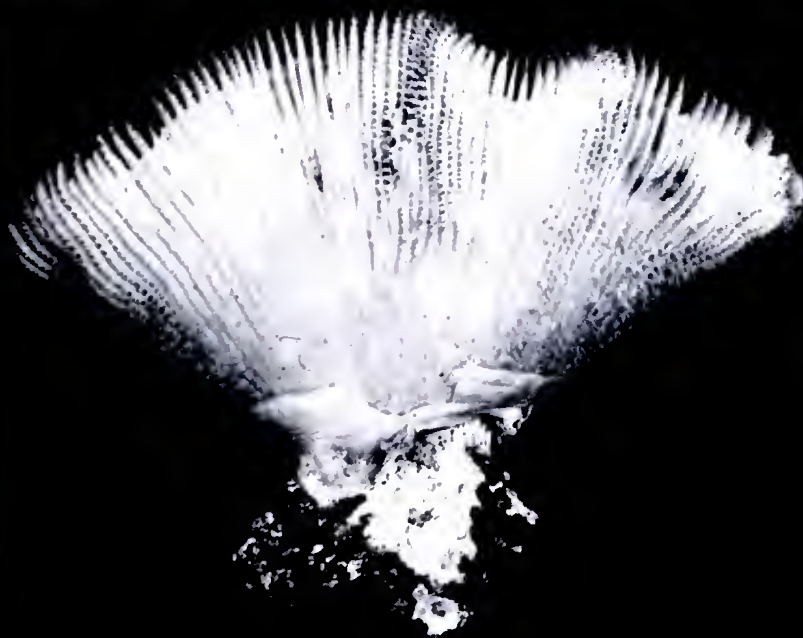


Fig. 409

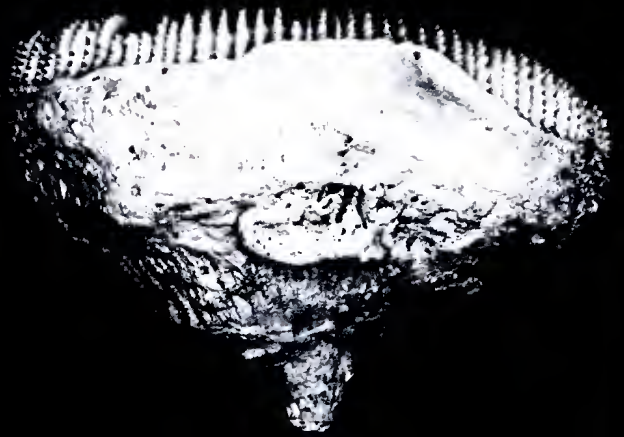


Fig. 410

Figs. 411, 412 *Trachyphyllia geoffroyi*, *in situ* at Lizard Island, Fig. 411 with mantle retracted, Fig. 412 with mantle expanded.

Fig. 413 *Trachyphyllia geoffroyi* from Swain Reefs, showing tentacles expanded at night.



