AUSTRALIAN INSTITUTE OF MARINE SCIENCE
MONOGRAPH SERIES

Volume 1

SCLERACTINIA OF EASTERN AUSTRALIA

PART I

Families Thamnasteriidae,
Astrocoeniidae,
Pocilloporidae

by

J. E. N. Veron

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Foreword

Many coral reefs of the tropical Indo-Pacific had been known long before 1770 when James Cook discovered and charted the vast reef complex off the north-eastern coast of Australia, later to be termed by Matthew Flinders the 'Great Barrier Reefs'. Since then the richness and variety of the organisms of this major tropical life province have become legendary and a focus of much study by biologists and geologists, especially during the last 85 years. No estimates are available of the diversity of reef-dwelling animals and plants, but certainly many thousands of species are involved. The scleractinian or stony corals, the principal reef-constructors, flourish here in a variety unknown elsewhere.

With the establishment of the Australian Institute of Marine Science in Townsville, North Queensland, it is appropriate that one of its first major scientific contributions should be a monographic enumeration and critical taxonomic study of the scleractinian corals, based upon very large, well-documented serial collections enabling an assessment of the specific significance of their well-known but not often considered intraspecific variations.

This volume is the first of a series of four monographs covering all reef-building species. As this first volume shows, many old species will fall and a few new species will be established; but most importantly this series will provide a stable, comprehensive taxonomic basis for future research in other fields of the reefs' complex biology and geology.

John W. Wells
Cornell University

I
Introduction

'Curiously, the reef-building coral fauna of the Great Barrier—its chief *raison d'être*—is not as well known as it should be, although systematics, by no means the sterile study some would have us believe, is a necessary prelude to any understanding of the Barrier's complex ecology.'

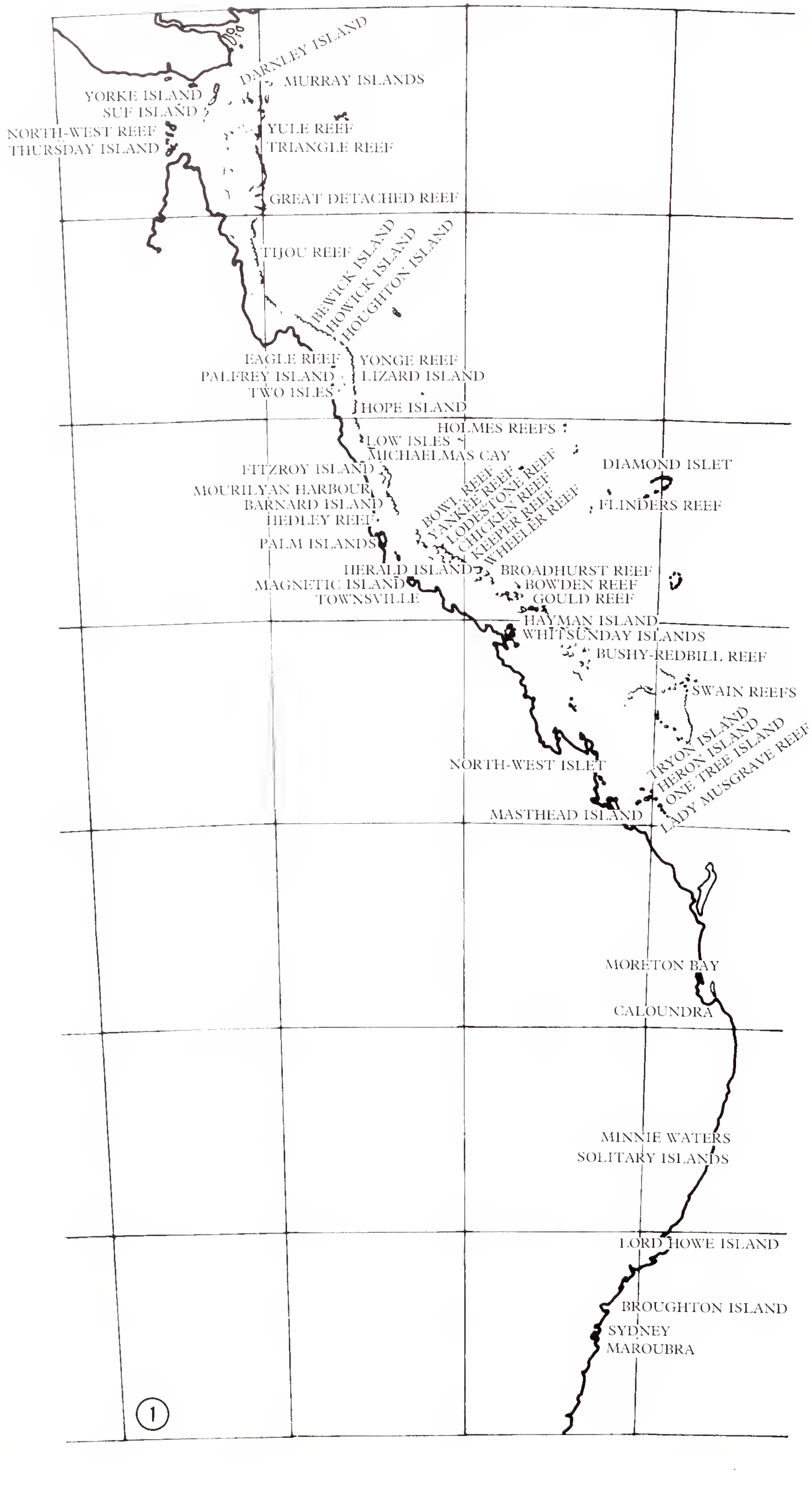
This statement, made by J. W. Wells in 1955, is still entirely valid twenty years later. It was only at the end of the last century that the coral fauna of North-East Australia started to arouse an interest amongst naturalists. Tenison-Woods and, some years later, Saville-Kent were pioneers in that field and both made valuable collections of corals in various parts of the Great Barrier Reef area. However, no comprehensive taxonomic report arose from their work, although a number of Saville-Kent's specimens have been dealt with by various scientists who contributed to the *Catalogue of Madreporarian Corals in the British Museum* (Brook, 1893; Bernard, 1903, 1905, 1906; Matthai, 1928). At the beginning of the century, Hedley and Taylor (1907) published a valuable contribution to the scleractinian fauna of the Great Barrier Reef. Five years later, the expedition of the Carnegie Institution to the Murray Islands was to provide the material for the first detailed and comprehensive papers, both published in 1918, on reef coral ecology (by Mayer) and taxonomy (by Vaughan). One of the major values of Vaughan's paper, apart from its thoroughness, was that it considered the coral fauna of one of the northernmost, and consequently one of the richest, parts of the Great Barrier Reef area.

In 1928–1929, members of the British Association Expedition to the Great Barrier Reef made a collection of corals, principally from Low Isles and nearby reefs. A taxonomic account of these corals was written by Crossland, and published in 1952, after his death. This study is of particular value because of the care with which collections were made at Low Isles, and also because Crossland had had extensive experience of coral reefs. His approach to coral taxonomy is therefore quite different from that of Vaughan, basically a geologist and paleontologist.

In more recent years, some attention has also been paid to the southern end of the Great Barrier Reef area, particularly to Heron Island (Salter & Besley, 1950; Salter, 1954). However, the most significant recent contribution to the knowledge of corals of eastern Australia is that of J. W. Wells. In a series of papers (Wells, 1955a, 1955b, 1962, 1964a; Stephenson & Wells, 1956), numerous additions to the coral fauna of this region were made, with special reference to Low Isles and Heron Island. But perhaps the greatest merit of some of these papers is that they provide a synthesis of knowledge of the corals of the Great Barrier Reef region, and give an overall picture of the distribution of genera, from north to south, within the Great Barrier Reef province. This last problem has been re-examined by one of us (Veron, 1974).

One should also mention the collections made during the *de Moor* Belgian expedition in 1967, but so far only one series of short papers, dealing exclusively with some species of *Goniastrea* has been published (Foidart, 1970a, 1970b, 1971).

The above-mentioned studies have led to a somewhat detailed knowledge of basically three areas in the Great Barrier Reef region: Murray Islands (09°S lat.) in the far north, Low Isles (16°20′S lat.) in the central position, and Heron Island (23°S lat.) at the southern end. To these three localities, Stephenson and Wells (1956) added


DARNLEY ISLAND
MURRAY ISLANDS
YORKE ISLAND
SUE ISLAND
NORTH-WEST REEF
THURSDAY ISLAND
YULE REEF
TRIANGLE REEF
GREAT DETACHED REEF
TIJOU REEF
BEWICK ISLAND
HOWICK ISLAND
HOUGHTON ISLAND
EAGLE REEF
PALFREY ISLAND
TWO ISLES
YONGE REEF
LIZARD ISLAND
HOPE ISLAND
HOLMES REEFS
LOW ISLES
MICHAELMAS CAY
DIAMOND ISLET
FITZROY ISLAND
MOURILYAN HARBOUR
BARNARD ISLAND
HEDLEY REEF
BOWL REEF
YANKEE REEF
LODESTONE REEF
CHICKEN REEF
KEEPER REEF
WHEELER REEF
FLINDERS REEF
PALM ISLANDS
HERALD ISLAND
MAGNETIC ISLAND
TOWNSVILLE
BROADHURST REEF
BOWDEN REEF
GOULD REEF
HAYMAN ISLAND
WHITSUNDAY ISLANDS
BUSHY-REDBILL REEF
SWAIN REEFS
TRYON ISLAND
HERON ISLAND
ONE TREE ISLAND
LADY MUSGRAVE REEF
NORTH-WEST ISLET
MASTHEAD ISLAND
MORETON BAY
CALOUNDRA
MINNIE WATERS
SOLITARY ISLANDS
LORD HOWE ISLAND
BROUGHTON ISLAND
SYDNEY
MAROUBRA
①

Moreton Bay as an area with a well-known coral fauna, and very recently Veron *et al.* (1974) published an account of the corals of the Solitary Islands (30°20′S lat.). It is to be noted, however, that both Moreton Bay and the Solitary Islands lie well outside the Great Barrier Reef area proper and the coral fauna is greatly reduced.

Previous knowledge of Great Barrier Reef corals was therefore primarily centred around three widely separated localities, each lying well within the line of the outer barrier reef.[1] Almost nothing was known of the corals of the barrier reef itself and little was known of the corals of the myriads of other islands and reefs which comprise the 2000 km long Great Barrier Reef province. Finally, it must be emphasised that these studies were almost exclusively based on collections from island reef flats or other waters accessible to non-divers.

Such methods and opportunities for field work are in very great contrast to those of the present study where the use of SCUBA and the research vessel *James Kirby* have allowed the authors to make their own direct observations and collections over a very increased range of depths, biotopes and geographic localities.

The field work and consequent collections on which the present studies are based were made during two voyages of R.V. *James Kirby* to the far northern islands and reefs of the Great Barrier Reef (the first voyage being Phase III of the Royal Society and Universities of Queensland Expedition to the Great Barrier Reef), as well as many shorter voyages to a variety of islands and reefs closer to Townsville. Other collections were made using islands as bases. These include the Murray Islands, Lizard Island, Low Isles, the Whitsunday Islands, Heron Island and, most importantly of all, the Palm Islands.

The collection, at present housed in the Department of Marine Biology, James Cook University, contains more than 10 000 specimens collected from the localities indicated in Fig. 1, including the principal collecting stations listed below. In addition, the coral collections of the Queensland Museum, including a collection identified by J. W. Wells, and the large collections of the Australian Museum were examined. Finally, the corals from the Great Barrier Reef Expedition 1928–29 were examined in the British Museum (Natural History), and those from the Murray Islands identified by Vaughan (1918) were studied in the U.S. National Museum.

Fig. 1 East Australian place names cited in the text.

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[1] The authors follow the widely accepted meaning of the term 'Great Barrier Reef'. This includes all the area of Queensland's continental shelf which is bounded by various coral reef formations. The term 'barrier reef' is applied only to outer reefs which form true barriers.

II
The Species Problem and Intraspecific Variation

It is now obvious to all coral taxonomists that, despite the rigid appearance of their calcareous skeletons, Scleractinia are highly plastic organisms, showing a considerable range of variations in all their skeletal characters. Gravier (1911), summarising the results of Pace (1903) and Wood-Jones (1907), could even write: 'Rien, en effet, ne reste stable chez ces animaux: ni l'aspect général de la colonie, ni le coenenchyme, ni même les calices.' Such a statement depicts the difficulties facing many scientists when attempting to apply to corals the Linnean species concept.

However, the early authors until about 1880 were not aware of this problem, mainly because they were working on single specimens, or on very small series. This unawareness of scleractinian polymorphism certainly led them to describe as new species what are only local varieties and, as a consequence, the present status of coral taxonomy is unnecessarily complex and obscure. Another deficiency of the early authors lies in the lack of accuracy of their descriptions, the only way to identify a specimen with any certainty being its comparison with the type specimen, as originally noted by Studer (1901): 'Bei der Aufzählung der Arten muss ich leider constatiren, dass es, ohne die Originalexemplare der Beischreibungen zur Hand zu haben, bis jetzt ausserordentlich schwer ist, eine Art mit Sicherheit zu identificiren.'

It was only when large collections were made available to taxonomists, enabling them to make comparisons within series of specimens, that the variability of skeletal characters became recognised as a major difficulty of coral classification. This brings us to the period of the first major oceanographic expeditions, and in particular we must mention here the *Challenger* expedition (1873–1876). It is the great merit of Quelch, in his report on the corals collected by the *Challenger* (1886), that he was the first to relate very clearly intraspecific variations with environmental factors. Indeed, after a comment on various environmental conditions, Quelch writes: 'It is certainly remarkable to notice the great amount of variation to which apparently one and the same species is liable, as is evident where large series of specimens are at hand; and it is probable that such variations are brought about by the influence of one or more of the above conditions.'

Ever since Quelch, coral taxonomists have been well aware of this problem and tried to deal with it in various ways. Duerden (1902, 1904) and Matthai (1914, 1923, 1926, 1928), for instance, attempted a detailed study of the soft parts, but they have not so far been followed in that direction. Bernard (1903, 1905, 1906), in his study of the Poritidae of the British Museum, abandons completely the Linnean binomial nomenclature and adopts a new taxonomic unit, the 'local form'. Of course, Bernard's treatment demonstrates the importance of the problem in its full scale, but it adds very little to our knowledge of coral taxonomy, and, seventy years later, one must recognise that his work has not been generally useful. In fact, Bernard's views were criticised soon after their publication, in particular by Gardiner (1904), who attempted to classify the skeletal variations into three categories: vegetative, continuous, and discontinuous (or specific). Bedot (1907) also pointed out that local varieties of well-known species have often unnecessarily been described as new species. A significant advance, much in line with the ideas developed by Quelch, was made in 1907 by Vaughan, who emphasised the necessity of studying variations in the Scleractinia as a prerequisite to a better understanding of coral taxonomy. According to him, these variations should be studied in three ways—in nature without experiment, in nature by experiment, and under artificial conditions. Vaughan also had several greater merits. He is responsible for one of the best definitions of the species as applied to corals; a species, he wrote, 'is a group of individuals connected among themselves by intergrading characters, and separated by distinct lacunae from all other individuals or groups of individuals'. Even more importantly, he recognised the need for physiological studies ('until more is known concerning the physiology of corals, we cannot understand the factors that determine their distribution') and he pointed out that growth form variations in corals may be either phenotypically or genotypically determined. Therefore, in many ways, Vaughan appears as a precursor of the modern trends in coral taxonomy. In the following few decades, however, these concepts were not widely used among scientists, who continued to follow a more traditional approach to coral taxonomy, with the exception of Umbgrove (1939, 1940), in his work on corals from the East Indies, and Crossland, in his report on corals collected by the Great Barrier Reef Expedition (1952).

In recent years, several authors, among them Kawaguti, Goreau and Yonge, applied to some coral species the physiological type of research suggested by Vaughan, but these studies were, from a taxonomic standpoint, limited. It was not until 1970 that Laborel, in his study of Brazilian corals, introduced the concept of 'écomorphoses' (intraspecific skeletal variations determined by environmental factors). However, the status of 'écomorphose' is not clearly defined by Laborel. This concept is more often applied to a group of individuals or populations living in given homogeneous environmental conditions, but some confusion still exists in Laborel's paper as to the relationships between 'écomorphoses' and terms such as 'forms' or even geographical sub-species. Laborel's contribution is nevertheless important, for it represents the introduction to scleractinian corals of a dual nomenclature (ecological versus morphotaxonomic) long in use amongst botanists. No such dualism has been developed so far in invertebrate taxonomy for the nomenclature of intraspecific categories. This probably results from the fact that zoologists have long been aware that geographic 'races' have ecological (and physiological) characteristics.

Two years later, Wijsman-Best (1972), in her study of New Caledonian Faviinae, made a further advance along the lines followed by Laborel. Wijsman-Best used the term 'ecotype' to characterise, from a classification standpoint, the interbiotope variations of colonies. A comprehensive study of these variations led her to consider as ecotypes of one species, groups of populations previously accepted as separate species.

Although the relationships (or hierarchy) between 'ecotype' and 'form' and even 'population' are not fully explicit, the overall concept is more rigidly delineated than in Laborel's work. In particular, there appears to be a converse and reciprocal relationship between 'ecotype' and 'biotope'.[2] A difficulty arises, however, from the use of the particular word 'ecotype'. Ever since it was introduced by Turesson (1922), 'ecotype' has implied a *genotypical* response to particular environmental conditions, whereas Wijsman-Best (1974) considered it a 'purely phenotypical term', in opposition to the general consensus.

The relative importance of *genotypically* and *phenotypically* (in particular *ecophenotypically*) determined variations have not yet been recognised, and various hypotheses have been put forward. Barnes (1973) suggested, for instance, that 'indeed, all growth forms may be under strict genetic control.' In any case, the word 'ecotype' is not satisfactory for characterising skeletal variations of reef corals.