Fig. 411▲

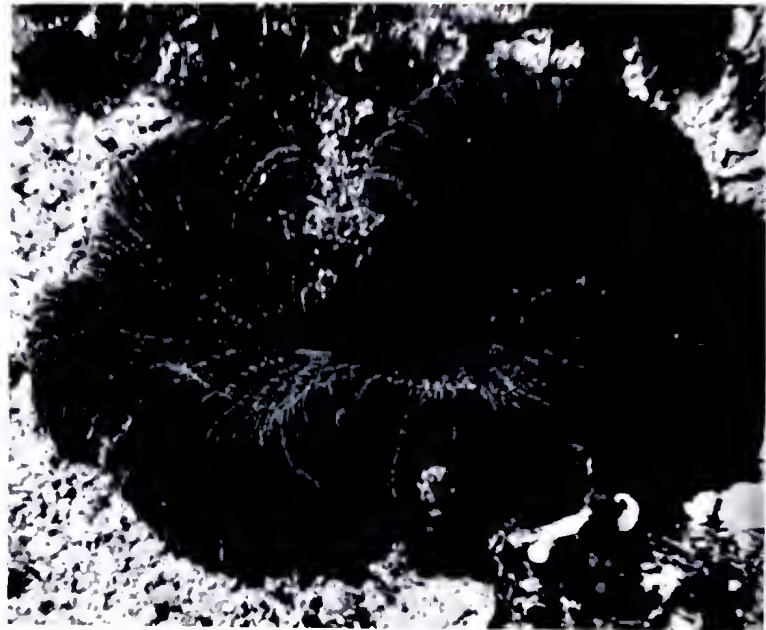


Fig. 412▲

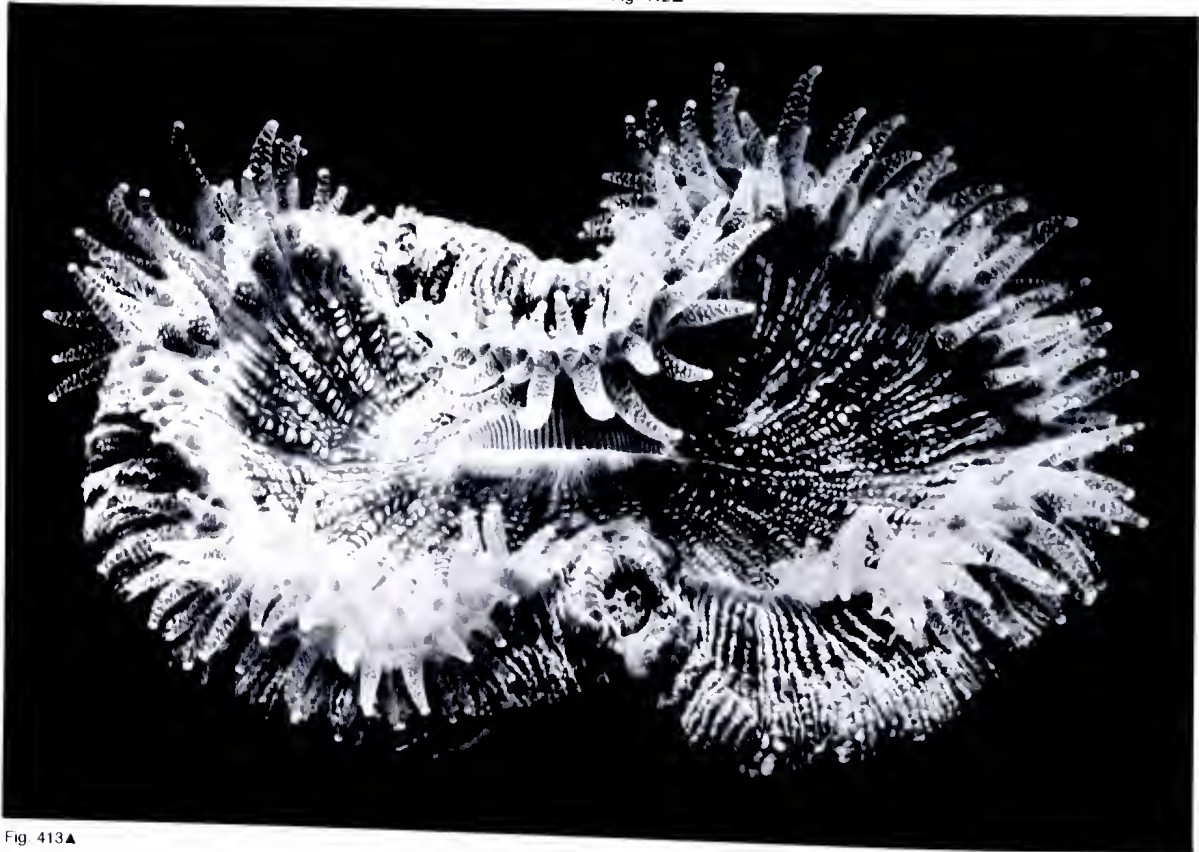


Fig. 413▲

- Fig. 414 *Caulastrea furcata* from the Whitsunday Islands (photo: J. Barnett).
- Fig. 415 *Favia laxa* from Lizard Island.
- Fig. 416 Adjacent colonies of *Favia* sp. 1 (right) and *Favia fava* (left) from the Whitsunday Islands.
- Fig. 417 The common 'mottled' colouration of *Favia fava*, from the Whitsunday Islands.
- Fig. 418 The common uniform brown colouration of *Favia fava* from Lizard Island.
- Fig. 419 *Favia fava* from the Whitsunday Islands (photo: T. Done).
- Fig. 420 Adjacent colonies of *Favia* cf. *amicorum* (left) and *Favia fava* (right) from Lizard Island.
- Fig. 421 *Favia* cf. *amicorum* from the Whitsunday Islands.
- Figs. 422, 423 *Favia pallida* from the Whitsunday Islands.
- Fig. 424 *Favia matthaii* from the Whitsunday Islands (Photo: T. Done).
- Fig. 425 *Favia matthaii* from Lizard Island.
- Fig. 426 *Favia rotumana* from Lizard Island.
- Fig. 427 *Favia maxima* from the Whitsunday Islands (Photo: T. Done).
- Figs. 428-430 *Favia lizardensis*: Figs. 428, 430 from Lizard Island; Fig. 429 from the Whitsunday Islands (Photo: J. Barnett).
- Fig. 431 *Favia* sp. 1 from the Whitsunday Islands, showing the mottled colour pattern similar to *Favia fava* (Figs. 417, 419) and *Favia* cf. *amicorum* (Figs. 420, 421).
- Fig. 432 *Favites abdita* from the Whitsunday Islands, showing the common hillocky growth form.
- Fig. 433 *Favites abdita* from Lizard Island, showing its most common colour pattern.
- Fig. 434 *Favites halicora* from Lizard Island.
- Fig. 435 *Favites flexuosa* from the Whitsunday Islands (Photo: T. Done).
- Figs. 436-438 *Favites rotundata*. Figs. 436, 437 from the Whitsunday Islands, Fig. 436 with polyps partly expanded (Photo: J. Barnett), Fig. 438 from Lizard Island.
- Fig. 439 *Favites complanata* from the Whitsunday Islands (Photo: T. Done).
- Figs. 440-442 *Favites pentagona*. Figs. 440, 441 from the Whitsunday Islands (Photo, Fig. 440 T. Done), Fig. 442 from Lizard Island.
- Figs. 443, 444 *Favites russelli*. Fig. 443 from Lizard Island, Fig. 444 from the Whitsunday Islands.
- Fig. 445 Adjacent colonies of *Favia maxima* (left) and *Favites bennettiae* (right) from the Whitsunday Islands (Photo: T. Done).
- Fig. 446 *Favites bennettiae* from the Whitsunday Islands (Photo: T. Done).
- Fig. 447 Adjacent colonies of *Oulophyllia crista* (right) and *Favites bennettiae* (left) from the Whitsunday Islands (Photo: T. Done).
- Fig. 448 *Favites bennettiae* from the Whitsunday Islands.
- Fig. 449 *Goniastrea retiformis* from Lizard Island.
- Fig. 450 *Goniastrea pectinata* from the Whitsunday Islands (Photo: T. Done).
- Fig. 451 *Goniastrea australensis* from the Whitsunday Islands (same biotope as Fig. 450).
- Fig. 452 *Goniastrea palauensis* from Lizard Island.
- Figs. 453, 454 *Platygyra daedalea* from the Whitsunday Islands (Photo: T. Done).

- Figs. 455, 456 *Platygyra lamellina*. Fig. 455 from the Whitsunday Islands (Photo: T. Done), Fig. 456 from Lizard Island.
- Fig. 457 *Platygyra sinensis* from the Whitsunday Islands (Photo: J. Barnett).
- Fig. 458 *Platygyra pini* from the Whitsunday Islands (Photo: T. Done).
- Fig. 459 *Platygyra zelli* from Lizard Island.
- Fig. 460 *Leptoria phrygia* from the Whitsunday Islands (Photo: T. Done).
- Fig. 461 *Oulophyllia crista* from the Whitsunday Islands (Photo: J. Barnett).
- Fig. 462 *Montastrea curta* from Lizard Island.
- Fig. 463, 464 *Montastrea magnistellata* from the Whitsunday Islands (photo, Fig. 464: T. Done).
- Fig. 465 *Montastrea valenciennesi* from Lizard Island.
- Fig. 466 *Leptastrea* cf. *bottae* from Lizard Island.
- Fig. 467 *Leptastrea purpurea* from the Whitsunday Islands.
- Fig. 468 *Leptastrea transversa* from the Whitsunday Islands.
- Figs. 469-472 *Leptastrea pruinosa*. Fig. 469 from Bushy Island-Redbill Reef with polyps expanded by day. Fig. 471 from Lizard Island. Figs. 470, 472 from the Whitsunday Islands.
- Fig. 473 *Cyphastrea chalcidicum* from Lizard Island.
- Figs. 474, 475 *Echinopora lamellosa* from Lizard Island.
- Fig. 476 *Echinopora horrida* from Lizard Island.
- Fig. 477 *Echinopora mammiformis* from Lizard Island.



Fig. 414▲

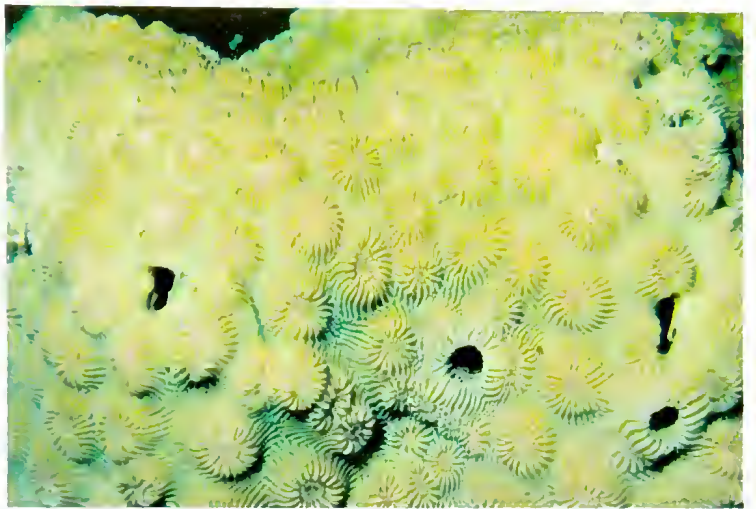


Fig. 415▲

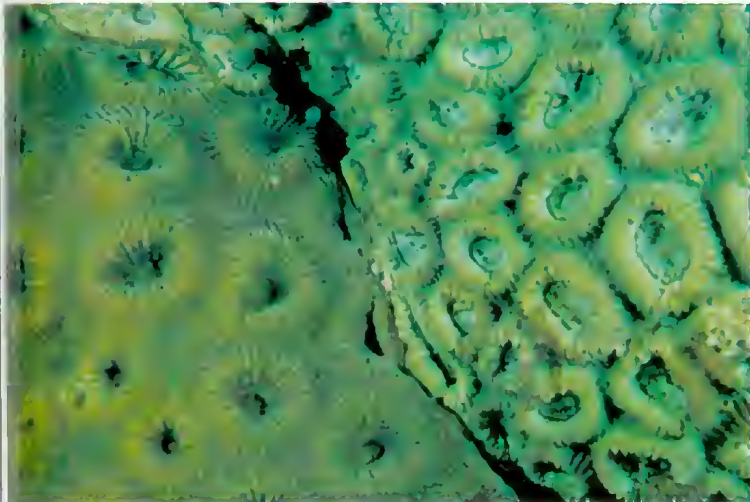


Fig. 416▲



Fig. 417▲

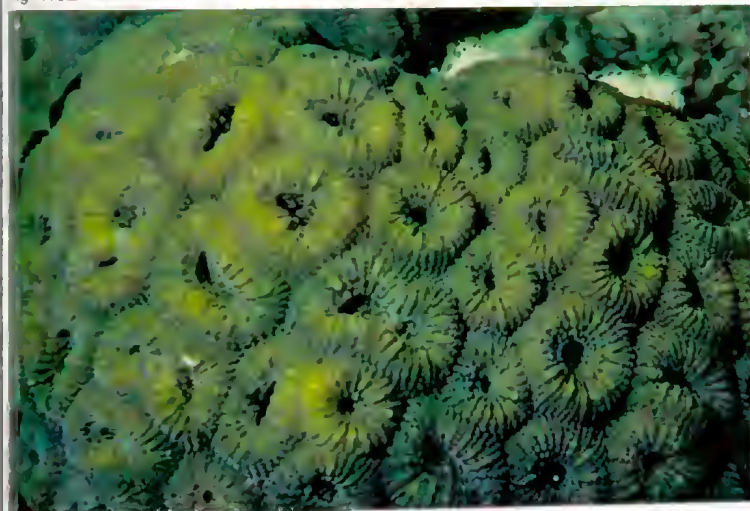


Fig. 418▲



Fig. 419▲

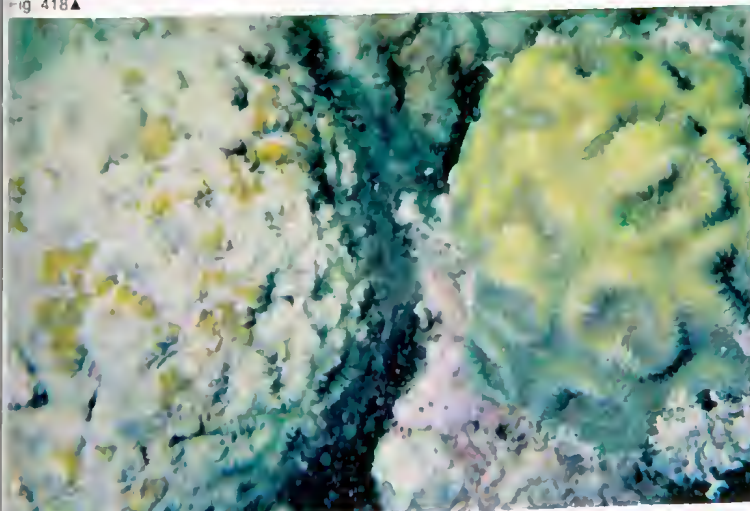


Fig. 420▲



Fig. 421▲

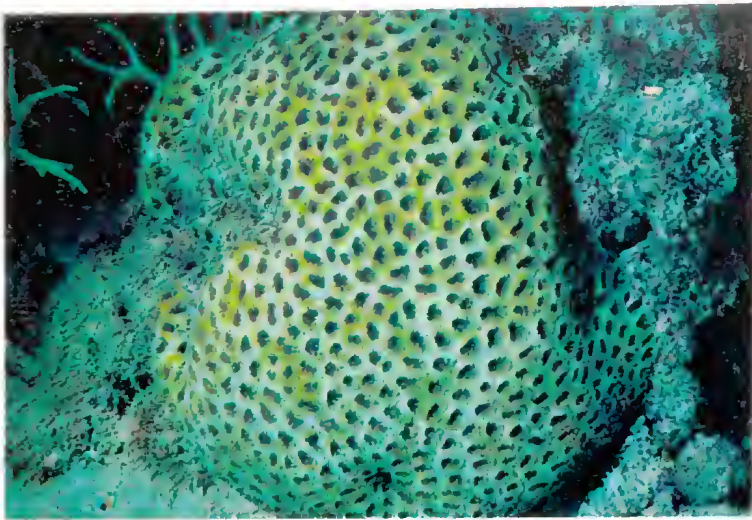


Fig. 422▲

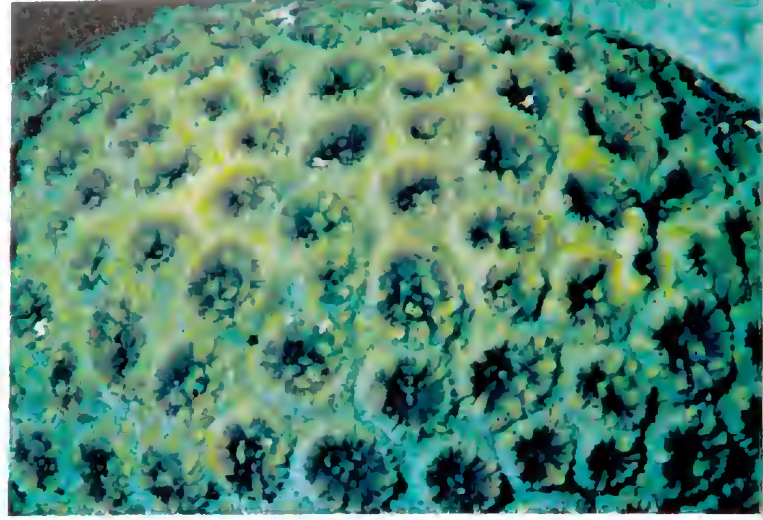


Fig. 423▲

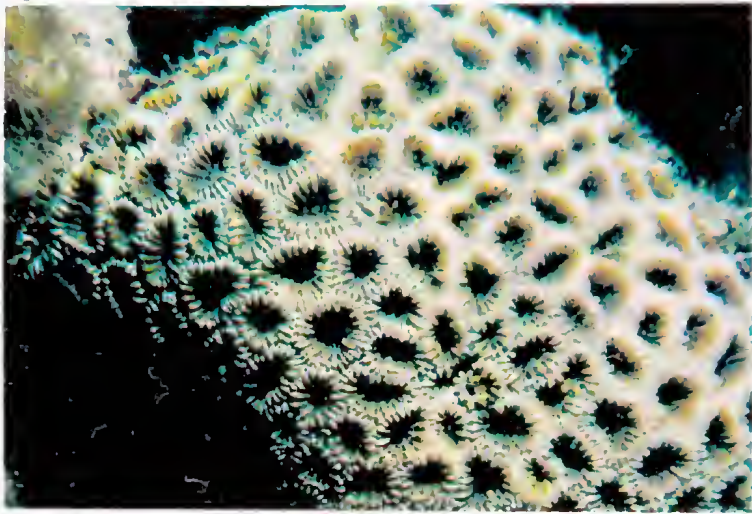


Fig. 424▲

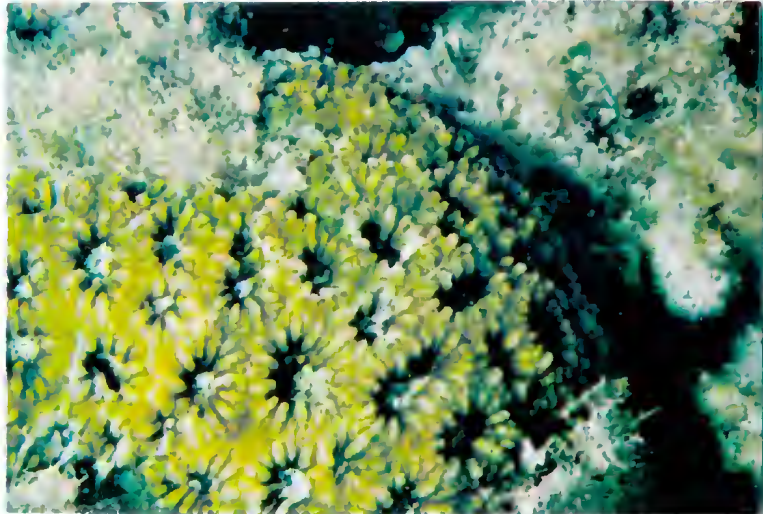


Fig. 425▲

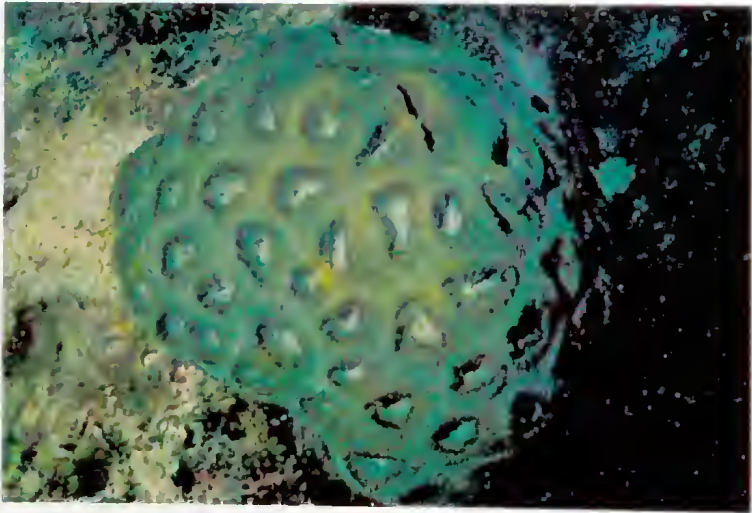


Fig. 426▲

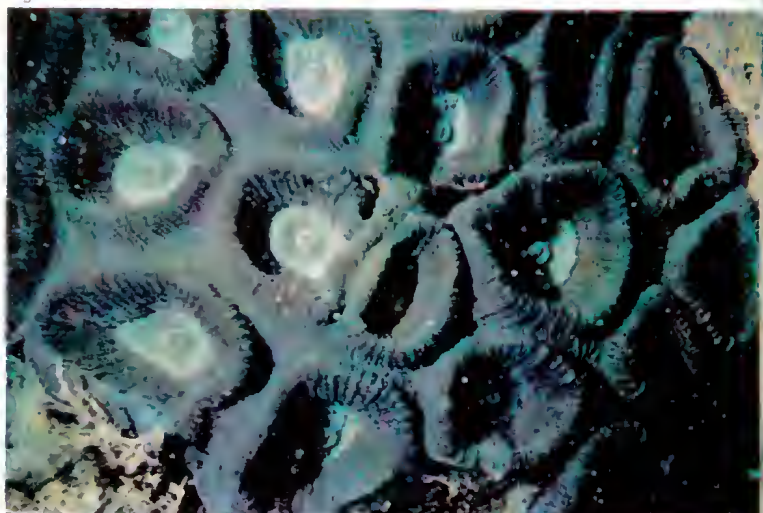


Fig. 427▲



Fig. 428▲

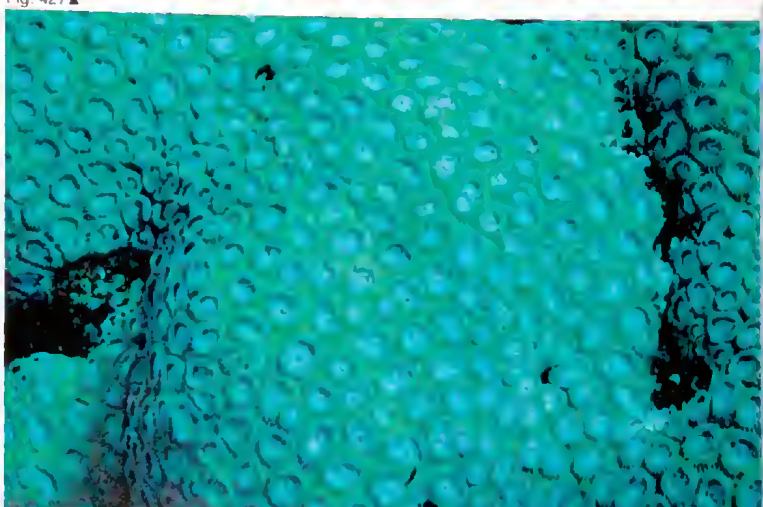


Fig. 429▲



Fig. 430▲

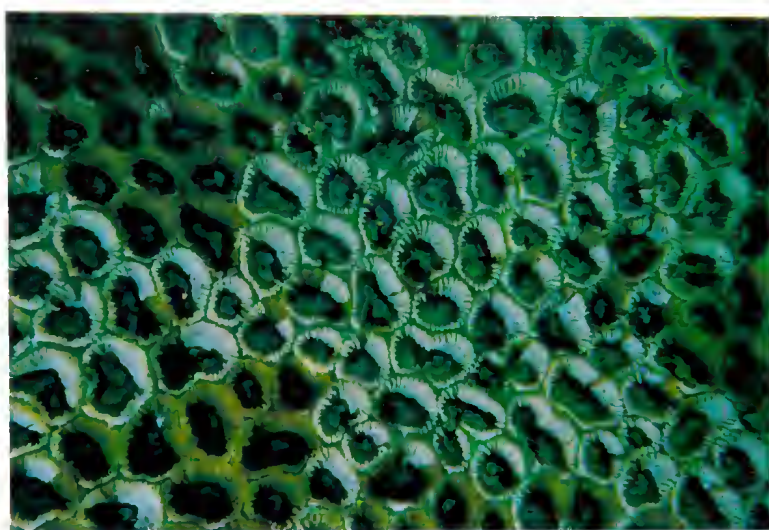


Fig. 431▲



Fig. 432▲

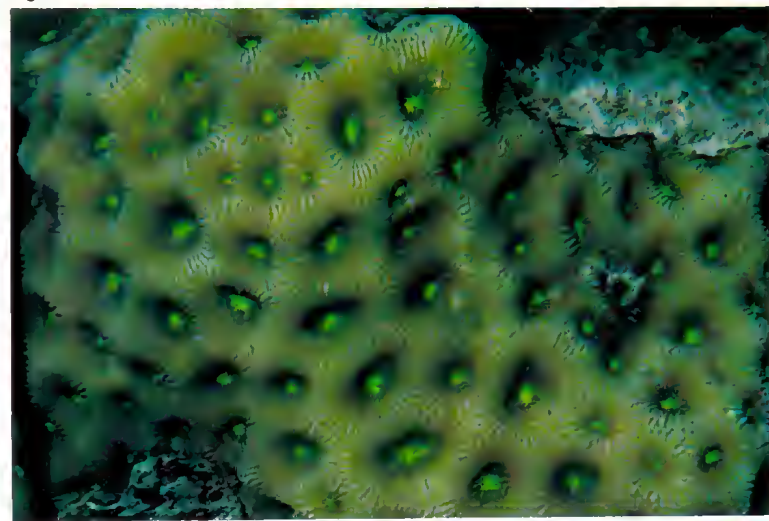


Fig. 433▲



Fig. 434▲

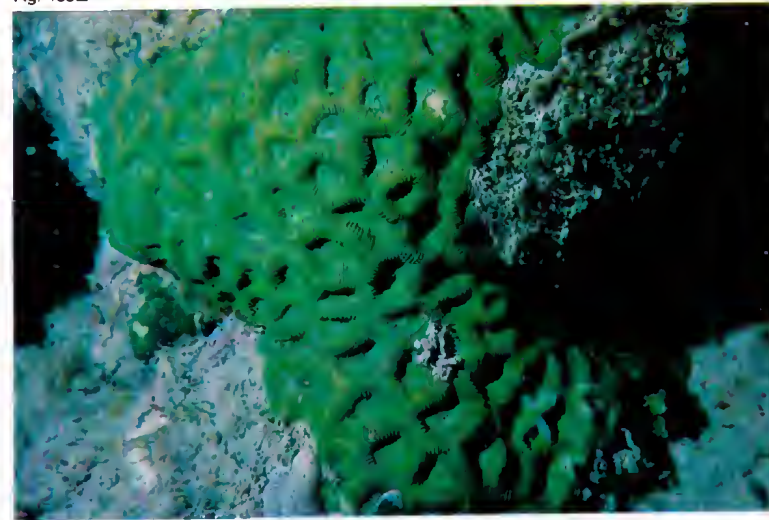