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[2] In this study, a 'biotope' is defined after Pérès (1961) as 'a geographical area with a variable surface or volume, which is under the influence of environmental factors, the dominant characteristics of which are homogeneous'. Pérès (1961) further describes a biotope as an area covered by a 'biocoenose', which can be defined as 'a group of living organisms, corresponding, by its composition, and by the number of species and individuals, to given average values of environmental factors. This is a group of organisms linked by mutual interaction, and which maintains itself by reproducing permanently in a given area.'

Another problem associated with the use of this word lies in the fact that, since Turesson, there has been an increasing tendency towards typological interpretation of this concept, thereby decreasing its interest (although a dualism between ecological and morphotaxonomic nomenclatures remains widespread in botany).

To avoid any possible misinterpretation of our own position, we use the more neutral word *ecomorph*, in a sense very similar to that of Laborel's own 'ecomorphose' and of Wijsman-Best's 'ecotype'.

Ecomorphs are hereby defined as intraspecific skeletal variations phenotypically and/or genotypically determined in response to specific ecological conditions.

We are well aware that this term has its limitations and that the ecomorph concept does not solve all the difficulties of coral taxonomy, but we believe it is an improvement over the previous situation. One major difficulty has been expressed by Mayr (1966) (writing about 'ecotypes', but the same is true of our 'ecomorphs'): 'unfortunately ecotypes are rarely discontinuous, rarely well delimited, often polyphyletic and always full of intraecotype variability'.

This derives from the fact that, in coral reefs in particular, it is hardly possible to find homogeneous environmental conditions, and therefore homogeneous populations. Chevalier (1971) mentions, quite rightly, that all the individuals of one and the same colony do not represent a homogeneous population. Indeed, the various parts of one colony are exposed to different conditions of illumination, hydrodynamics, sedimentation and action of commensals or parasites; hence the variations, purely phenotypically-determined in this case, that may frequently be observed in different parts of the one colony.

Various 'techniques' are presently being attempted in the field of coral taxonomy to overcome the difficulties of the 'species problem', especially intraspecific variability, e.g. numerical taxonomy (Powers, 1970), interspecific aggression and immunological techniques (Lang, 1971) and statistical treatment (multivariate analysis) (Wallace, 1974) on *Acropora*. In some cases, such studies are of interest for the solution of limited problems, but we believe that they are unlikely to be useful on the larger scale required for comprehensive taxonomic studies. Another approach which is of general application for the whole order involves a study of the histological structure and ultrastructure of skeletal elements. Such methods, which are generally favoured by paleontologists, were refined by use of ultra-polished thin sections by Chevalier (1971). However, intraspecific variations are frequently given taxonomic status by being typified as 'varieties' (a twice-ambiguous word) which are only loosely related to specific environmental conditions, a very major weakness of this approach.

Although there is some merit in Chevalier's approach, more than a thousand hours spent underwater examining corals in their environment, and the further examination of more than ten thousand specimens with detailed ecological data, have convinced us that the ecomorph is a biological reality and so, consequently, are the species 'units' which we have used below.

III
Methods

The precise methods of study of any species or group of species depended (a) on the taxonomic problems encountered, (b) the number and variability of relevant specimens present in the collection, and (c) the abundance and accessibility of relevant specimens in the field.

Initially, all taxonomic studies were based on series of specimens collected by the authors because they were of taxonomic interest (i.e. collections of category 2, below). If for any reason these collections and observations proved inadequate, further study was undertaken which usually involved making collections specifically designed to investigate further the range of growth forms of the species or group of species under consideration (i.e. collections of category 3, below). In addition, other study methods or combinations of study methods were frequently used. Thus, for example, the skeletal characteristics of some species were studied using various quantitative methods; in other species, polyps were studied histologically or photographically, the latter both *in situ* and in aquaria.

The final account of a species or group of species given in these publications represents a synthesis of all information derived from various combinations of these methods. Details are given with the discussion of each species.

Synonymy

The synonymy given in these publications is designed to serve the dual purpose of combining the synonymies of previous authors and proposing the new synonymies determined from the present studies. In the former case, conclusions of previous taxonomists have usually been accepted without restudying type specimens, provided that original species descriptions and opinions expressed by other authors do not appear to contradict those conclusions. In the latter case, the synonymy of previously recorded east Australian 'species' is listed together with very clear cases of synonymy with other Indo-Pacific 'species'.

It is emphasised that the synonymies of many if not most of the species discussed in the present publications are likely to be far from complete.

The Collection of Specimens

The collections on which this study is primarily based are of three different categories:

1. General collections. These were made by the authors or by assistants and colleagues, primarily to aid in the compilation of distribution records. In most cases, the collectors aimed to collect one representative specimen of as many species as possible from each locality.

2. Collections for general taxonomic study. Collections were made by the authors of specimens which are, for some reason, of taxonomic interest.

3. Collections for specific taxonomic study. Very detailed collections were made by the authors for the study of intraspecific growth form variations, as described below. Localities selected for this work include the islands referred to in the Introduction as well as three outer barrier reefs—Great Detached Reef, Tijou Reef and Bowl Reef.

Collections from 'principal collecting stations' (see below) were of categories 2 and/or 3, or 1, 2 and/or 3. Collections involving more than one category were made simultaneously, during successive dives, or sometimes during different voyages.

After collection, all specimens were numbered and given a locality number. Specimens from collection categories 2 and 3, which include all collections from the principal collecting stations had their colour, depth and the principal parameters of their environment recorded. Where appropriate, detailed notes were made of the differences between the microhabitats of different colonies.

All specimens were cleaned in a solution of equal parts by weight of sodium hypochlorite and sodium carbonate, then washed, dried, labelled and stored in 'polythene' bags. They are at present housed in the Department of Marine Biology, James Cook University. All specimens specifically mentioned or photographed in these publications, including type specimens, are being temporarily kept at the Australian Institute of Marine Science.

Photography

Close-up photographs were made with a Zeiss Tessovar photomacroscope, using incident light or light transmitted through the specimen from below. Photographs of whole specimens were made with 35mm cameras using diffuse fluorescent illumination.

Underwater photographs were made with Nikonos, Minolta or other 35mm cameras, or a Hasselblad 6 × 6cm camera, using standard techniques.

IV

The Determination of Intraspecific Growth Form Variation

The delineation of closely allied species and the subsequent study of growth form variations within species were made by direct underwater observation combined with the collection of specific reference specimens for laboratory study (collections of category 3, above). These underwater observations and collections were made with the following objectives:

1. To determine growth form variation within a single colony.

Samples were collected from large colonies which occupy more than one microhabitat, usually by growing over, around, and under a horizontal overhang (e.g. Fig. 2). Samples were also collected from large colonies exhibiting growth form variations between their centres and peripheries. These samples were used to determine intraspecific variations which are entirely phenotypic.

Fig. 2 A single large colony of *Seriatopora hystrix*, Wheeler Reef, collecting station 22.

2. To determine growth form variation within a single biotope.

Samples were collected of colonies growing close to each other in very uniform conditions within generally uniform biotopes such as flat reef crests, flat sandy lagoons and flat muddy bays around islands. Under these conditions, intraspecific growth form variation is minimal and these samples (e.g. Fig. 3) were therefore used to separate allied species with a maximum of reliability.

3. To determine variation among interconnected biotopes.

Series of samples were collected specifically to illustrate the gradual change in growth form that occurs between adjacent biotopes.

Fig. 3 Adjacent colonies of *Pocillopora damicornis* and *Pocillopora verrucosa*, Bowl Reef, collecting station 10 (× 0.7).

All information derived from these three forms of observation and collection were combined to differentiate between closely allied species and to determine the extent of growth form variation of species *within a single locality*.

The full extent of intraspecific growth form variation was studied by comparing results obtained by the above methods from many different localities which were specifically selected to incorporate both a maximum diversity of biotopes, as described below, and a wide geographic range within the Great Barrier Reef.

V
Principal Collecting Stations and Biotopes

General localities for collecting were usually selected according to a compromise between accessibility and suitability for the type of collection to be undertaken. Each locality was the site of one or more principal collecting stations (for collections of categories 2 or 3, above), each of which involved one or more biotopes. Very seldom was more than one biotope studied per collecting station.

In this work, emphasis has been placed on the study of environmentally-induced growth form variations, as these are considered by the authors and others (e.g. Laborel, 1970; Wijsman-Best, 1972) to be basic to the understanding of species variability and, consequently, species recognition. The following, therefore, is an attempt broadly to categorise the principal biotopes studied and list the relevant principal collecting stations. It is emphasised, however, that each and every biotope considered is itself a constantly changing, endlessly complex combination of microhabitats. The following brief and inevitably unsatisfactory account attempts to convey general impressions only. Descriptions of individual biotopes are not given.

Unless otherwise stated, depth ranges indicated are those recorded at the time of collection. Different collections at the same station refer to different depth ranges (indicated) or to other slight differences in collecting areas.

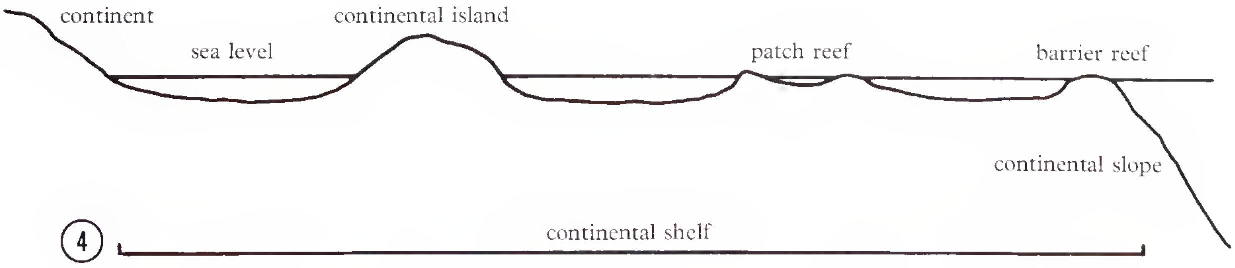
The Great Barrier Reef province can be divided lengthwise into three principal zones (Fig. 4): (a) outer reefs, including barrier reefs, (b) inner reefs and associated cays, and (c) high islands.

OUTER REEFS INCLUDING BARRIER REEFS

Three groups of biotopes were studied (Fig. 5):

(A) Biotopes of reef fronts (Fig. 6). Such biotopes are maximally exposed to wave action. The water is clear and almost continually turbulent. The substrate consists of hard, well-cemented wave-worn reef rock. The coral cover is usually rich and relatively homogeneous and is closely cropped by wave action. Such biotopes were found at collecting stations:

Fig. 4 Simplified diagrammatic cross-section of the Great Barrier Reef.



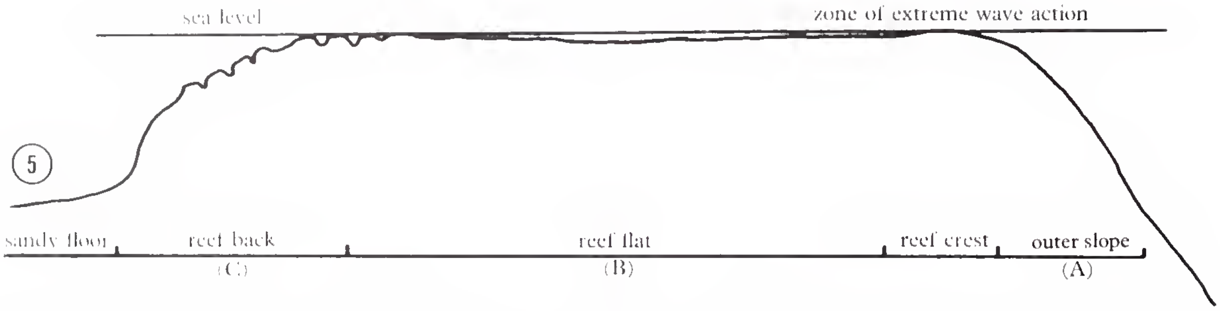
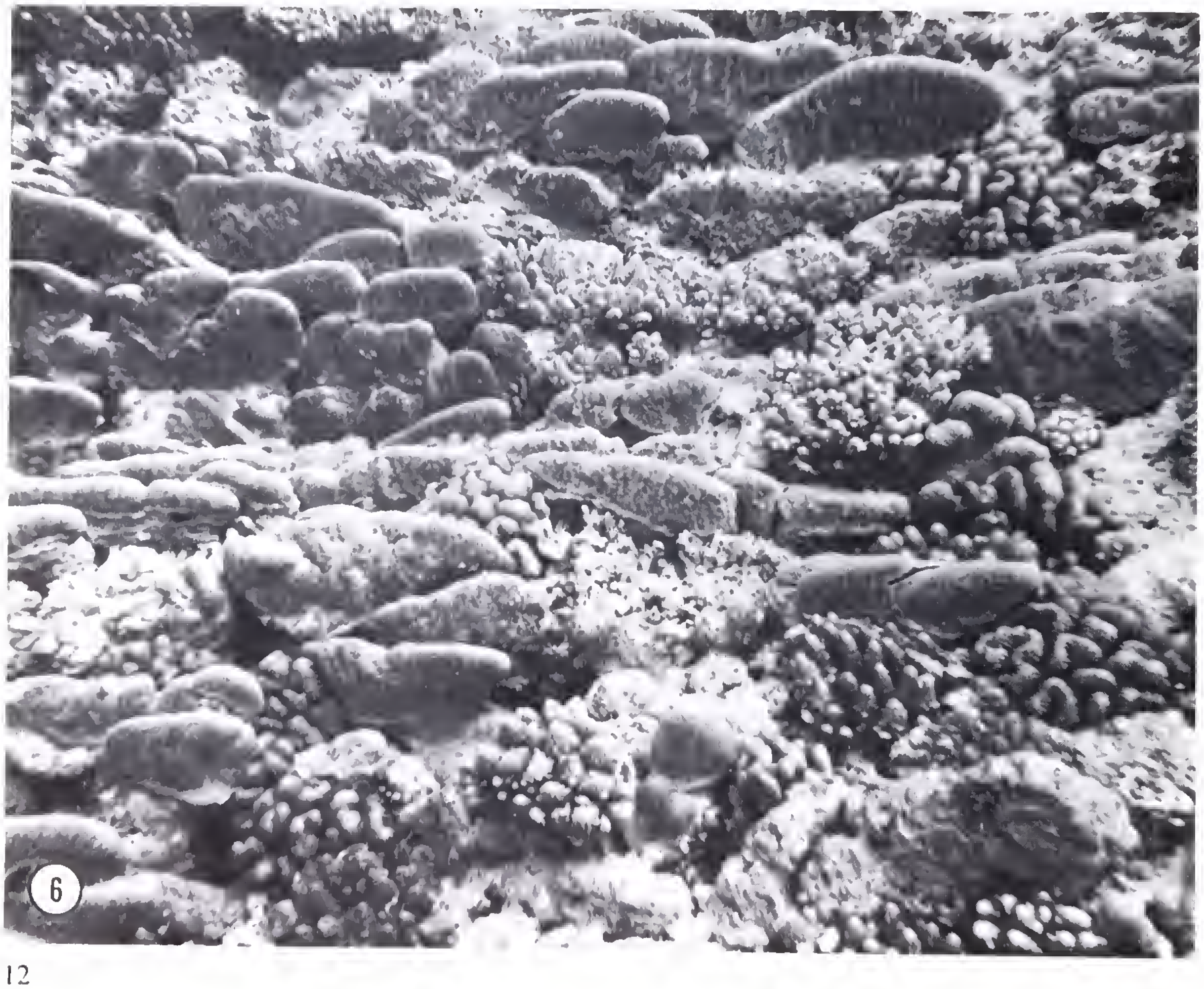


Fig. 5 Diagrammatic cross-section of an outer barrier reef, showing the approximate location of the three groups, A, B and C, of biotopes studied.

1. *Great Detached Reef;* outer slope, exposed to strong to extreme wave action, steeply sloping cemented reef rock substrate; three collections by SCUBA, 5, 10 and 15m below the reef front.
2. *Tijou Reef;* outer slope, exposed to strong to extreme wave action, steeply sloping cemented reef rock substrate; five collections by SCUBA, on the reef front and 5, 10, 15 and 10–20m below the front.
3. *Yonge Reef;* outer slope, exposed to strong to extreme wave action, steeply sloping reef rock substrate; one collection by SCUBA, 0–35m.
4. *Bowl Reef;* outer slope, exposed to strong to extreme wave action, gently sloping cemented reef rock substrate; two collections by SCUBA, 2–4 and 10m.

(B) Biotopes of reef flats and very shallow lagoons that are normally protected from strong wave action but which are exposed to slight tidal currents (e.g. Fig. 7).

Fig. 6 The outer slope of an outer barrier reef, collecting station 1.