Fig. 435▲

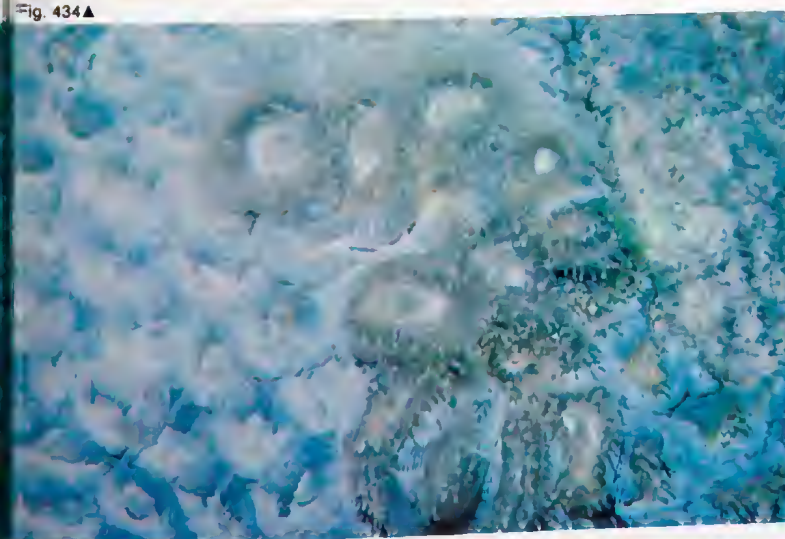


Fig. 436▲

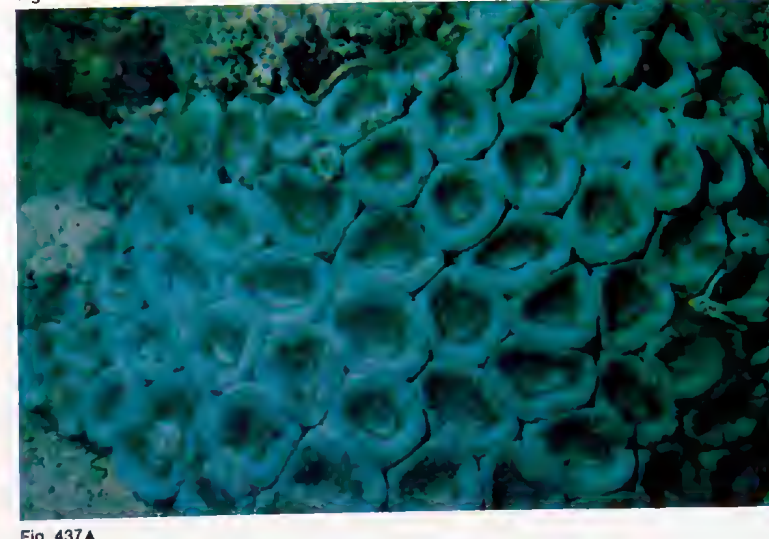


Fig. 437▲



Fig. 438▲

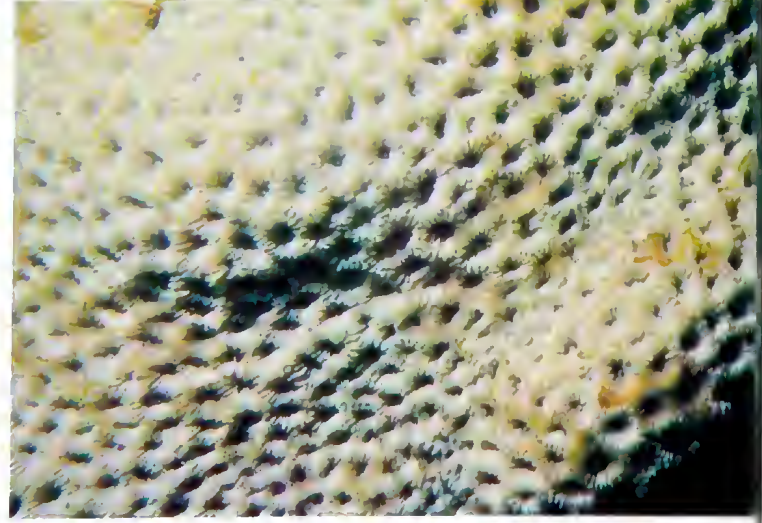


Fig. 439▲



Fig. 440▲

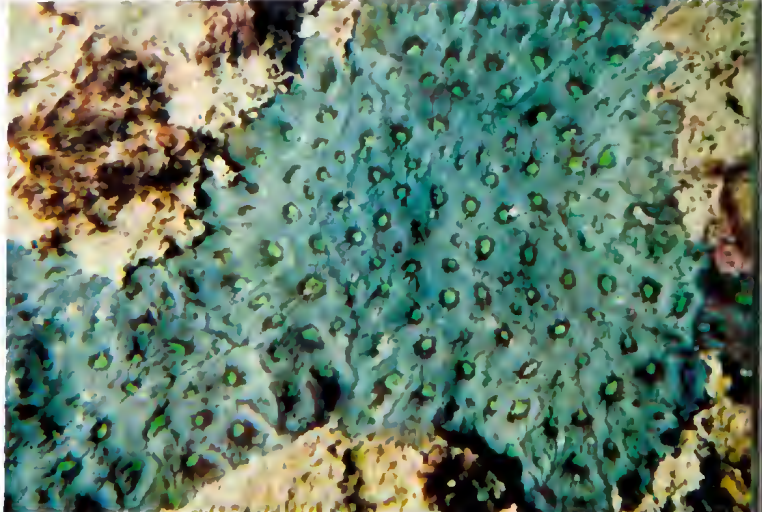


Fig. 441▲

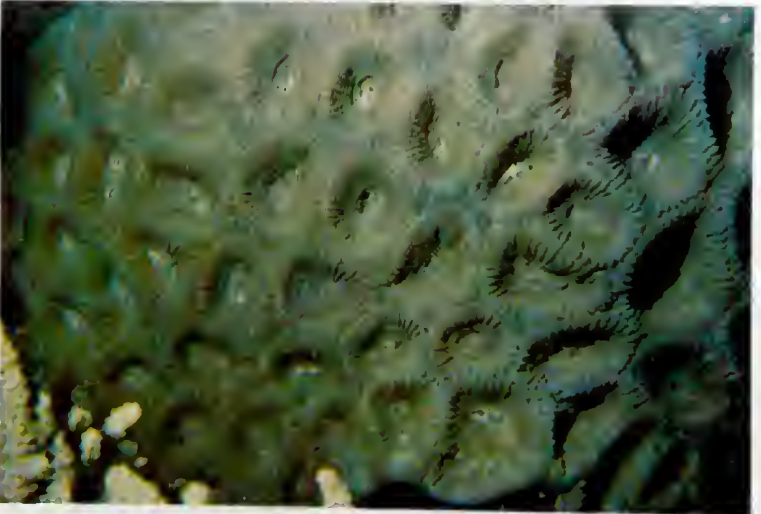


Fig. 442▲



Fig. 443▲



Fig. 444▲



Fig. 445▲



Fig. 446▲



Fig. 447▲

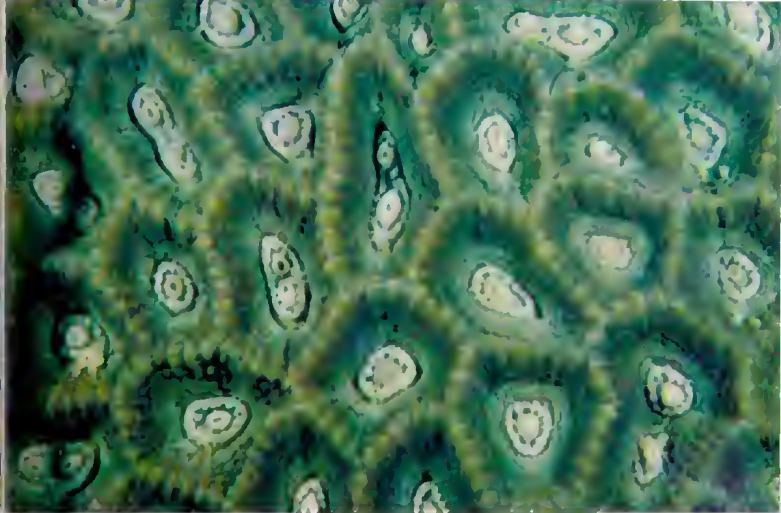


Fig. 448▲



Fig. 449▲

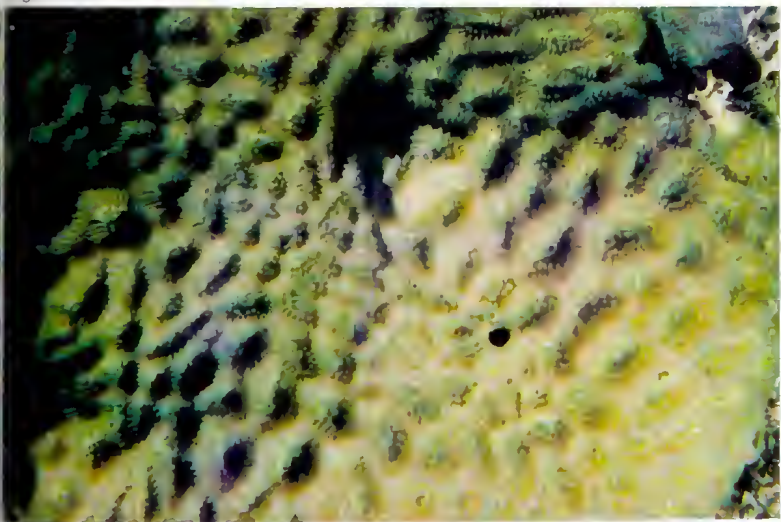


Fig. 450▲

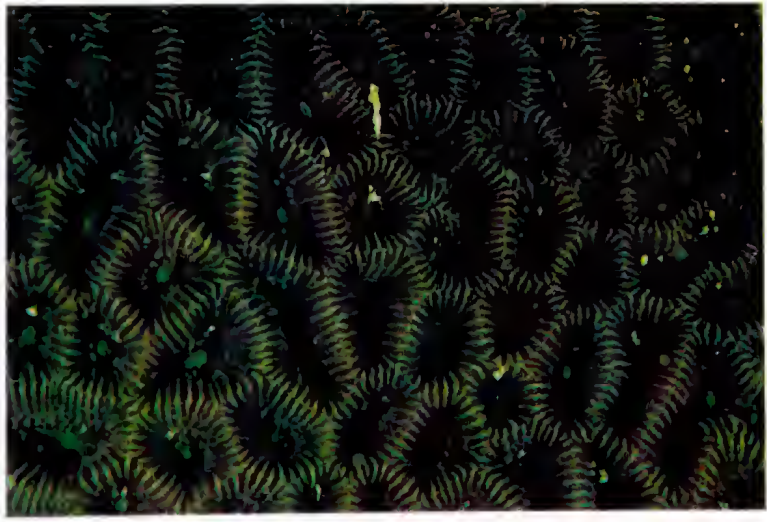


Fig. 451▲



Fig. 452▲



Fig. 453▲



Fig. 454▲



Fig. 455▲



Fig. 456▲



Fig. 457▲

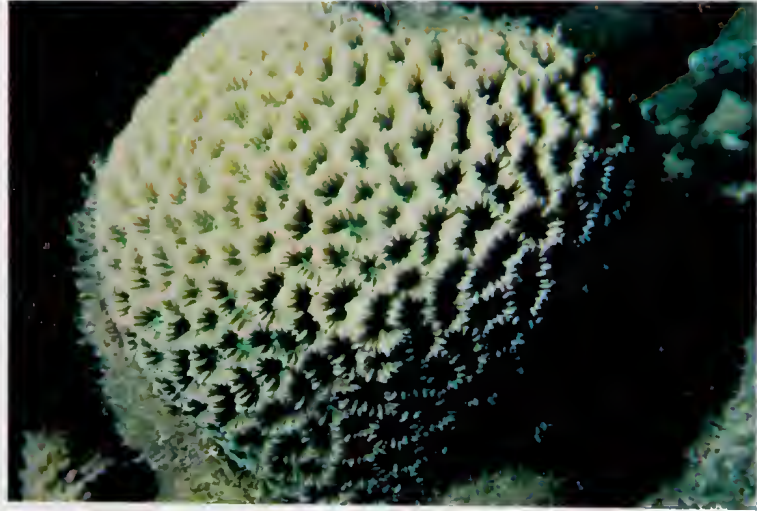


Fig. 458▲



Fig. 459▲



Fig. 460▲



Fig. 461▲



Fig. 462▲



Fig. 463▲



Fig. 464▲



Fig. 465▲



Fig. 466▲



Fig. 467▲



Fig. 468▲

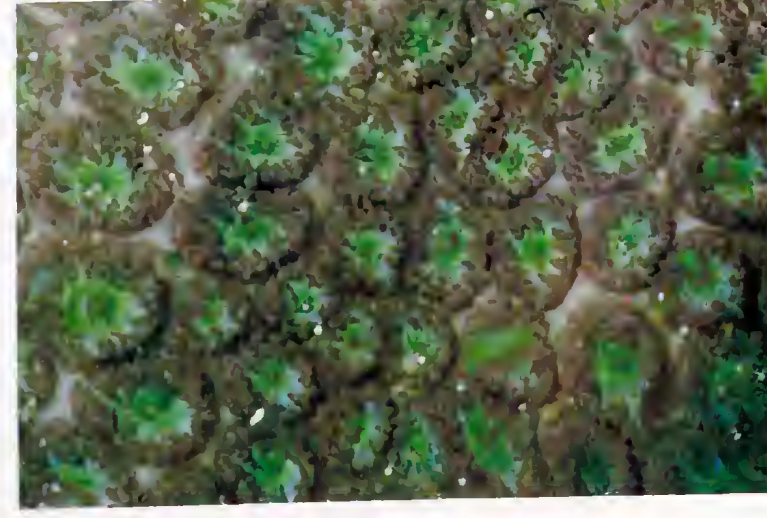


Fig. 469▲

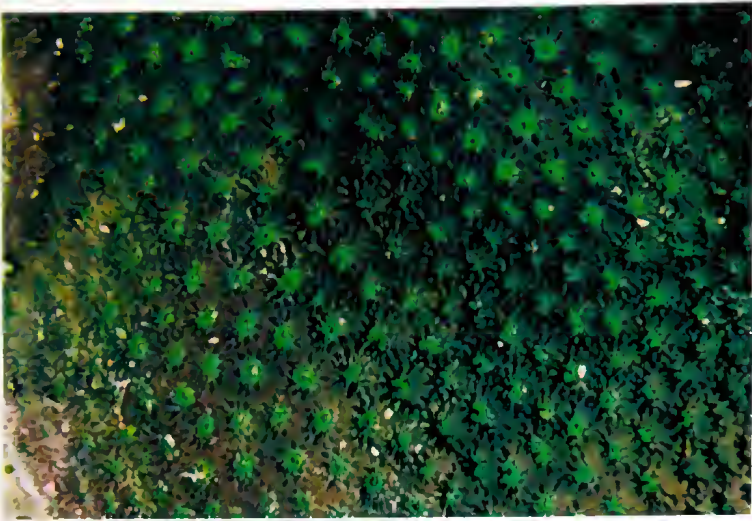


Fig 470▲

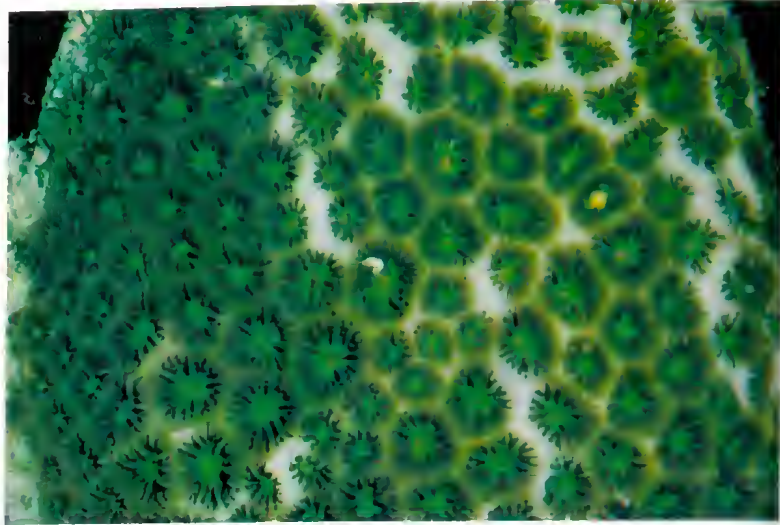


Fig 471▲



Fig 472▲

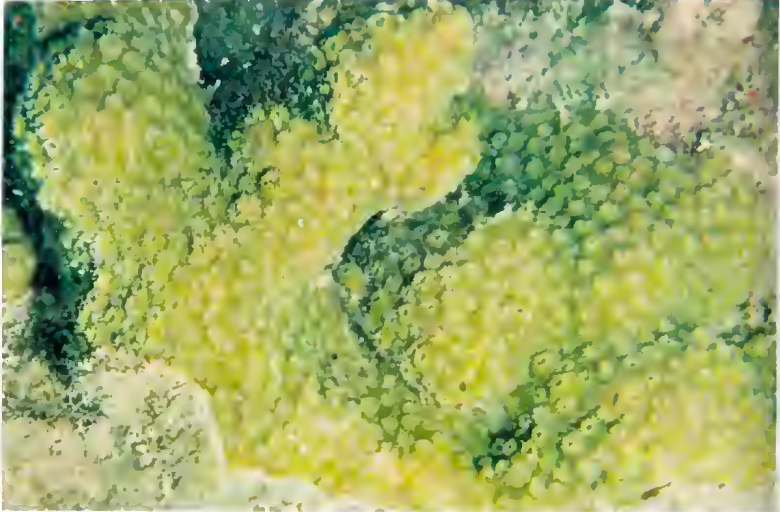


Fig 473▲



Fig 474▲



Fig 475▲

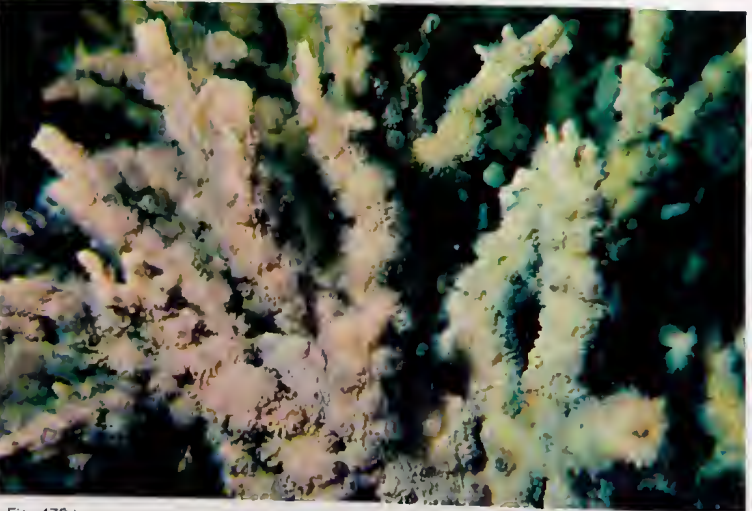


Fig 476▲



Fig 477▲

V

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VII

Index

For the purpose of uniformity of contemporary spelling, the diphthong *ae* (or the corresponding digraph *ae*) which appears in the endings of some generic names has been transliterated into its modern equivalent *e*, representing the single vowel for which it stands. Original spellings are retained for names no longer in common usage.

<i>abditā, Favites</i>	54-59, 61, 67	<i>favistella</i>	87
" <i>Madrepora</i>	54	<i>(Pissicella) favulus</i>	86
" <i>Prionastraea</i>	55	<i>flexuosa</i>	61