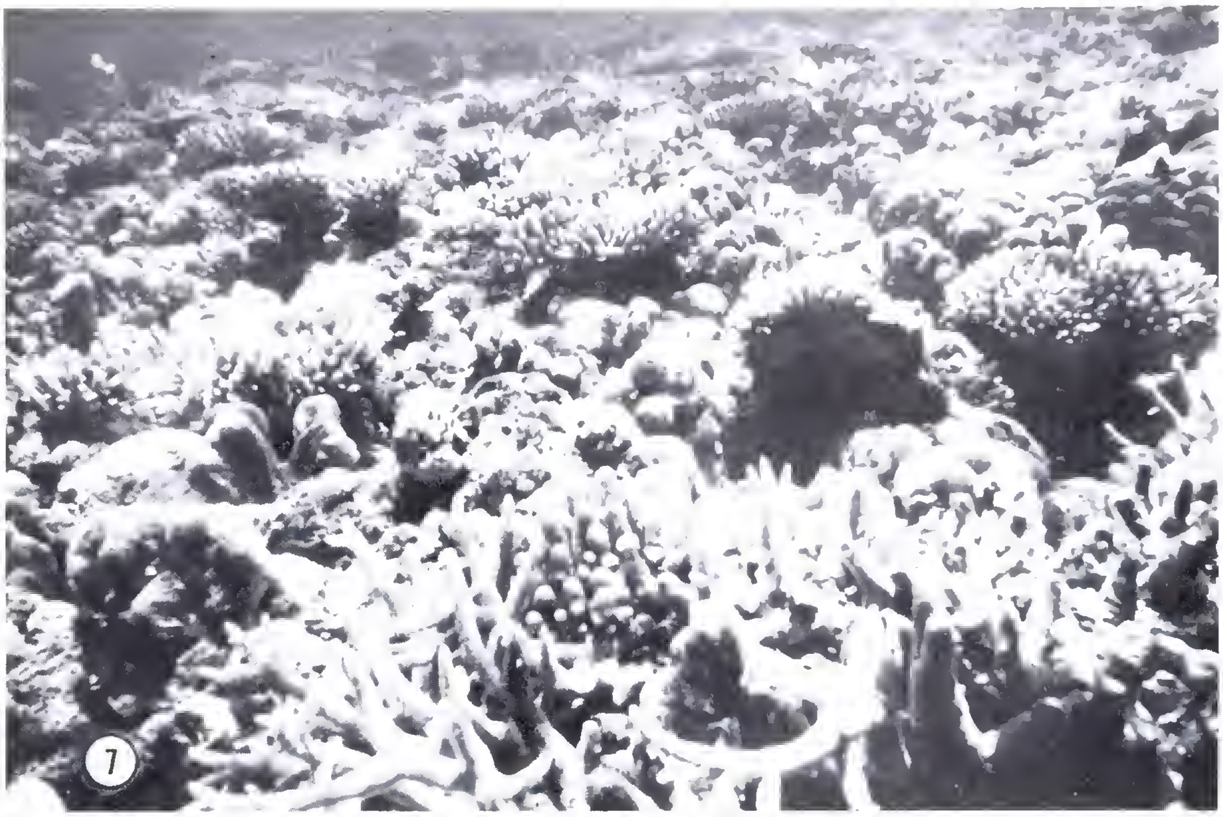
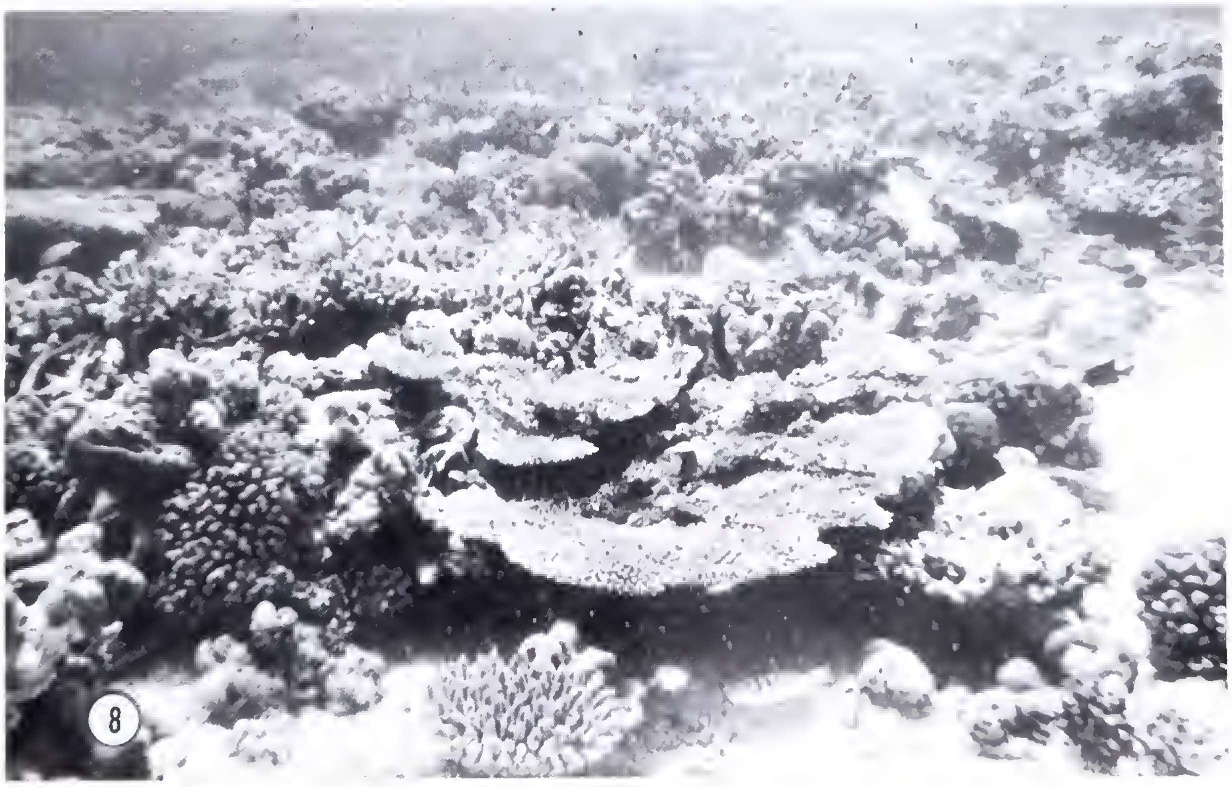


Fig. 7 The reef flat of an outer barrier reef, collecting station 6.

The substrate consists of eroded reef rock, sand or coral debris. The water is usually clear; the temperature may be markedly higher than that of the surrounding sea. The coral cover is usually sparse and very irregular. Such biotopes were found at collecting stations:

5. Great Detached Reef; reef flat, exposed to tidal currents and slight wave action, sand and rubble substrate; one collection by SCUBA, 300m behind the front, at 1m depth.
6. Tijou Reef; reef flat, exposed to moderate currents and slight wave action, reef rock

Fig. 8 The reef back of an outer barrier reef, collecting station 9.



merging onto sand substrate; three collections by SCUBA, 300, 450 and 600m behind the front, 1–2m.

(C) Biotopes of reef backs (e.g. Fig. 8). These are usually well protected from strong wave action but may be exposed to tidal currents. The substrate usually consists of rugged, eroded reef rock extending from the reef flat to the sandy ocean floor. It is usually broken up into a complex of small valleys, caves and overhanging ledges. The benthic fauna is usually rich and its diversity reflects the multitude of microhabitats available. Such biotopes were found at collecting stations:

7. The barrier reef NE from Murray Islands, W side; reef back, protected, steeply sloping reef rock substrate; one collection by SCUBA, 5m.
8. Tijou Reef; reef back, protected, broken reef rock merging onto sand; one collection by SCUBA, 5–10m.
9. Yonge Reef; reef back, semi-protected, substrate of broken reef rock merging onto sand; two collections by SCUBA, 0–6m.
10. Bowl Reef; reef back, protected, substrate of rugged reef rock with a sandy floor; two collections by SCUBA, 1–10 and 22m.

INNER REEFS AND ASSOCIATED CAYS AND LAGOONS

The variety of biotopes included here are such that general descriptions are seldom widely applicable. In this study, corals from 3 diverse groups of biotopes were selected for study, primarily because they appeared to be protected from environmental extremes.

(D) Biotopes of semi-enclosed lagoons. These are characteristically well protected from wave action and from currents. The substrate usually consists of coarse sand and coral rubble, the water is usually clear. The coral cover is usually very heterogeneous, often delicate; ramous growth forms are dominant. Such biotopes were found at collecting stations:

11. Lizard Island, in lagoon near Palfrey Island; protected, sand substrate; one collection by SCUBA, 0–9m.
12. Low Isles, N side; protected, semi-enclosed lagoon, substrate of broken reef rock and flat, soft sand; one collection by SCUBA, 5–7m.

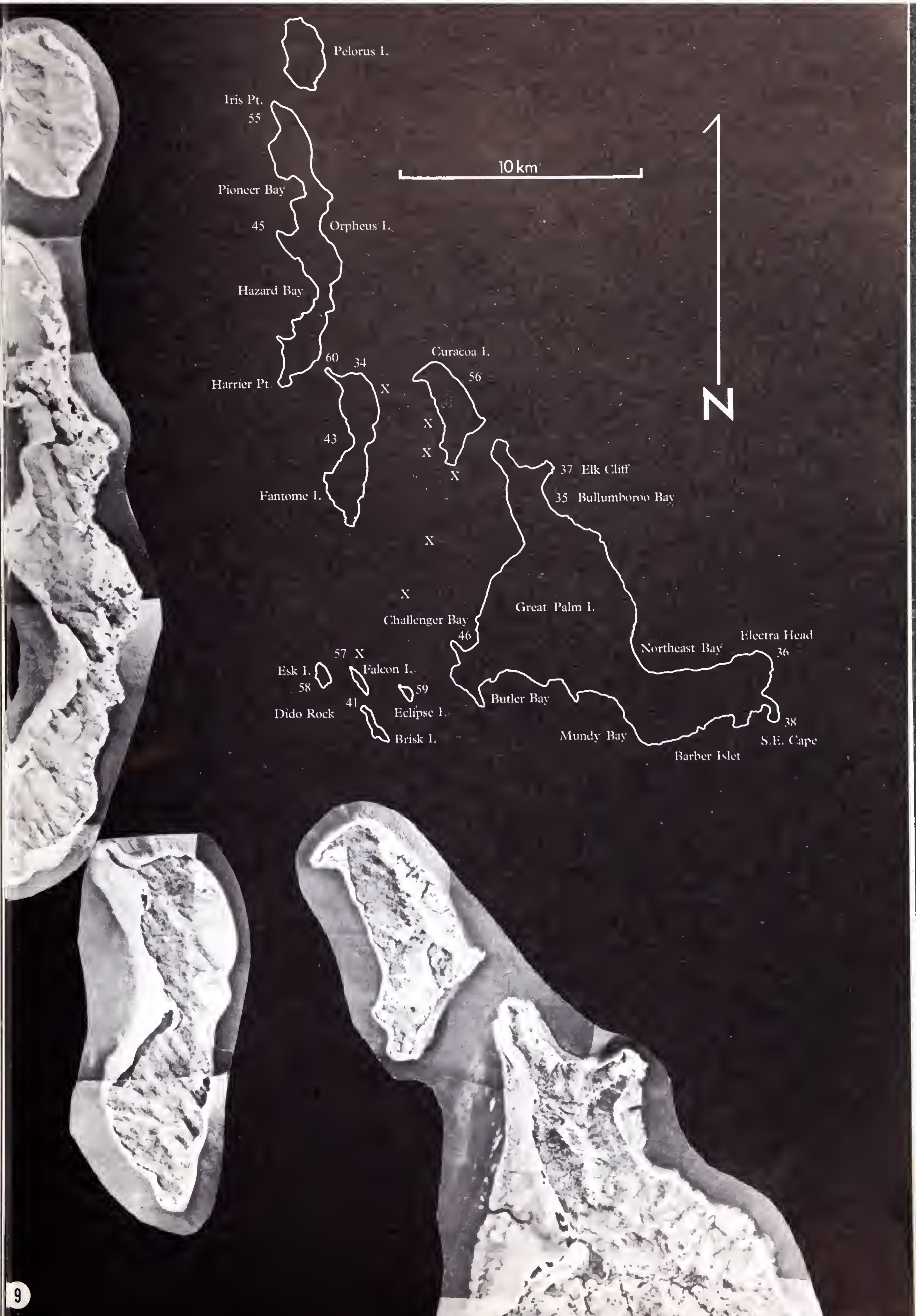
(E) Biotopes of sloping reef areas having substrates of rubble and/or partially cemented reef rock, a good circulation of clear water and protection from strong wave action. Under such circumstances, coral growth is usually prolific and diverse. Biotopes of the following collecting stations can be loosely grouped here:

13. Yorke Island, N side; well protected, substrate of reef rubble merging onto soft sandy floor; two collections by SCUBA, 2–15m.
14. North-West Reef, S side; semi-protected from wave action but exposed to moderate currents, well cemented reef rock merging onto sandy floor; one collection by SCUBA, 2–10m.
15. Howick Island, W corner; semi-protected, substrate of broken reef rock merging onto sand; one collection by SCUBA, 3–10m.
16. Houghton Island, W corner; semi-protected, substrate of broken reef rock merging onto sand; one collection by SCUBA, 3–22m.

(F) Biotopes of reef backs. These are essentially similar to biotopes of the backs of barrier reefs (C). Such biotopes were found at collecting stations:

Fig. 9 Aerial photograph of the northern part of the Palm Islands complex. Inset: map of the whole Palm Islands complex. Numbers indicate locations of principal collecting stations of the Palm Islands. Dredge samples were taken from localities indicated with a cross.

6


Pelorus I.
Iris Pt.
55
10 km
Pioneer Bay
45
Orpheus I.
Hazard Bay
60
34
Curacoa I.
56
Harrier Pt.
X
N
X
43
X
X
37 Elk Cliff
Fantome I.
35 Bullumboroo Bay
X
X
Great Palm I.
Challenger Bay
46
Electra Head
Northeast Bay
36
57 X
Esk I.
Falcon I.
58
59
41
Dido Rock
Eclipse I.
Butler Bay
38
Mundy Bay
S.E. Cape
Brisk I.
Barber Islet

17. Sue Island, SW and NW sides; semi-protected, broken reef rock merging onto muddy floor; two collections by SCUBA, 2–10m.
18. Bewick Island, NE corner; protected, substrate of fringing reef merging onto sand; one collection by SCUBA, 0–12m.
19. Eagle Reef, W side; well protected, substrate of reef rock merging onto soft sand; one collection by SCUBA, 0–5m.
20. Eagle Reef, S end; semi-protected, substrate of reef rock merging onto soft sand; one collection by SCUBA, 0–15m.
21. Keeper Reef, NW corner; protected, substrate of broken reef rock on a flat sandy floor; one collection by SCUBA, 2–10m.
22. Wheeler Reef, W side; semi-protected from wave action, exposed to currents of approximately 1m/second; one collection by SCUBA, 1–10m.

HIGH ISLANDS

Complexities of the coastline of high (continental) islands, and particularly groups of high islands such as the Palm Islands, provide the greatest diversity of marine habitats, and consequently the greatest diversity of benthic fauna, to be found within the Great Barrier Reef. For this reason, many detailed studies, including the majority of collections of category 3 (above), were carried out at the Palm Islands near Townsville. The principal collecting stations of the Palm Islands complex are indicated in Fig. 9.

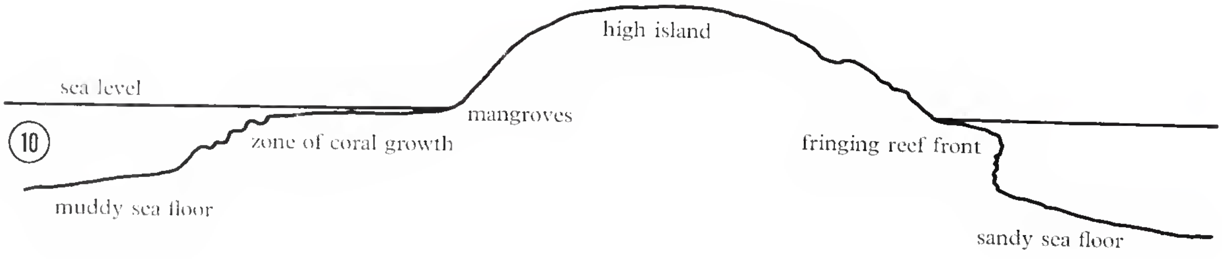
Five major groups of biotopes were studied (Fig. 10):

(G) Biotopes of sandy, or partly sandy, flat ocean floor. Biotopes studied were protected from wave action and exposed to slight currents of slightly turbid water. Very uniform biotopes may be many km^2 in area. Benthic fauna is always very sparse. Such biotopes were found at principal collecting stations:

23. Flat sea floor between Maer Island (Murray Islands) and the barrier reef; protected substrate of sand or mud; three collections by dredging, 42, 50 and 75m.
24. Lizard Island, NW side; semi-protected, substrate of soft sand; one collection by SCUBA and one by dredging, both 20m.
25. Palm Islands; mostly semi-protected, substrate of mud, sand or rubble; seven collections by dredging over a distance of 9.5km, 20–46m (Fig. 9).

(H) Biotopes of the front of fringing reefs. Well-defined fringing reefs occur around rocky shorelines exposed to wave action and/or currents. They are usually shaped approximately as indicated in Fig. 10, with the reef front steeply sloping to overhanging. The substrate is consolidated reef rock. Such fringing reefs are very

Fig. 10 Diagrammatic cross-section of a high island and associated reefs, showing the approximate location of the five groups, G, H, I, J and K, of biotopes studied.



different from the 'zones of coral growth' which occur on the sheltered sides of most major high islands (see below).

26. Maer Island (Murray Islands), SW side; semi-protected, steeply sloping fringing reef; one collection by SCUBA, 5–20m.

27. Maer Island (Murray Islands), E side; exposed to moderate wave action, moderately sloping fringing reef merging onto sandy floor; two collections by SCUBA, < 5 and 5–12m.

28. Dewar Island (Murray Islands), S side; exposed to moderate wave action, near vertical fringing reef; one collection by SCUBA, 1–10m.

29. Dewar Island (Murray Islands), SE side; exposed to moderate wave action, fringing reef substrate merging onto sandy floor; two collections by SCUBA, 2–5 and 15–27m.

30. Wyer Island (Murray Islands), NW side; protected, substrate of fringing reef and coral rubble; one collection by SCUBA, 0–25m.

31. Darnley Island, W side; protected, fringing reef merging onto sandy floor; two collections by SCUBA, 2–5 and 2–10m.

32. Lizard Island, NE side; semi-protected, vertical fringing reef merging onto soft sandy floor; one collection by SCUBA, 1–22m.