<i>Acanthastrea hillae</i>	203	<i>fragilis</i>	36
<i>Acanthelia</i>	182, 183	<i>fuscoviridis</i>	54
<i>Acanthelia horrida</i>	194	<i>guettardi</i>	136
<i>Acanthopora</i>	182	<i>halicora</i>	59
<i>Acanthopora horrida</i>	194	<i>heliopora</i>	153
<i>acropora, Favia</i>	21	<i>henrichii</i>	54
" <i>Heliastrea</i>	20	<i>intersecta</i>	21
" <i>Madrepora</i>	20, 21	<i>lamarckiana</i>	137
<i>acuticollis, Favites</i>	53, 54, 59	<i>laperousiana</i>	137
" <i>Prionastraea</i>	53	<i>magnifica</i>	83
<i>adduensis, Favia</i>	68	<i>microphthalma</i>	167, 176
<i>aequicostatus, Heterocyathus</i>	208	<i>ocellina</i>	173
<i>affinis, Astraea</i>	25	<i>ordinata</i>	33
" <i>Favia</i>	25, 41	<i>pallida</i>	41
" <i>Parastrea</i>	25	<i>pandanus</i>	36
<i>agassizi, Leptastrea</i>	155, 156	<i>parvistella</i>	80
<i>aiharai, Caulastrea</i>	11	<i>pectinata</i>	87
<i>amarantum, Trachyphyllia</i>	207	<i>purpurea</i>	158
<i>amarantus, Trachyphyllia</i>	208	<i>puteolina</i>	36
<i>amicorum, Favia</i>	27, 29, 30-33	<i>quadrangularis</i>	137
" <i>Parastrea</i>	32	<i>retiformis</i>	79
<i>amplior, Favia</i>	33	<i>robusta</i>	54
" <i>Parastrea</i>	33	<i>rotumana</i>	40
<i>ananas, Astraea</i>	32	<i>rudis</i>	68
<i>annuligera, Montastrea</i>	4, 137, 139-141, 143	<i>sinuosa</i>	87
" <i>Orbicella</i>	139	<i>solidior</i>	137
<i>Antillia</i>	207	<i>speciosa</i>	36
<i>Antillia constricta</i>	208	<i>spongia</i>	79
<i>geoffroyi</i>	208	<i>tesserifera</i>	65
<i>lonsdalei</i>	208	<i>versipora</i>	36, 149
<i>lonsdaleia</i>	208	<i>virens</i>	51, 54
<i>sinuata</i>	208	<i>Astracosmilia</i>	11
<i>Antillophyllia</i>	3, 207	<i>Astrées</i>	1
<i>Aphrastraea</i>	1, 2	<i>astreiformis, Astroria</i>	98
<i>Aphrastraea deformis</i>	68	" <i>Coeloria</i>	100
<i>arabica, Coeloria</i>	103	" <i>Maeandra</i>	100
<i>armata, Plesiastrea</i>	21	" <i>Platygyra</i>	100
<i>aspera, Cyphastrea</i>	176	<i>astrinus, Favites</i>	50
" <i>Favia</i>	26	<i>Astroria</i>	98
" <i>Goniastrea</i>	4, 79, 83-86	<i>Astroria astreiformis</i>	98
" <i>Oulophyllia</i>	119, 123, 124	<i>daedalea</i>	98
" <i>Phymastrea</i>	144	<i>esperi</i>	98
" <i>Ulophyllia</i>	118	<i>sinensis</i>	105
<i>Astraea affinis</i>	25	<i>stricta</i>	105
<i>ananas</i>	32	<i>australensis, Coeloria</i>	92
<i>cellulosa</i>	33, 36	" <i>Goniastrea</i> .. 79, 89, 91, 92-95, 105, 118	
<i>cerium</i>	87	" <i>Prionastraea</i>	92
<i>deformis</i>	68	<i>Barabattoia</i>	11
<i>denticulata</i>	33, 36	<i>Barabattoia goroensis</i>	32, 33
<i>eximia</i>	79	<i>mirabilis</i>	27, 29, 32, 33

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