33. Lizard Island, SE side; vertical fringing reef merging onto soft sandy floor, one collection by SCUBA, 1–22m.

34. Fantome Island (Palm Islands), N and NW sides; semi-protected, fringing reef sloping steeply onto sandy floor; five collections by SCUBA, 3–10, 10–15, 15–20, 20–24 and 5–20m.

35. Bullumbooroo Bay, Great Palm Island; exposed to moderate wave action and currents, fringing reef sloping steeply onto sandy floor; one collection by SCUBA, 2–15m.

Fig. 11 The intertidal mud flat of Hazard Bay, Orpheus Island, Palm Islands at a low tide (photograph: P. Saw).

36. Electra Head, Great Palm Island; as for station 35; four collections by SCUBA, 0–3, 0–3, 3–15 and 3–15m.
37. Elk Cliff, Great Palm Island; as for station 35; one collection by SCUBA, 0–15m.
38. South-East Cape, Great Palm Island; as for station 35; two collections by SCUBA, 5–18 and 18–20.

(I) Biotopes of intertidal and sub-tidal mud flats. These frequently occur between mangrove areas or soft sandy beaches and the 'zone of coral growth' on the sheltered (usually western) side of islands (Fig. 11). Many such areas are not fully drained at low tide; other areas are exposed only at low spring tides. The water is turbid and frequently much warmer than that of the surrounding sea. Coral growth is usually restricted; colonies frequently form so-called 'micro-atolls'.

39. Bewick Island, NE corner; intertidal mud flats; one collection.
40. Houghton Island, W corner; intertidal mud flats; four collections.

(J) Biotopes of the zone of coral growth on the protected side of high islands. These zones occur between intertidal mud flats and the muddy or sandy ocean floor. They are usually shaped as indicated in Figs. 9 and 10. The substrate is usually poorly cemented rubble with sand and/or mud. The water is frequently turbid, coral cover is usually dense and very diverse, both in species and growth form. Such biotopes were found at collecting stations:

41. Falcon Island (Palm Islands), SW end; protected, substrate of fringing reef and sand; two collections by SCUBA, 1.5 and 1.5–10m.
42. Esk Island (Palm Islands), SW side; protected, reef sloping onto muddy floor; one collection by SCUBA, 1–22m.
43. Fantome Island (Palm Islands), W side; very well protected substrate of flat mud with zone of coral growth at 2–10m; three collections by SCUBA, 0–2, 2–10 and 13–15m.

(K) Biotopes of muddy ocean floors frequently occur adjacent to the above-described zone of coral growth and are characterised by flat, soft mud, calm, turbid water and poor light penetration. Such biotopes were found at collecting stations:

44. Lizard Island, N side; semi-protected, substrate of flat, soft mud; one collection by SCUBA and one by dredging, both 28m.
45. Orpheus Island (Palm Islands), W side; very well protected, substrate of flat mud; three collections by SCUBA, 1–5, 5–13 and 5–10m.
46. Challenger Bay, Great Palm Island; very well protected, flat muddy substrate; one collection by SCUBA, 5–10m.

Collections were also made from localities substantially differing from those above.

(L) The upper continental slope.

47. Two km E of the barrier reef NE from Murray Islands; exposed to currents up to approximately 1m/sec, substrate of mud or rubble and *Halimeda* sand, on continental slope; one collection by dredging, 170m.
48. Five km E of Bowl Reef; near the continental slope exposed to currents of approximately 1m/sec, substrate of *Halimeda* sand and rubble; two collections by dredging, 55m.

(M) Tidal channels between reefs exposed to high currents.

49. Between two reefs of the barrier reef NE from Murray Islands; exposed to strong currents, protected from waves, flat, cemented substrate; one collection by dredging, 43m.
50. Outer edge of the channel between two reefs of the barrier reef NE from Murray Islands; exposed to strong currents, flat, cemented substrate; two collections by dredging, 41–48 and 50–57m.
51. Tijou Reef, S end; exposed to moderate wave action and strong currents, steeply

sloping reef rock substrate; one collection by SCUBA, 2–25m.
52. Yankee Reef, NW corner; steeply sloping reef rock exposed to strong currents; one collection by SCUBA, 1–25m.

(N) Sea grass beds.

53. Thursday Island, SW corner; protected from wave action, exposed to moderate currents, substrate of mud with sea grasses; one collection by SCUBA, 6m.
54. Thursday Island, E end; protected from wave action but exposed to moderate currents, substrate of mud with sea grasses in shallow areas; two collections by SCUBA, 4–10m.

(O) Rugged walls of high islands.

55. Orpheus Island (Palm Islands), NW point; semi-protected, steeply sloping substrate of large rocks and soft mud; four collections by SCUBA, 3–10, 10–18, 18–22 and 22–25m.
56. Curaçoa Island (Palm Islands), N side; exposed to moderate wave action and currents, substrate of rugged rock merging onto sandy floor; one collection by SCUBA, 1–25m.

(P) Semi-protected sand and rubble banks.

57. Falcon Island (Palm Islands), N end; semi-protected, substrate of coral rubble and sand; one collection by SCUBA, 5–10m.
58. Eastern slope of sandbank north of Dido Rock (Palm Islands); substrate of steeply sloping sand and rubble; one collection by SCUBA, 1–25m.
59. Eclipse Island (Palm Islands), N side; semi-protected, substrate of coral rubble; one collection by SCUBA, 10–12m.

(Q) Miscellaneous.

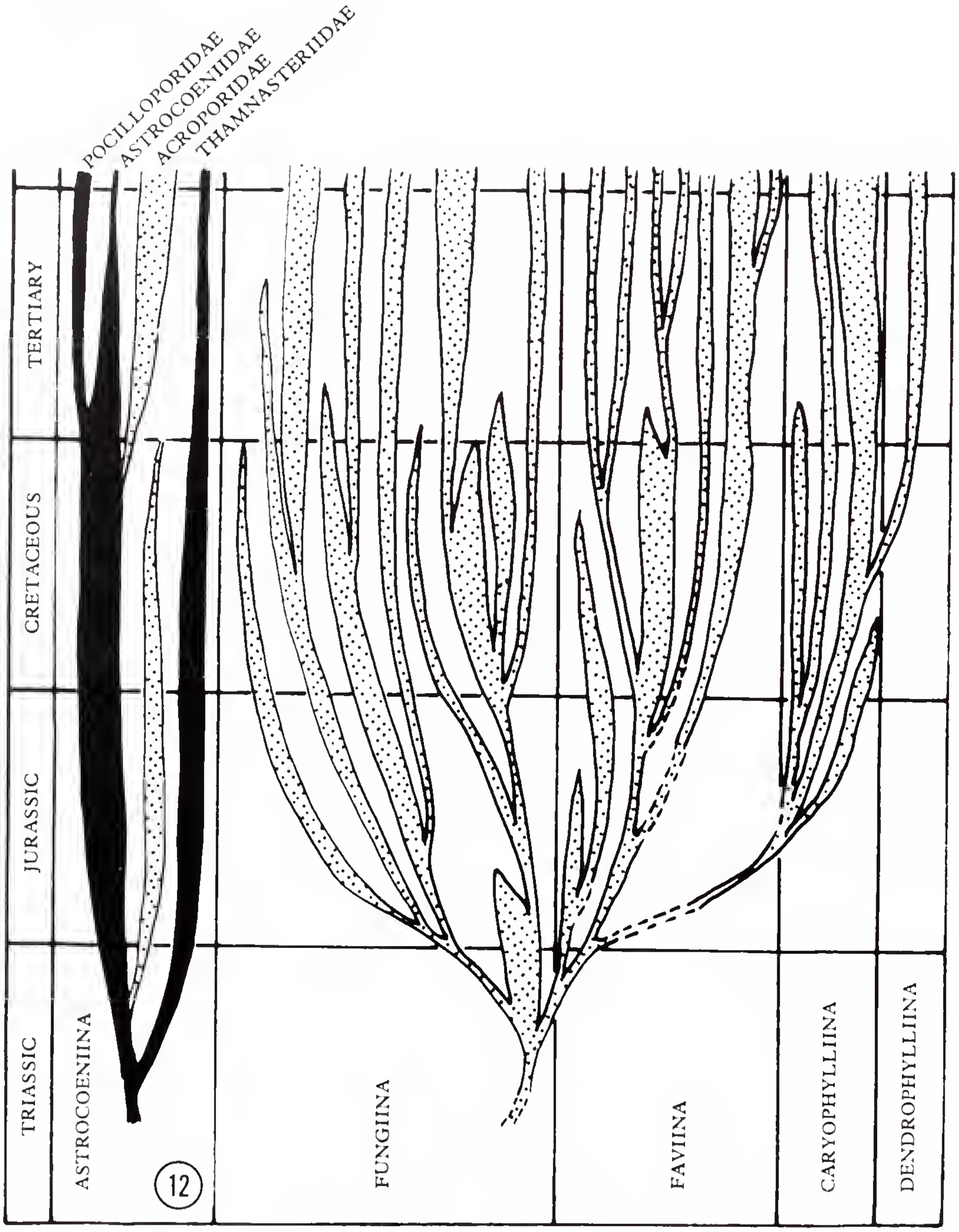
60. Between Orpheus and Fantome Islands (Palm Islands) (see Fig. 9); protected from wave action but exposed to moderate currents, substrate of coarse sand; two collections by SCUBA, 5 and 10m.

VI

Suborder Astrocoeniina

The three families considered in this study belong to Suborder Astrocoeniina Vaughan & Wells, 1943, a taxonomically isolated group of scleractinian corals with a known fossil history extending from the middle Triassic (Wells, 1956). Of the four extant families, three form a relatively homogeneous group while the fourth, comprised of the surviving genus *Psammocora*, represents an early offshoot (Fig. 12).

Fig. 12 Evolutionary pattern of the Scleractinia after Wells, 1956, showing the families considered in the present paper, in black, and illustrating the separation of the Astrocoeniina from the rest of the Scleractinia.



VII
Family Thamnasteriidae Vaughan & Wells, 1943

The family Thamnasteriidae, which includes only one living genus, *Psammocora,* was originally placed by Vaughan & Wells in the suborder Fungiina. This treatment is in agreement with a long-accepted opinion that *Psammocora* (included by Lamarck in his *Pavonies*) has close relationships with *Pavona* and *Coscinaraea.* Perhaps the best demonstration of the affinities of *Psammocora* and *Coscinaraea* is provided by *Coscinaraea exaesa* (Dana), which has been described and recorded over more than a century as *Psammocora exaesa* Dana. The family Thamnasteriidae was subsequently placed by Wells (1954, 1956) in the suborder Astrocoeniina. The most convincing evidence to support this change is to be found in the septal structures, which are characterised by a small number of single trabeculae, and in the tentacles, which are similar to those of some genera of the family Pocilloporidae. These arguments are certainly valid, but it must be pointed out that the wall structure (which is synapticulothecal), the high degree of septal fusion, as well as typically thamnasteroid structures such as the uniting of septocostae or biseptal laminae, are characters also found in the families Agariciidae and Siderastreidae. The inclusion of the family Thamnasteriidae in the suborder Astrocoeniina, where it remains isolated, is therefore considered questionable. Perhaps a comprehensive revision of the three families (Thamnasteriidae, Siderastreidae, Agariciidae) would provide a more definitive answer.

GENUS *PSAMMOCORA* DANA, 1846

Type species *Psammocora obtusangula* (Lamarck, 1816)

The genus *Psammocora,* the only living genus of the family Thamnasteriidae, is characterised by the ramification of the septocostae and the presence of collines. The variations of the latter character have been used to define three subgenera (Vaughan & Wells, 1943):

sub-genus *Psammocora* with collines rounded, enclosing several calices or series,
sub-genus *Stephanaria* Verrill 1867, with collines enclosing only one calice or series,
sub-genus *Plesioseris* Duncan 1884, with collines high and acute.

Although *Plesioseris* Duncan (as well as *Meandroseris* Rousseau) were originally considered as distinct genera, Gardiner (1898) suggested that they be absorbed into *Psammocora.* Indeed, the distinction between *Psammocora (Psammocora)* and *Psammocora (Plesioseris)* is unclear, owing to the wide range of variation in the development of the collines, even in a single species. For instance, *Meandroseris australiae* Rousseau (type species of the subgenus *Plesioseris*) is very close to, if not identical with, *Psammocora profundacella* Gardiner, which, according to Pillai (1972) belongs to the subgenus *Psammocora* (and this is doubtful).

Likewise, the distinction between the subgenera *Psammocora* and *Stephanaria* is questionable. In most specimens of *P. (Stephanaria) digitata,* for instance, the collines are hardly developed and it is not possible to decide whether they enclose only one, or several calices or series.

Therefore, the subdivision of *Psammocora* into three subgenera does not appear to improve the taxonomy of the genus, or to be useful for the classification of the species.

Psammocora contigua (Esper, 1797)

Synonymy (partly after van der Horst, 1921).

Madrepora contigua Esper, 1797.

Psammocora contigua (Esper, 1797); Dana (1846); Edwards & Haime (1851); Ortmann (1888); Gardiner (1898, 1905); Whitelegge (1898); van der Horst (1921, 1922); Hoffmeister (1925); Faustino (1927); Eguchi (1935); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939, 1940); Matthai (1948c); Crossland (1952); Stephenson & Wells (1955); Nemenzo (1955); Searle (1956).

?*Psammocora planipora* Edwards & Haime, 1851; von Marenzeller (1907); Edwards & Haime (1860); Klunzinger (1879); Ortmann (1888, 1889); Bassett-Smith (1890); van der Horst (1922); Umbgrove (1940).

?*Psammocora obtusangula* (Lamarck, 1816); Dana (1846); Edwards & Haime (1851); Gardiner (1898); Hoffmeister (1925).

Psammocora plicata (Dana, 1846); van der Horst (1922); Umbgrove (1940).

?*Psammocora frondosa* Verrill, 1864.

Psammocora ramosa Quelch, 1886; Umbgrove (1940).

Psammocora gonagra Klunzinger, 1879; Gardiner (1898); Vaughan (1918); van der Horst (1922); Umbgrove (1940); Stephenson & Wells (1955); Scheer (1967).

Psammocora divaricata Gardiner, 1905; van der Horst (1921).

Psammocora vaughani Yabe, Sugiyama & Eguchi, 1936; *non* Wells (1955).

Material Studied

Darnley Island (2 specimens), **Murray Islands** (2 specimens), **Bewick Island** (2 specimens), **Lizard Island** (3 specimens), **Two Isles, Hope Island** (3 specimens), **Low Isles**, **Palm Islands** (18 specimens).

These localities include collecting stations 7, 8, 11, 23, 39, 42 and 48. Additional records from the Queensland Museum include (as *P. gonagra* and *P. contigua*): **Fitzroy Island**, **Bushy-Redbill Reef**, **Heron Island**, **Tryon Island**, **Lady Musgrave Reef** and **Flinders Reef**.

Previous Records from Eastern Australia

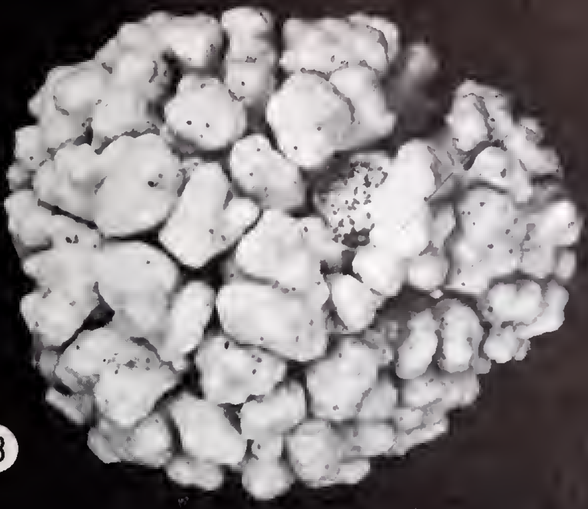
Murray Islands (as *P. gonagra*), Vaughan (1918); Mayer (1918); **Low Isles** (as *P. gonagra* or *Psammocora* sp.), Yonge (1930); Marshall & Orr (1931); Stephenson *et al.* (1931); Yonge & Nicholls (1931a, 1931b); Yonge *et al.* (1932); Stephenson & Stephenson (1933); Manton (1935); (as *P. contigua*), Crossland (1952); Stephenson & Wells (1955); **Heron Island**, Salter (1954); **North-west Islet** (as *P. gonagra*), Hedley (1927).

Characters and growth form variation

In clear, protected waters, colonies up to 50cm across and 13cm high are common. They are composed of bifacial, irregularly-shaped or twisted anastomosing plate-like or rod-like branches of very variable width (Figs. 13–18). Those occurring in turbid waters or in areas exposed to currents are usually very stunted, having compact branches which

Figs. 13–18 *Psammocora contigua* (× 0.6).

Fig. 13 From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.
Fig. 14 From Two Isles.
Fig. 15 From Falcon Island, Palm Islands, collecting station 57.
Fig. 16 From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.
Fig. 17 From Bewick Island.
Fig. 18 From Low Isles.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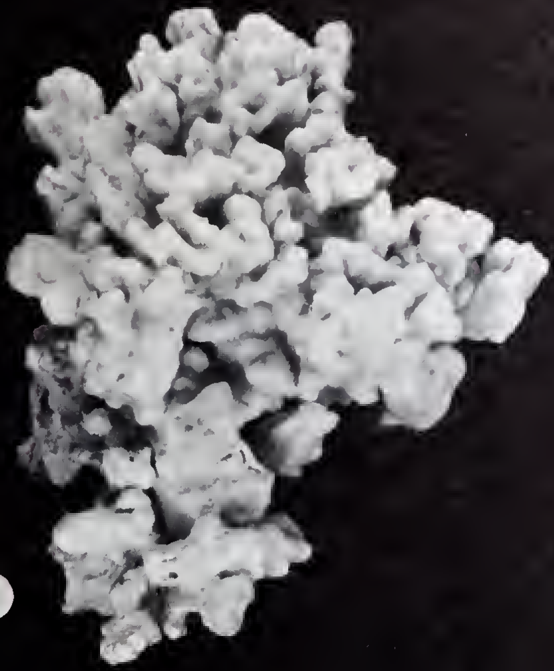
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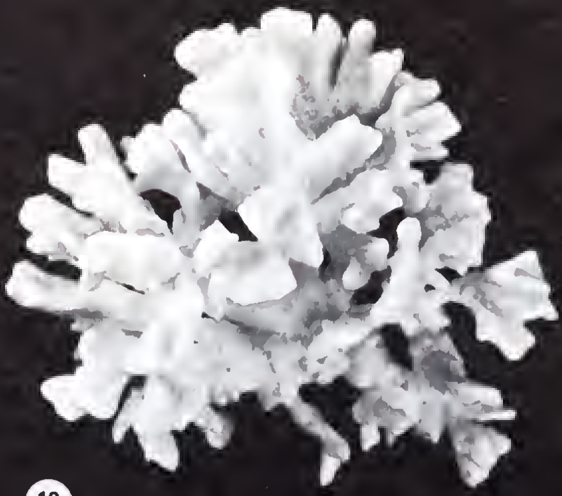
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are very variable in shape, although seldom plate-like (Figs. 14–16). Colonies exposed to strong currents have short, thick, submassive arms. Seven such specimens from collecting station 60 were free-living coralliths (Fig. 13). This species has not been observed in reef situations exposed to strong wave action.

Despite its variability of growth form, this species is usually distinguished from others of the genus by having anastomosing branches. The synonyms *divaricata* and *vaughani* refer to growth forms which clearly belong to opposite ends of the *P. contigua* range. In both cases, the fine structure is completely compatible with that of *P. contigua* (compare Fig. 19 [the holotype of *P. divaricata*], 20, 21 [the holotype of *P. vaughani*] and 22).

Calices form slight fossae, 1–2mm apart, in the otherwise smooth colony surface and frequently form rows centred in shallow valleys. The columella is of variable height and prominence. It may be peg-like and covered with granulations, or composed of

Figs. 19–22 *Psammocora contigua*

Fig. 19 Calices near the tip of a branch of the holotype of *Psammocora divaricata* (× 5.0).

Fig. 20 Calices near the tip of a branch of *Psammocora contigua* from between Orpheus and Fantome Islands, Palm Islands, collecting station 60, (× 5.0), illustrating similarities with *P. divaricata*.

Fig. 21 Calices of the holotype of *Psammocora vaughani* (× 10.0).

Fig. 22 Calices of *Psammocora contigua* from Darnley Island, collecting station 31, (× 10.0), illustrating similarities with *P. vaughani*.


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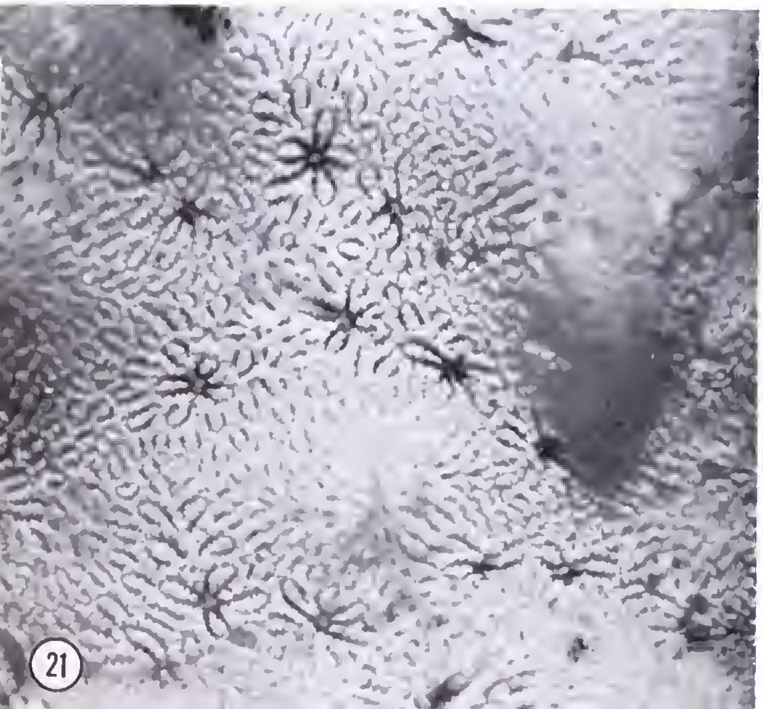
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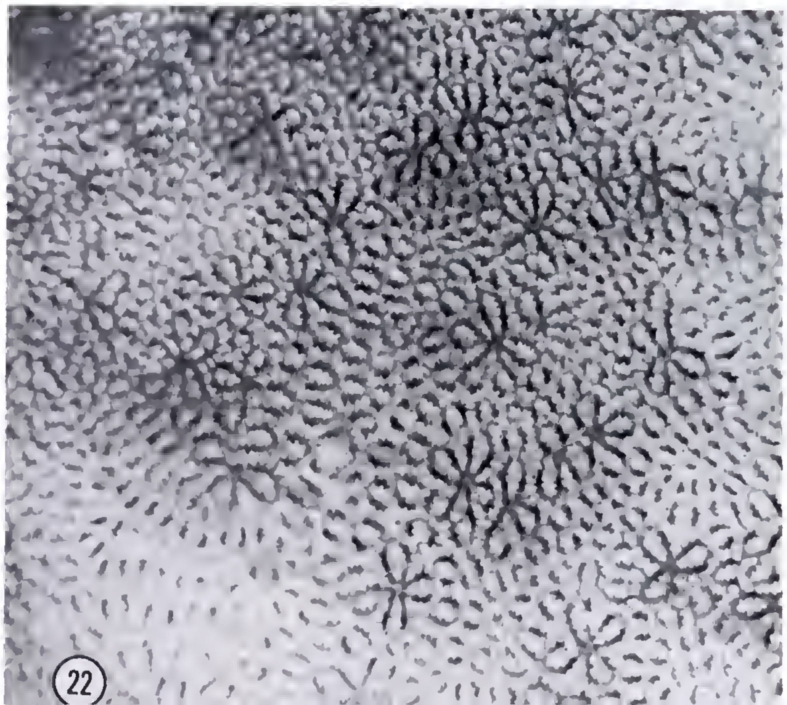
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loose trabeculae. A deep-seated, compound, synapticular ring sometimes surrounds the columella. Interlocking septa and coenenchymal lobes are uniformly covered by, or are composed of, masses of minutely branching granules. The number of septa varies from about 5 to 25. The colour of the living colony varies from pale to dark grey-brown.

Distribution

Widely distributed throughout the Indo-Pacific.

Bathymetric Range

0–26m (present study only).

Psammocora nierstraszi van der Horst, 1921

Synonymy

Psammocora nierstraszi van der Horst, 1921; Wells (1954).

?*Psammocora samoensis* Hoffmeister, 1925.

Material Studied

1 specimen from a reef between south **Yule** and **Triangle Reef**.

Previous records from Eastern Australia

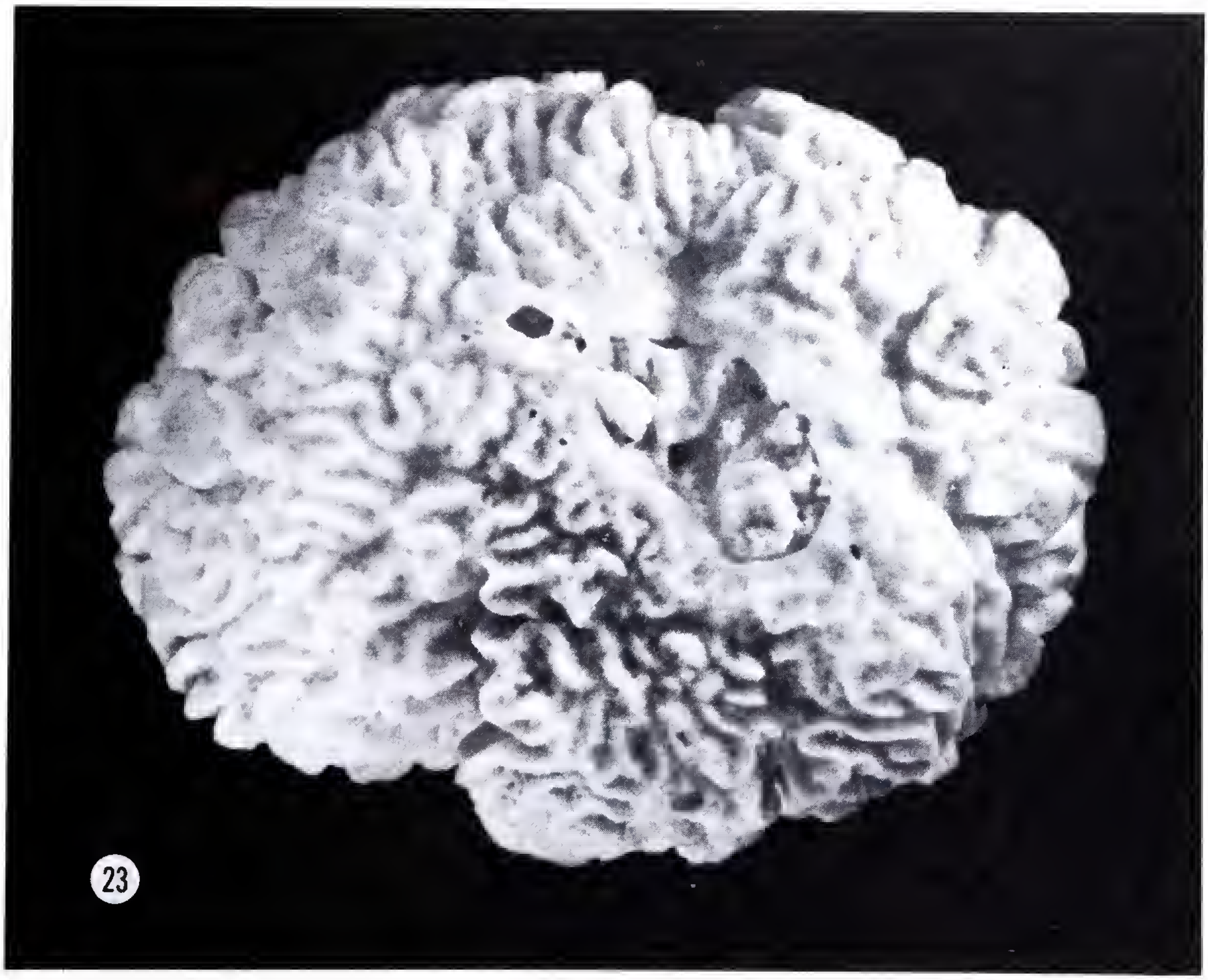
Not previously recorded.

Characters

The corallum is massive, an almost spherical corallith (Fig. 23). It is covered with irregular, high, acute ridges, which bear little relation to the corallites. These are not enclosed by the ridges in well-defined series, as in *Psammocora profundacella* for instance.

Figs. 23, 24 *Psammocora nierstraszi*

Figs. 23, 24 (overleaf) From barrier reef south of Yule Entrance (× 1.5, × 10.0 respectively).



The ridges are continuous (even more so than in *Psammocora samoensis* Hoffmeister) and single 'conical knobs', as described by van der Horst, are exceptional. The corallites (Fig. 24) have no true walls, but rows or rings of synapticulae are visible. The septa are numerous at the periphery of the corallites. They are disposed in groups, arising from the fusion of their inner ends; 10–12 septa reach the columella. Petaloid structures are present in many corallites. The septal margin and the septal sides are densely granulated. The columella is present, composed of several vertical rods.

Discussion

As already suggested by Wells (1954), *Psammocora samoensis* Hoffmeister, appears to be synonymous with *P. nierstraszi* van der Horst, the only difference being more continuous, higher and sharper ridges in the former. In the only specimen examined, the ridges are still more continuous than in the specimen figured by Hoffmeister (pl. 5, Figs. 3b and 3c). Although *Psammocora samoensis* is known by a very limited number of specimens, it is tentatively suggested that it could be merely an ecomorph of *P. nierstraszi*, occurring on reef flats in agitated waters.

Psammocora (Plesioseris) samoensis Hoffmeister from Nemenzo (1955) appears to be *P. profundacella*, judging from the figure (Pl. VI, Fig. 5) and from his description. Indeed, Nemenzo describes the collines as 'conspicuous, acute, usually enclosing a group or series of calices', a character which is more typical of *P. profundacella*.

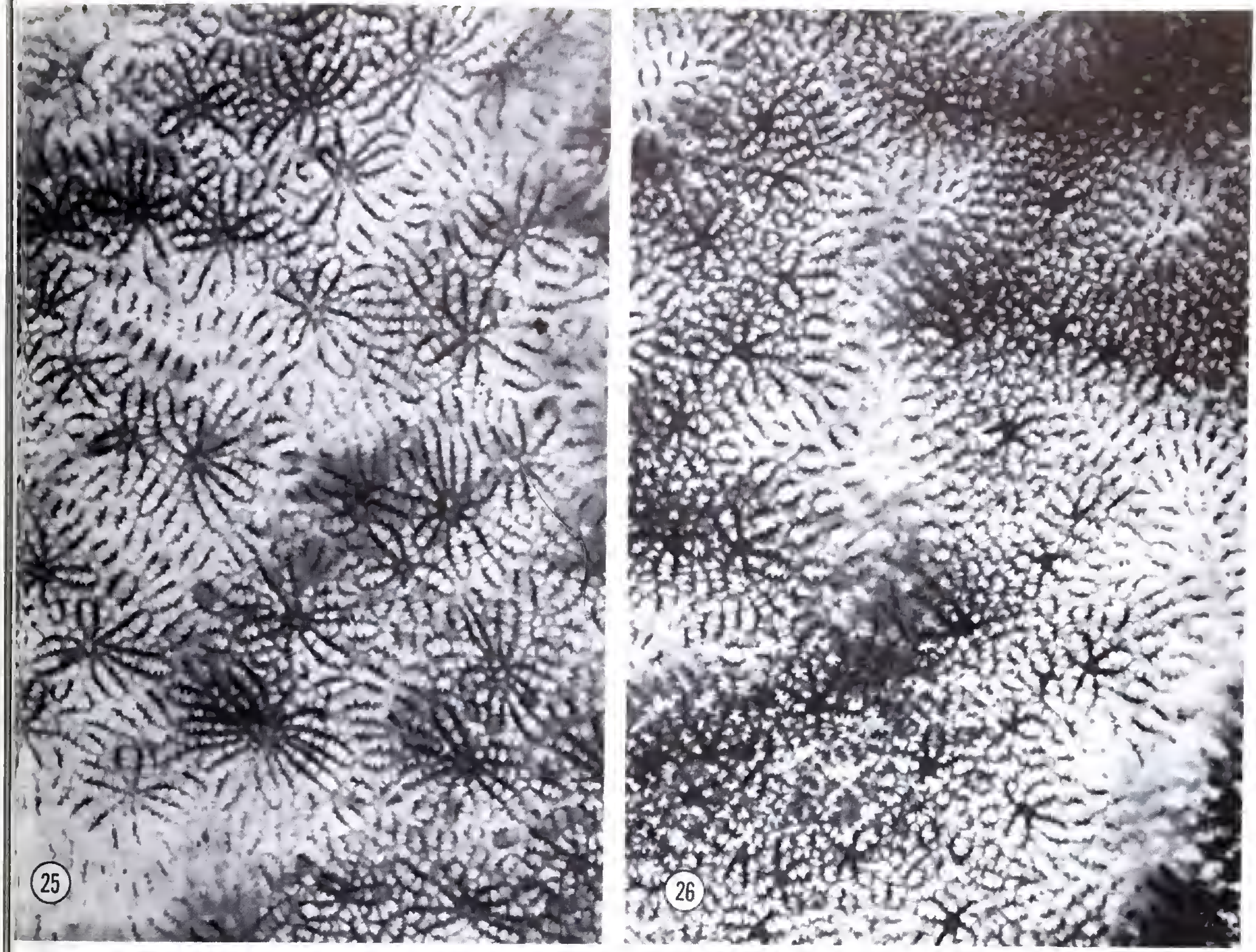
The relationship between *P. nierstraszi* and *P. superficialis* is discussed with the latter species.

Distribution

Aldabra, Maldives, Indonesia, Great Barrier Reef, Samoa, Marshall Islands.

Bathymetric Range

0–35m.



Figs. 25, 26 *Psammocora superficialis*
Fig. 25 *Psammocora superficialis* holotype (× 10.0).
Fig. 26 From Falcon Island, Palm Islands, collecting station 41, (× 10.0).

Psammocora superficialis Gardiner, 1898

Synonymy

Psammocora superficialis Gardiner, 1898; Hoffmeister (1925); Yabe, Sugiyama & Eguchi (1936); Gardiner & Waugh (1939).

Psammocora vaughani Yabe, Sugiyama & Eguchi, 1936: *sensu* Wells (1955b).

Material Studied

Murray Islands (3 specimens), **Palm Islands** (2 specimens), **Minnie Waters,**[3] **Solitary Islands**.

Previous records from Eastern Australia

Several localities in the vicinity of **Moreton Bay** (as *P. vaughani*), Wells (1955b).

Characters

We include in this species a series of specimens with a heterogeneous appearance. The corallum is primarily a thick encrusting lamina with free margins, tending to become massive towards the centre.

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[3] Locality from specimen held at the Australian Museum.

The corallum is covered with irregular, scattered ridges which bear little or no relation to the corallites. These ridges show a considerable degree of variation in their development; in some specimens they are almost nonexistent, being reduced to low collines separating the corallites; in others (e.g. Fig. 26 from the Palm Islands) they get close to the *profundacella-haimeana* condition. The length of these ridges is also highly variable, from mere hydnophoroid protuberances to continuous ridges.

The corallites are more or less regularly distributed over the corallum and are only rarely in series (Figs. 25, 26). The septa frequently fuse together and only 6 to 12 reach the central fossa. Petaloid septa are present in all specimens, but they are less conspicuous in lightly calcified coralla. In some specimens, the pronged arrangement of the septa is similar to that described by Hoffmeister for *P. samoensis.* The thecal structure is somewhat similar to that of *Psammocora profundacella*, the wall being replaced by a row of synapticulae which are less prominent than in *P. profundacella*. Another row of synapticulae occurs a short distance either side of the 'false wall'.

When the skeletal elements are thickly calcified, these structures are no longer visible from above and the intercalicular areas appear as undifferentiated, strongly echinulated coenenchyme.

The columella is often reduced to a central spine, as mentioned by Gardiner.

Discussion

As already mentioned by Wells (1954), *P. superficialis* is close to *P. nierstraszi,* the latter having higher and, except in the form *samoensis*, more irregularly developed ridges. The other distinctive character, according to Wells, is the size of the corallites, which remain small in *P. nierstraszi* (1mm).

The affinities with *P. profundacella* have already been emphasised in the above discussion.

Distribution

Mozambique, Gulf of Aden, Japan, Carolines, Great Barrier Reef, Funafuti, Samoa.

Bathymetric Range

0–38m.

Psammocora explanulata van der Horst, 1922

Synonymy

Psammocora explanulata van der Horst, 1922; Wells (1954).

Material Studied

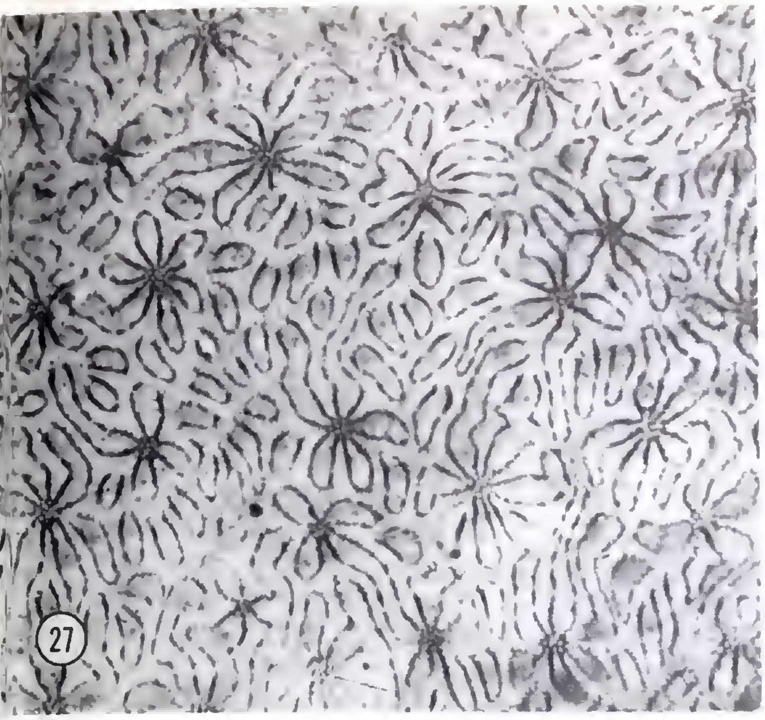
Palm Islands (2 specimens), collecting station 55.

Previous records from Eastern Australia

Not previously recorded.

Figs. 27–32 *Psammocora explanulata*

Fig. 27 From Orpheus Island, Palm Islands, (× 5.0).
Fig. 28 Same specimen as Fig. 27 (× 3.0).
Fig. 29 From Orpheus Island, Palm Islands (× 6.0), showing similarity with van der Horst's type.
Fig. 30 Same specimen as Fig. 29 (× 5.0).
Fig. 31 Same specimen as Fig. 27 (× 10.0).
Fig. 32 Same specimen as Fig. 29 (× 17.0).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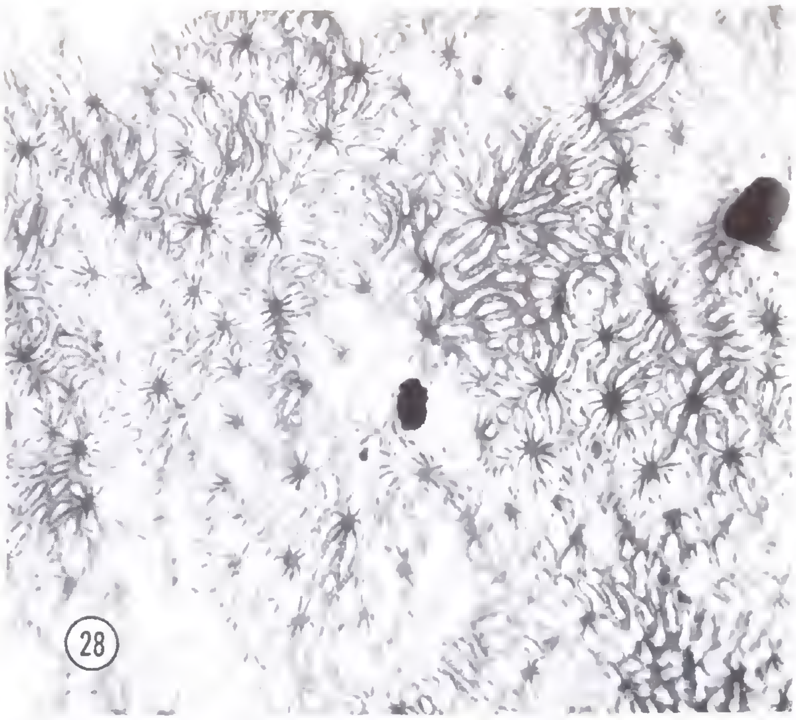
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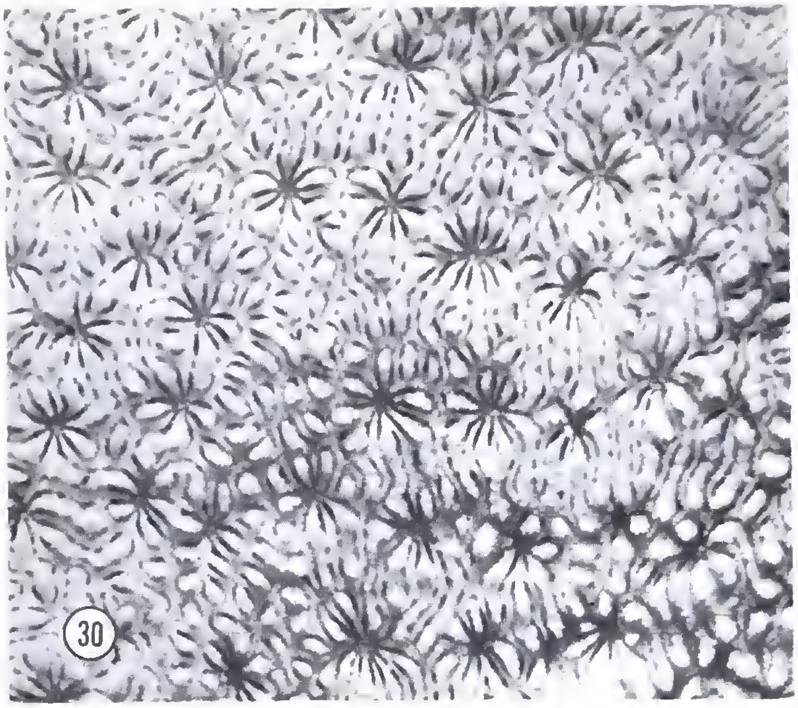
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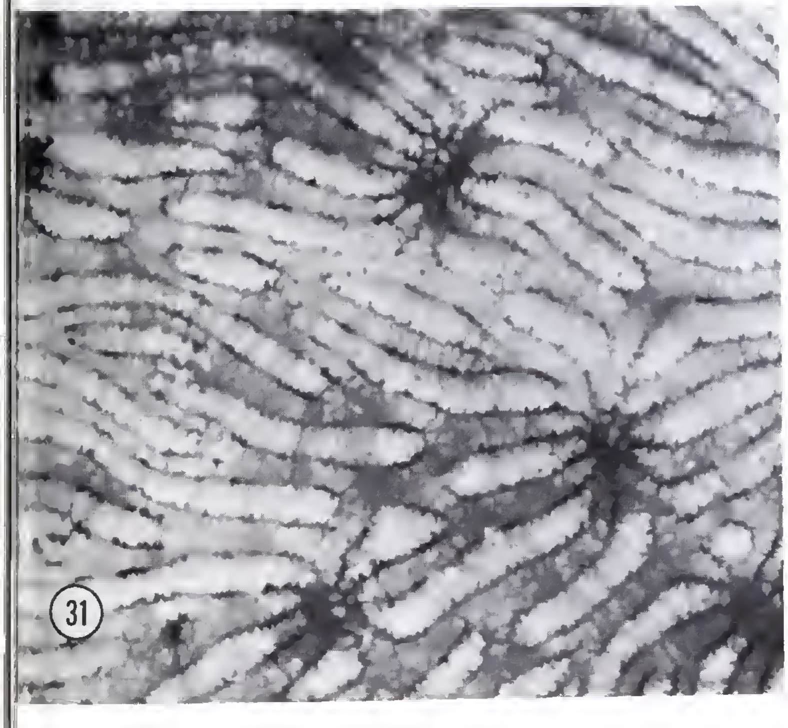
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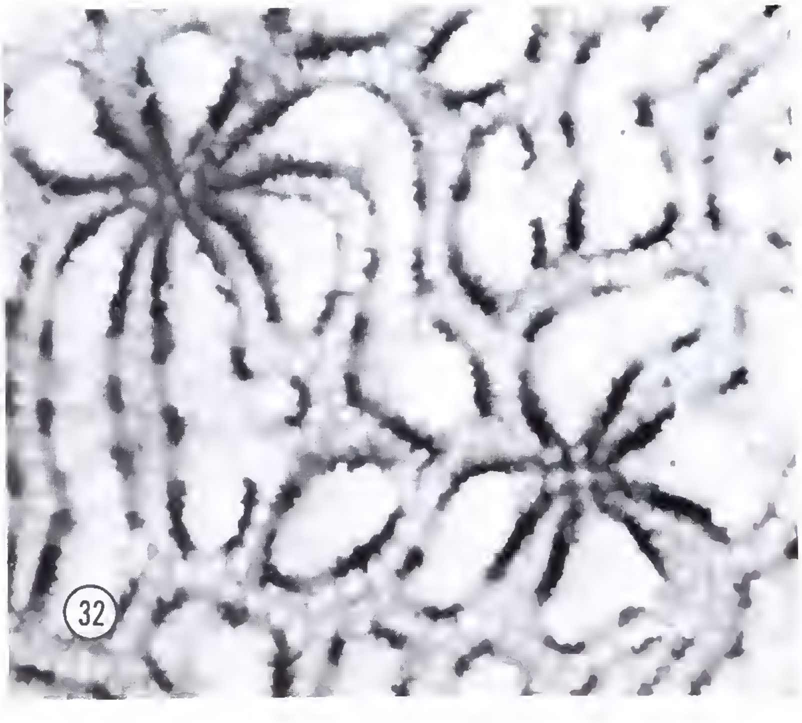
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Characters

The two coralla examined were primarily encrusting and closely attached to the substratum. Their maximum thickness was approximately 10mm towards their centres. The structure of both specimens (Figs. 27–32) agrees in every respect with van der Horst's comprehensive description, which is as follows:

> 'Corallum incrusting and thin. The thickest part of the colony is 8mm, but here the corallum is dead and covered again by a living layer. For the rest the maximum thickness is 3mm, but is ordinarily less. The surface of the corallum is smooth, without protuberances or crests [Figs. 27, 28]. The calicles are sunken just a little in the centre. They are large and easily visible, with clearly radiating septa [Figs. 29, 30]. Number of septa 12 to 18, the principal ones often thickened. The columella is well developed, consisting of several papillae. The calicles are irregularly scattered; the distance between the calicular centra is 2–4mm, at the edge of the corallum often more. The edge of the septa and septo-costae is densely covered with small, rough, often arborescent teeth. The coenenchym is richly developed.
>
> The separate septo-costae, as well as the septa, are clear to the naked eye, in the same way as in *Ps. exesa*. Generally they are parallel to each other, united in groups, and connected also by parallel rows of synapticula [Figs. 31, 32]. The groups of septo-costae are not parallel to each other; extending in different directions, quite independently of the direction of the septa in the calicles; septa and septo-costae may join at the periphery of the calicles at any angle.
>
> In some parts of the corallum thinner septo-costae form a network, surrounding short and thick ones, exactly as in other species of *Psammocora* (e.g. *Ps. contigua)* and in *Polyphyllia* [Fig. 30]. Also in the groups of longer, parallel septo-costae smaller sometimes alternate, but not always.'

The only complementary remark to be added to van der Horst's description is that, just as in the only specimen from Marshall Islands (Wells, 1954), the primaries (which are often petaloid) are markedly exert above the general surface of the corallum.

Distribution

Indian ocean (Providence, Amirante, La Réunion), Pacific ocean (Great Barrier Reef, Marshall Islands).

Bathymetric Range

10 (present study) to 92–144m (Wells, 1954).

Psammocora digitata Edwards & Haime, 1851

Synonymy (partly after van der Horst, 1922)

Psammocora digitata Edwards & Haime, 1851

Psammocora exaesa Dana, 1846: *sensu* Edwards (1860); Brüggemann (1879); Quelch (1886); Rehberg (1892); Gardiner (1905); van der Horst (1921, 1922); Yabe & Sugiyama (1935b); Eguchi (1935); Yabe, Sugiyama & Eguchi (1936); Crossland (1952); Nemenzo (1955).

Psammocora togianensis Umbgrove, 1940; Wells (1950, 1954); Searle (1956); Pillai, Vine & Scheer (1973).

Material Studied

Darnley Island, Sue Island (4 specimens), **Yorke Island, Thursday Island, Tijou Reef** (2 specimens), **Palm Islands** (7 specimens), **Bowl Reef, Broadhurst Reef, Keeper Reef.**

These localities include collecting stations 11, 13, 16, 22, 34, 44, 48, 49, 56 and 59.

Previous records from Eastern Australia

Low Isles (as *P. exaesa*), Crossland (1952); **Heron Island** (as *P. exaesa*), Salter (1954).

Taxonomic history and characters

This species, so easily recognised both underwater and by skeletal characters, has long been the centre of another taxonomic wrangle. The *P. exaesa* Dana of the authors listed above, which is well illustrated by Yabe, Sugiyama & Eguchi (1936) and Crossland (1952), all appear to be one species, the type specimen of which, according to Wells (1954), 'seems to be a *Coscinaraea* closely allied to *C. fossata*'. Certainly it is not the type of the species considered here.

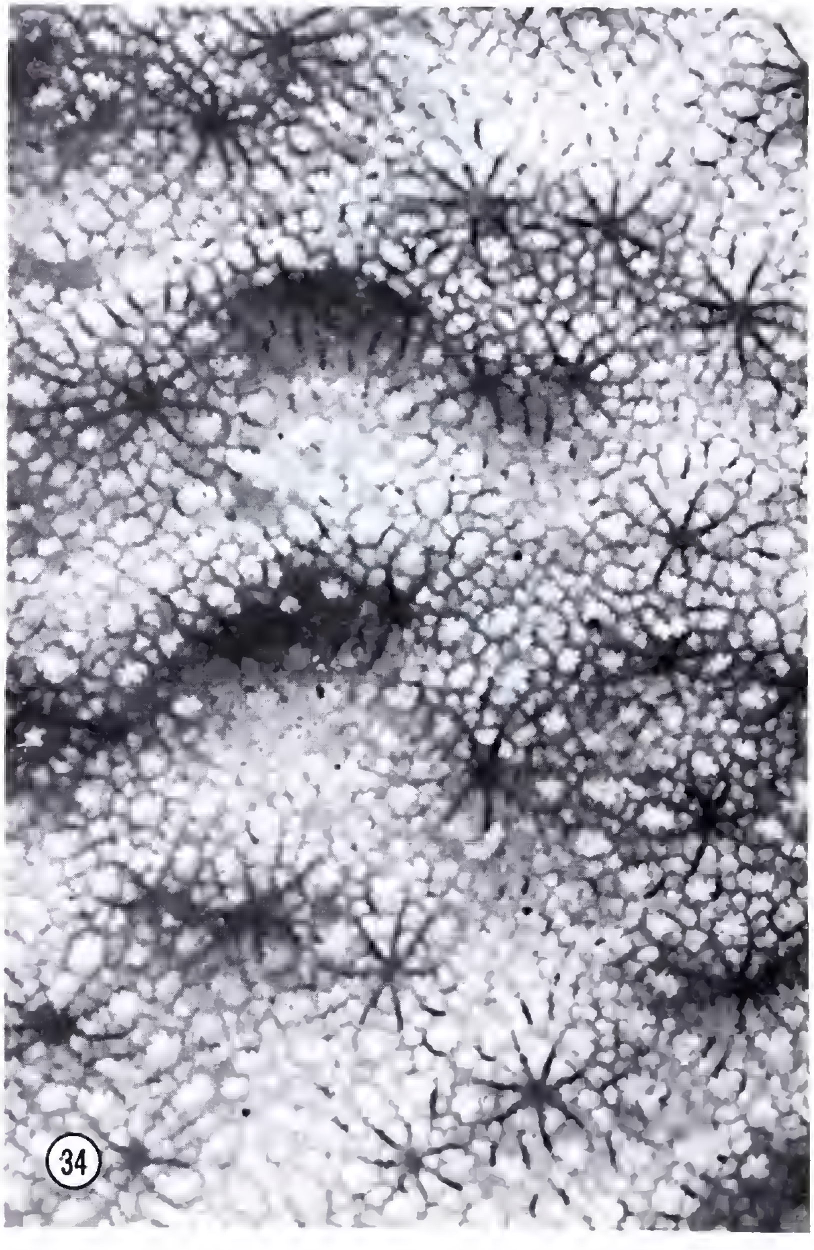
A second area of confusion is with *P. togianensis* Umbgrove. In his *nova species* description, Umbgrove (1940) states that *P. togianensis* 'belongs to the group of branching *Psammocoras*. The growth type resembles *Psammocora divaricata* Gardiner and still more *P. digitata*.' He then describes a species with a growth form not remotely like *P. divaricata,* a synonym of *P. contigua* (see above). He does say, however, that 'the structure of the calices most resembles those of *Psammocora exaesa* Dana as figured by Gardiner (1905, pl. XCII) and by Yabe *et al.* (1936, pl. XLIV)'.

Wells (1956) comments that the separation of *P. togianensis* from *P. digitata* 'seems justified', pointing out that the calice diameters of the holotypes of the two are 'a little more than 2mm' and '3–4mm' respectively. He adds: 'A more reliable distinction seems to be in the number of septa that reach the columella: rarely more than 6 or 7 in *P. digitata,* rarely less than 8 and often 12 in *togianensis.*'

Type specimens of *P. exaesa, P. togianensis* and *P. digitata* have all been examined. Photographs of the latter two 'species' are included here (Figs. 33, 34).

Of the 16 specimens in the present collection, calices were 0.7–5.2mm in diameter and contained 3–15 septa independently reaching the calice centre. The range of

Fig. 33 Holotype of *Psammocora digitata* (× 10.0).
Fig. 34 Holotype of *Psammocora togianensis* (× 10.0).



diameters of average calices, however, was a relatively uniform 2.0–3.3mm (mean: 2.75mm). These contained 7–10 (mean: 8.4) septa which independently reached the calice centre. The depth of the calices was relatively uniform within coralla but varied among them, some being flush with the surface, some forming distinct fossae.

Viewed from above (Fig. 35), most septa are either single, bifurcated or trifurcated. Some are petaloid, terminating in small, blunt, vertical monticules which give the calice a regular, flower-like appearance. Others are straight-sided, extending through the septo-theca either to terminate in similar small, blunt monticules or to unite in an irregular fashion with other septo-costae to form the complex matrix of the coenenchyma. Both the inner and outer margins of the septa are united by deep-seated, inconspicuous, synapticular rings. The columella is inconspicuous and consists of a small pinnacle or a few twisted trabeculae. Except for the synapticular rings, these structures are all covered by very irregular granules which are themselves covered by fine denticles.

Colonies are usually very uniform in colour over their whole surface. Colours range from pale to medium purple-grey or grey-brown.

Growth form variation

Small colonies may be encrusting, occasionally forming thick, horizontal plates (Fig. 38). Larger colonies form vertical, irregularly shaped columns, circular or elliptical in cross section, approximately 1.5–6.5cm in diameter (Figs. 36, 37). Dome-shaped, ramose colonies up to 2.5m in diameter have been observed in protected shallow biotopes. Otherwise, growth form is relatively uniform over a wide range of environments.

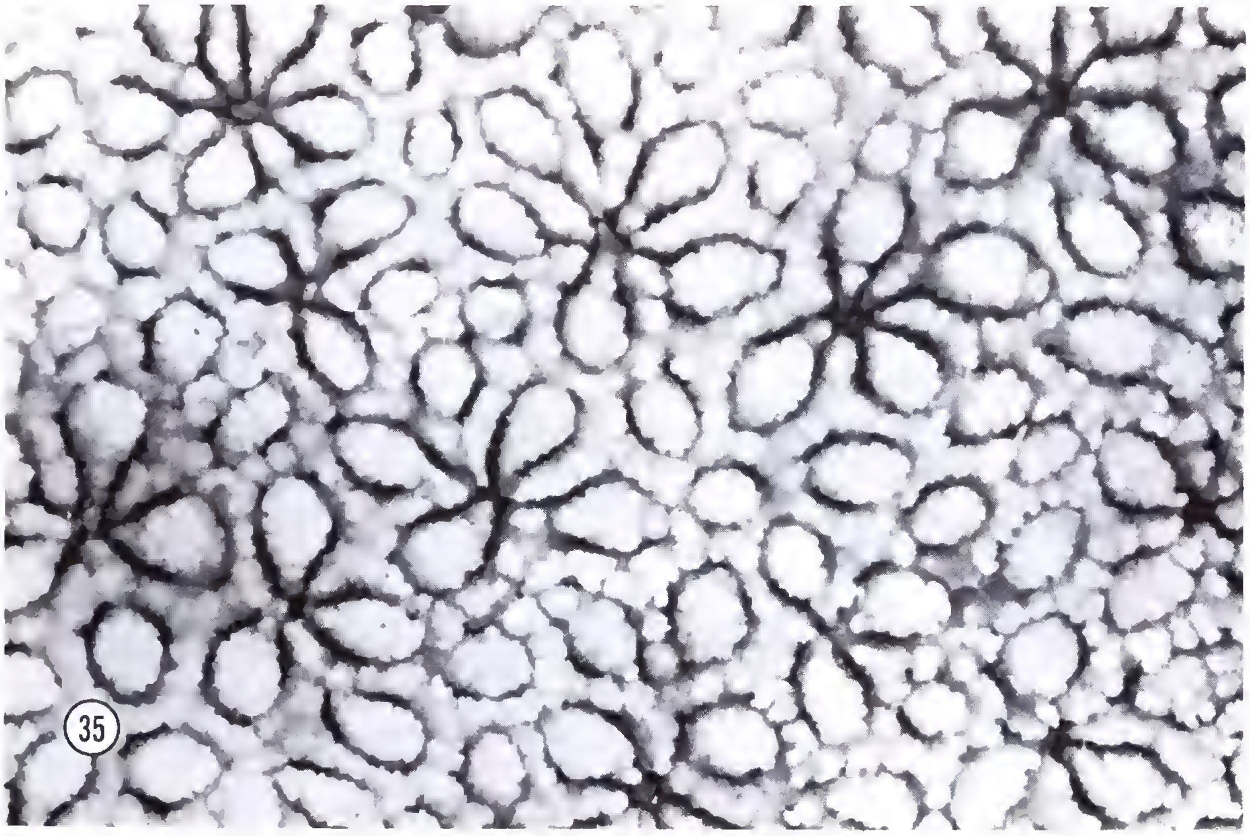


Fig. 35 *Psammocora digitata*, same specimen as Fig. 37 (× 13.0).

Distribution

Widely distributed in the Indo-Pacific from the Seychelles Islands to the Fiji Islands.

Figs. 36–38 *Psammocora digitata*

Fig. 36 From Barber Island, Palm Islands, (× 0.6).
Fig. 37 From Darnley Island, collecting station 31, (× 0.6).
Fig. 38 From Broadhurst reef (× 0.6).

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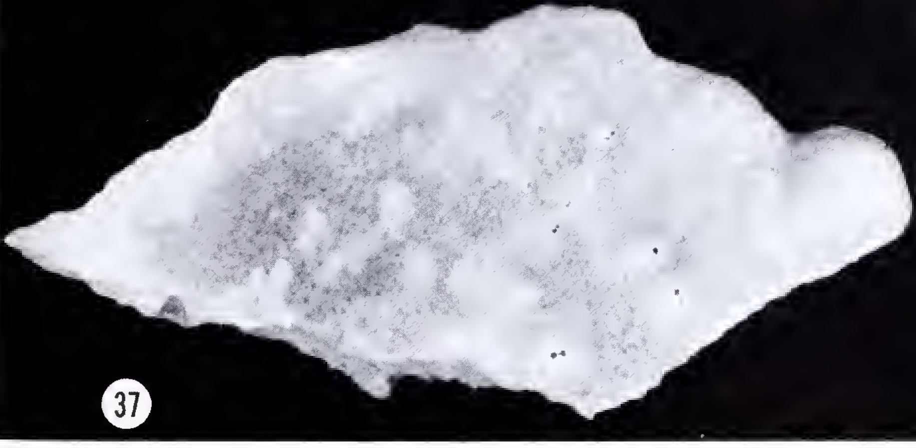

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Bathymetric Range

0–28m (present study only).

Psammocora haimeana Edwards & Haime, 1851

Synonymy (Two spellings of the species, *haimeana* and *haimiana* are not separated.)

Psammocora haimeana Edwards & Haime, 1851; Edwards & Haime (1860); Klunzinger (1879); Ortmann (1888); Bassett-Smith (1890); Gardiner (1898, 1905); van der Horst (1921, 1922); Umbgrove (1939); Wells (1950, 1954); Wells & Davies (1956); Scheer (1964).

Material collected

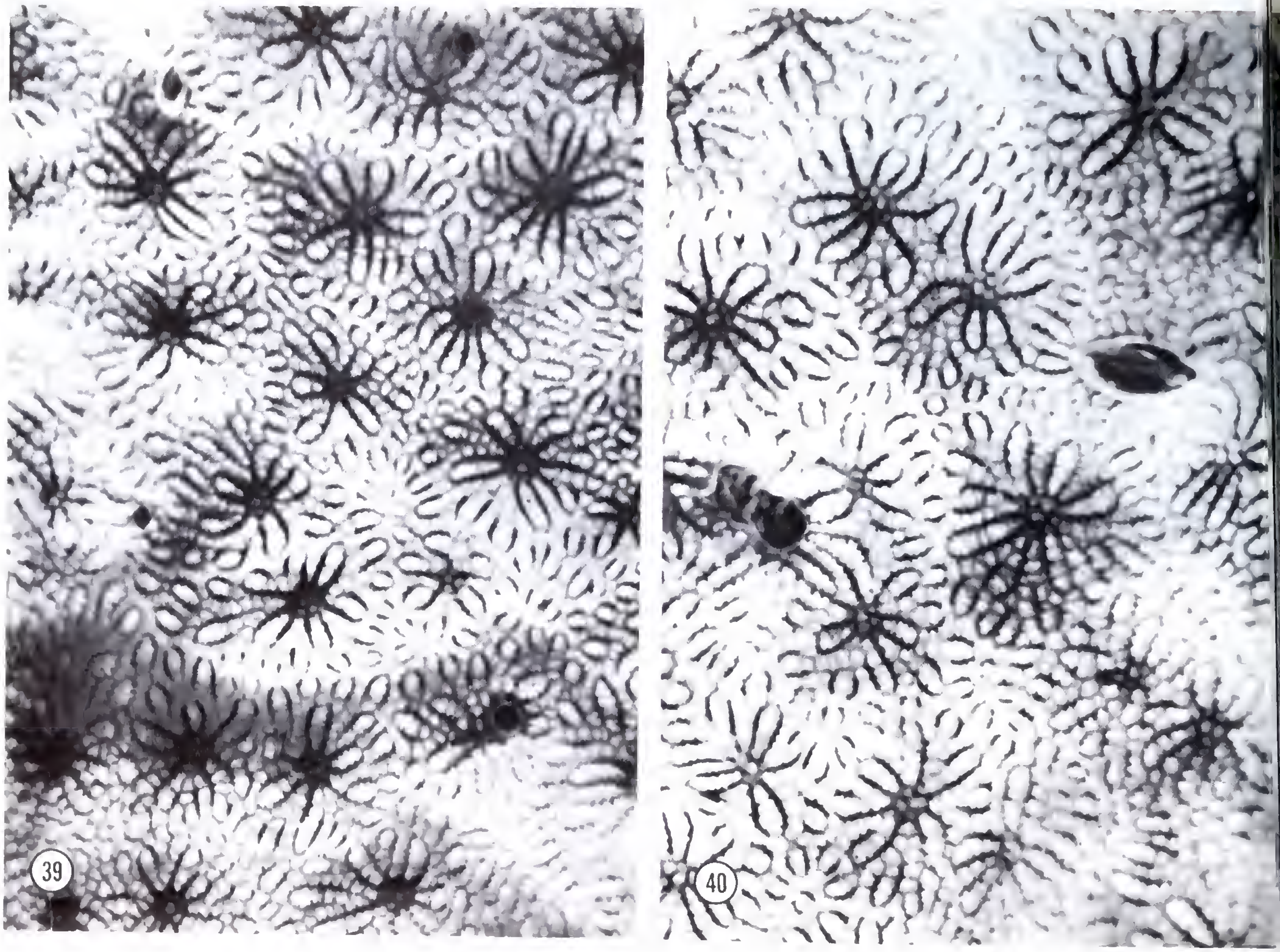
Tijou Reef, Yonge Reef, Palm Islands.
These localities include collecting stations 2 and 3.

Previous records from Eastern Australia

Not previously recorded.

Characters

The three small specimens collected agree well with Umbgrove's (1939) and Gardiner's (1898) descriptions (Figs. 39, 40). Calices are irregularly polygonal, 2.5 to 4mm across, and form distinct fossae or short valleys. Approximately 12 septa reach the


Figs. 39, 40 *Psammocora haimeana* From south Great Palm Island (× 10.0, × 12.5 respectively).

columella: 'up to 6 of these (usually less) bifurcate or trifurcate towards the periphery of the calice. Along the calicular margins usually 24 septa may be counted in full grown calices. The outer ends are slightly thicker than the inner ends. Interseptal loculi are narrow.' (Umbgrove, 1939). The septa are finely granulated, the columella is small and granulated and is surrounded by a series of small paliform lobes. The coenenchyme is granulated, reticular and continuous with, although distinct from, the septa.

Distribution

South Africa, Madagascar, Red Sea, Maldives, Cocos Keeling Islands, Indonesia, Great Barrier Reef, Marshall Islands.

Psammocora profundacella Gardiner, 1898

Synonymy

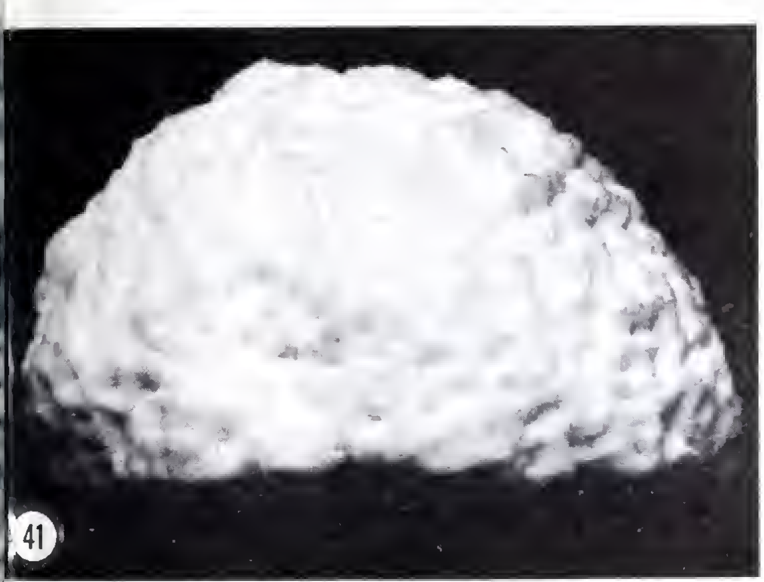
Psammocora profundacella Gardiner, 1898; Vaughan (1918); Matthai (1924); Yabe, Sugiyama & Eguchi (1936); Crossland (1948); Nemenzo (1955).

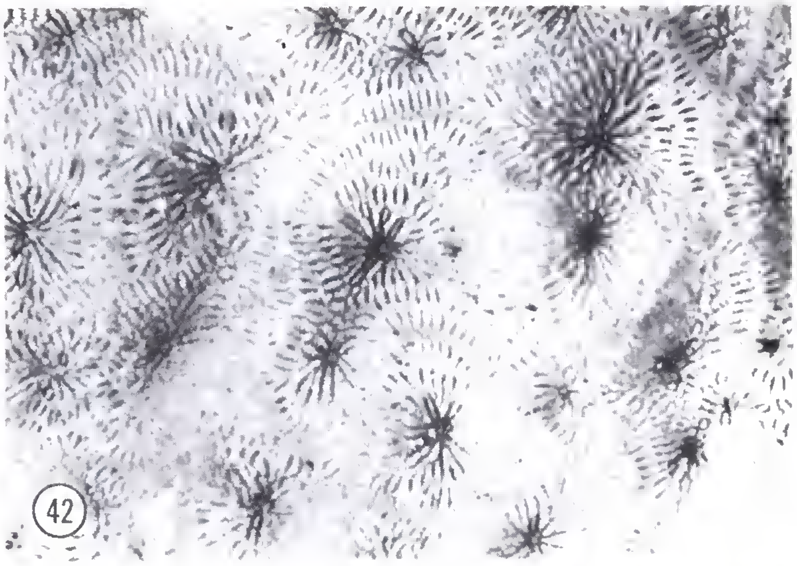
Material Studied

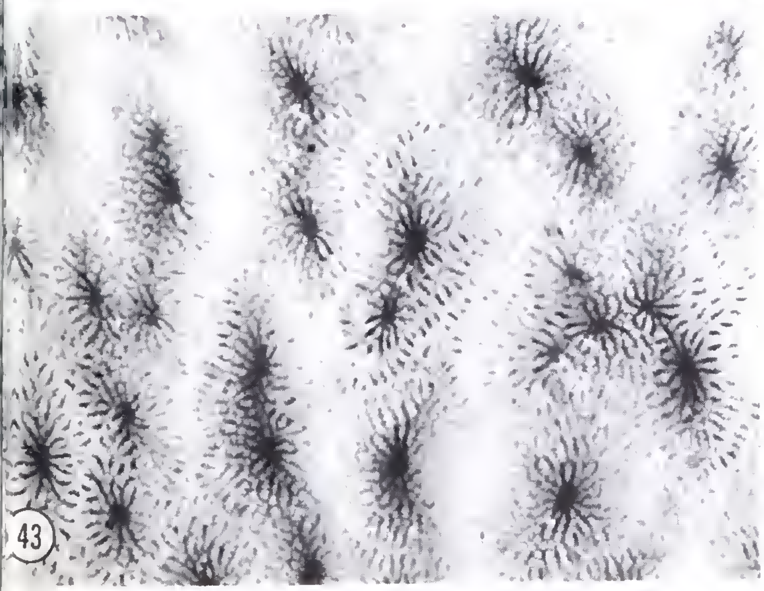
Darnley Island (4 specimens), **Murray Islands** (3 specimens), **Yule Reef** (3

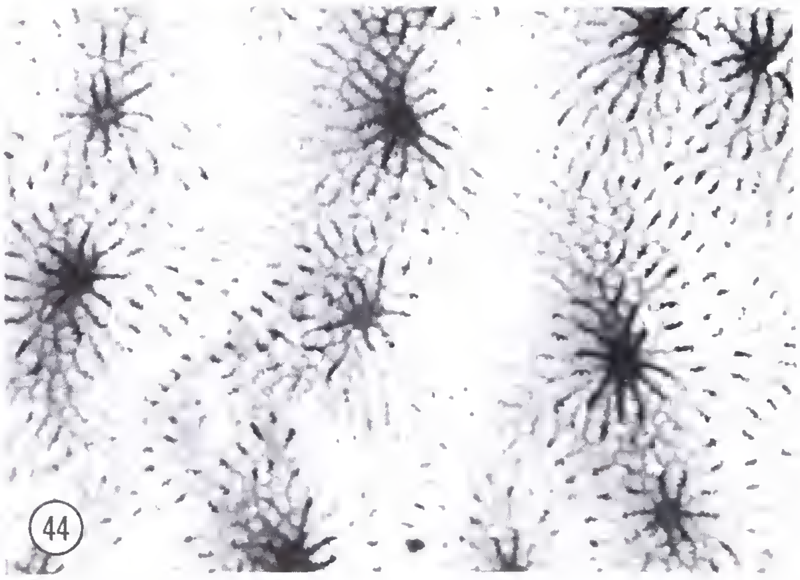
Figs. 41–44 *Psammocora profundacella*

Fig. 41 Part of holotype (× 1.5).
Fig. 42 Holotype (× 6.6).
Figs. 43, 44 From Yorke Island (× 6.2, × 10.0 respectively).









specimens), **Tijou Reef, Lizard Island.**

These localities include collecting stations 74, 76, 81, 82, 83, 85, 88 and 97.

Previous records from Eastern Australia

Heron Island, Salter (1954).

Characters

Colonies are thick, encrusting, tending to become submassive. The upper surface is usually irregular and is often deformed by action of commensals or parasites (serpulids, vermetid gastropods, lamellibranchs and cirripedes). The corallites have well-defined boundaries; they are single or in series, 2–3mm wide and separated by intermediate ridges. The numer of septa is variable, decreasing by fusion from the margin to the centre of the corallites. The septa are perforate, with dentate margins and spinulose sides; 8–12 septa reach the calicular fossa. The wall between two adjacent corallites ('false wall replacing a true theca', according to Gardiner) is basically synapticulothecal, but solid. The upper part of this false wall reaches the top of the ridges. On each side of the wall, within each corallite or series of corallites, there is at least one conspicuous row of synapticulae. This disposition gives to the corallum its typical appearance, even to the naked eye. The columella is generally reduced to a few papillae or is almost absent.

The holotype is illustrated, Figs. 41, 42.

Variations

Variations in growth form are of little significance, particularly when considering the infestation of our specimens with various commensals which are responsible for the knob-like protuberances and tubes over the upper surface of the coralla. The disposition of the ridges shows a certain degree of variation: in some specimens they circumscribe a few, or even only one, corallite, thereby coming close to the '*haimeana*' condition, but in most cases, short series of up to 4–5 calices are present.

Some variation has also been noticed in the height of these ridges, ranging from barely observable structures to well-developed collines up to 2mm high, with either rounded or sharp upper edges. Variation was also observed in the number of septa, as already mentioned, and in their thickness and ornamentation (Figs. 43, 44). In particular, the 'petaloid' or 'thamnasteroid' septa, with an elliptical outline so characteristic of the genus *Psammocora,* is not a reliable character. They are scarce in a few specimens, very abundant in others. In one specimen, petaloid septa are totally absent from one half of the corallum and constantly present in the other half.

Discussion

A number of the above-mentioned variations have already been noticed by Crossland (1948), who describes a specimen from Mauritius with 'crisply outlined polygonal calices, generally single'. By this character, which is also present in some specimens of our series, *Psammocora profundacella* appears closely allied to *P. haimeana,* particularly when the ridges are high and acute. However, as only three specimens of the latter species are present in our collection, its affinities with *P. profundacella* cannot be appreciated, although data from the literature suggest that *P. haimeana* is a well-defined species with little intraspecific variation. Another species to be considered here is *P. superficialis,* which, judging by the calicular structure (wall and synapticular rings in particular), is close to *P. profundacella.* In *P. superficialis,* the ridges are less developed, irregular, and are distributed independently of the corallites.

Psammocora profundacella also appears to come close to, or to be identical with, *Meandroseris australiae* Rousseau, judging from the description and figure. This similarity was mentioned by Gardiner himself, but he considered *P. profundacella* a new species on the grounds that it has more septa (about thirty instead of twenty), less regularly arranged series and, according to Duncan, a true wall. The validity of the first two characters as bases on which to separate species is questionable. The latter character would be more valid, however, if it were to be confirmed by the examination of Rousseau's specimen. It would be an unusual, if not abnormal, character for a *Psammocora*.

Distribution

South Africa (Durban), Inhaca, Mauritius, Andamans, Great Barrier Reef, Philippines, Taiwan, Japan, Funafuti, Fanning Island.

Bathymetric Range

2–28m (present study only).

VIII
Family Astrocoeniidae Koby, 1890

The family Astrocoeniidae is represented in the Indo-Pacific by only one living genus, *Stylocoeniella*. Although it is a small family, its homogeneity remains doubtful, and we strongly support Wells's (1966) statement that *Stylocoeniella* is certainly closely allied to *Actinastrea (Astrocoenia)*, and that both genera are nearer to the Pocilloporidae than to the stylocoeniid corals. Further evidence of this situation is supported by the genus *Palauastrea* Yabe & Sugiyama, 1941, which we revive (p. 70) and which to a certain extent represents an intermediate between *Stylocoeniella* and *Stylophora*.

GENUS *STYLOCOENIELLA* YABE & SUGIYAMA, 1935

Type species *Stylocoeniella armata* (Ehrenberg, 1834)

Generic synonymy

Stylocoenia	Yabe & Sugiyama, 1933.
Astrocoenia	Wells, 1935.
Stylocoeniella	Yabe & Sugiyama, 1935a.

The genus *Stylocoeniella* includes two living species: *Stylocoeniella armata* (Ehrenberg) and *Stylocoeniella guentheri* (Bassett-Smith), both of them being present in our collections. These two species are not conspicuous (small sized, encrusting colonies, often in crevices) and this may explain the fact that they are not well represented in most collections, although they are widely distributed throughout the Indo-Pacific.

Stylocoeniella guentheri Bassett-Smith, 1890

Synonymy

Stylophora guentheri Bassett-Smith, 1890.

Stylocoeniella sp. Wells, 1964b.

Stylocoeniella guentheri (Bassett-Smith, 1890); Wells (1966).

Material studied

Murray Islands (2 specimens), **Mourilyan Harbour**, **Palm Islands** (13 specimens).

These localities include collecting stations 27, 28, 34, 38, 43, 55 and 57.

Previous records from Eastern Australia

Not previously recorded.

Characters

Wells (1966) has already pointed out the similarities between *Stylocoeniella guentheri* and *Stylophora*, which are confirmed by the examination of our specimens, particularly in the characters of the coenenchyme. One must also make the comparison, as Wells did, between the styliform pillars of *Stylocoeniella guentheri*, which are clearly related to one of the primary septa, and the hoods of *Stylophora*.

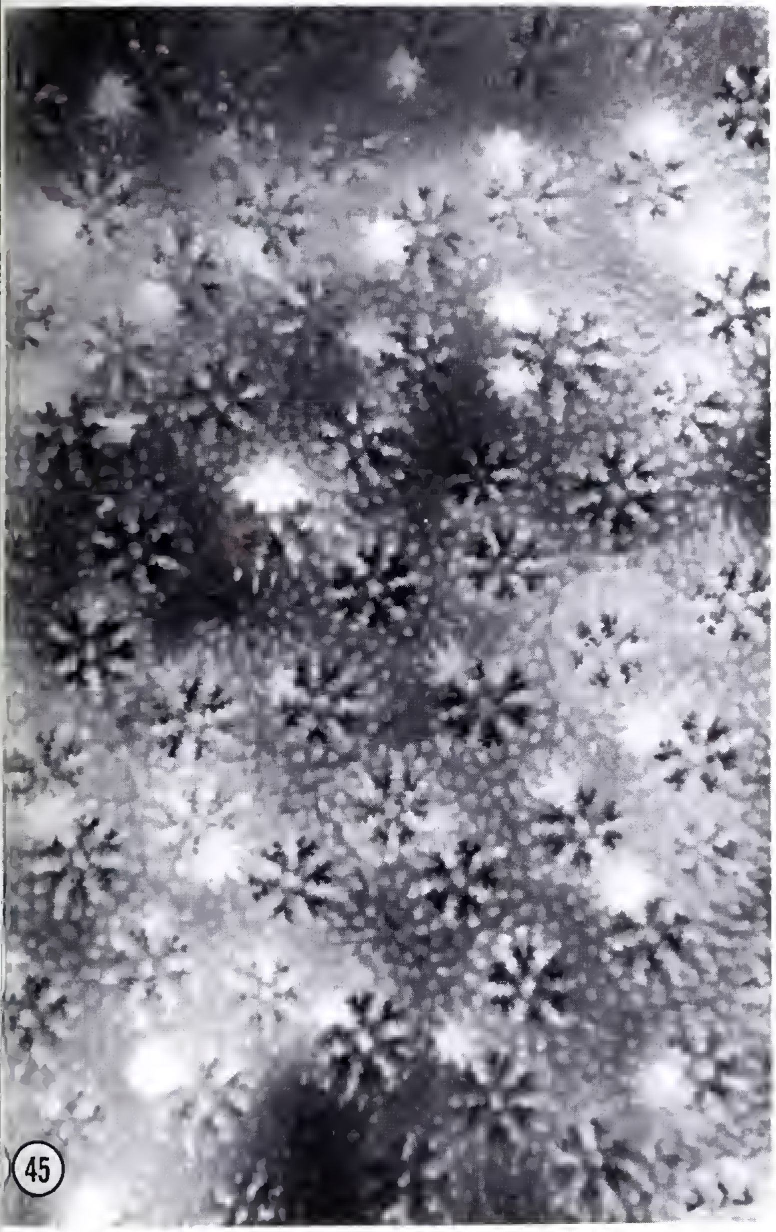
However, on the basis of the septal structure and dentation (Figs. 45, 46) *S. guentheri* is obviously closer to *Stylocoeniella armata* than to any species of *Stylophora*. In both *S. armata* and *S. guentheri*, the intercorallite pillar structure is similar, and, despite a convergence with the hoods of *Stylophora* in the latter species, they seem to be a morphologically distinct process.

There is some similarity between *S. guentheri* and deep water forms of *S. armata*, the latter having a well developed spinous coenenchyme and pillars standing close to the calice. However, they are separated on the basis of septal structure, *S. guentheri* having a weakly developed second cycle, *S. armata* having a second cycle almost as well developed as the first cycle.

Most colonies are deformed by infestations of the serpulid worm *Spirobranchus giganteus* (Pallas) (Fig. 47). Most specimens have an encrusting growth form (Fig. 48), others are massive with knob-like or column-like vertical expansions up to 7cm high which are sometimes fused (Fig. 49).

Distribution

From Madagascar to Marshall Island. (Tuléar, Addu, Macclesfield Bank, Great Barrier Reef, Taiwan, Eniwetok.)



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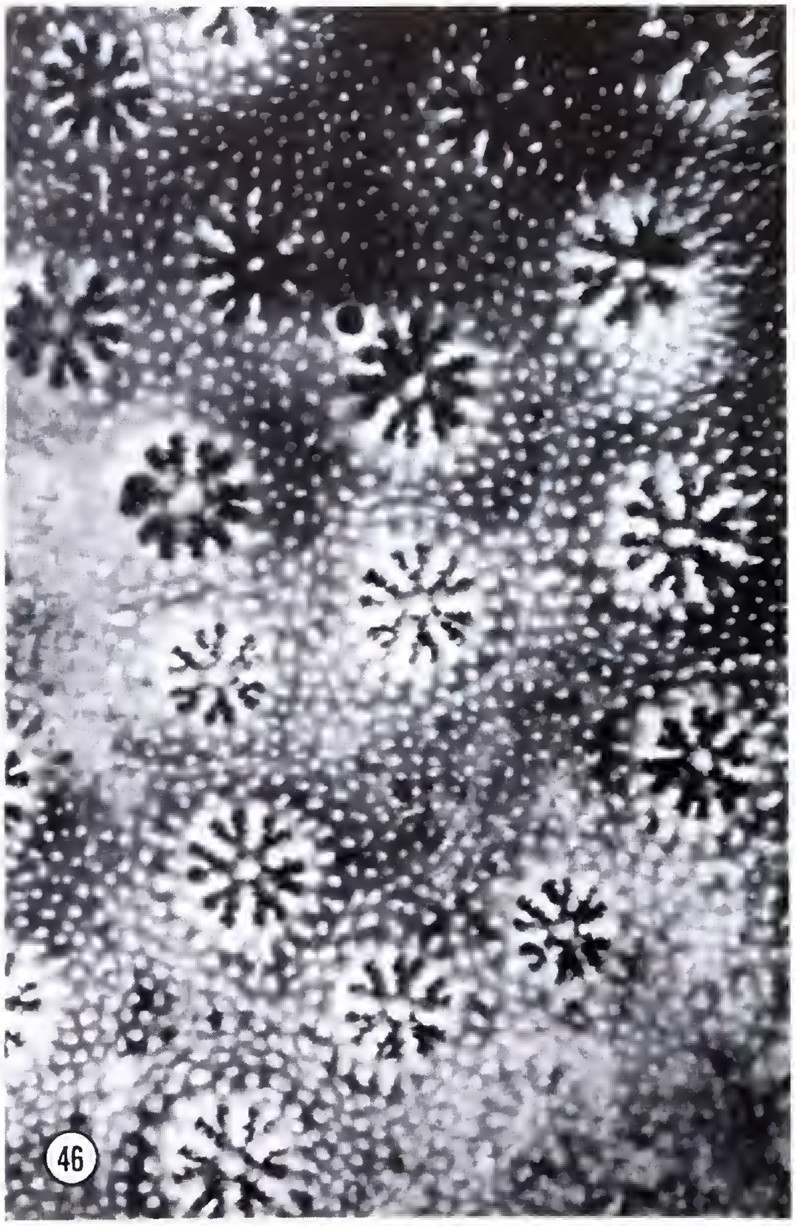

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Figs. 45, 46 *Stylocoeniella guentheri*

Figs. 45, 46 Calices of the corallum illustrated in Fig. 48 (× 12.8, × 18.0 respectively).


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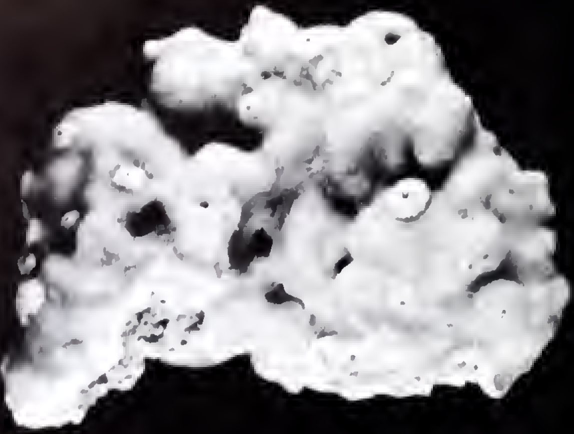
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Bathymetric range

0–58m, 0–15m (present study).

Stylocoeniella armata (Ehrenberg, 1834)

Synonymy

Porites armata Ehrenberg, 1834.

Stylophora armata (Ehrenberg, 1834); Edwards & Haime (1850); Klunzinger (1879); von Marenzeller (1907).

Stylocoenia hanzawai Yabe & Sugiyama, 1933.

Astrocoenia hanzawai (Yabe & Sugiyama, 1933); Wells (1935).

Stylocoeniella hanzawai (Yabe & Sugiyama, 1933); Yabe & Sugiyama (1935a); Yabe, Sugiyama & Eguchi (1936); Nemenzo (1964).

Stylocoeniella armata (Ehrenberg, 1834); Wells (1950, 1954, 1966).

Material studied

North-west Reef, Great Detached Reef (2 specimens), **Tijou Reef** (2 specimens), **Low Isles, Palm Islands** (2 specimens), **Bowl Reef, One Tree Island** (3 specimens).

These localities include collecting stations 2, 5, 12, 14 and 45.

Previous records from Eastern Australia

Torres Strait and **Albany Pass**, Wells (1935); **Heron Island**, Salter (1954); 7 records south to 23°S lat., Wells (1955a).

Characters

Although only twelve specimens were examined, there is some degree of variation in the development of the intercalicular pillars which are so characteristic of the genus, but on an average, they are quite conspicuous (Fig. 50) except for one small colony which was dead and partly encrusted. Corallites are mostly cerioid or subcerioid. Within part of one colony the corallites were mostly square in their outline; in another mostly cerioid specimen, the calices were separated in some places by a narrow strip of spinous coenenchyme. Septa are in two cycles, and are generally subequal or only slightly different in size; paliform lobes are present, sometimes only slightly marked.

All the present specimens were collected in relatively shallow water (12m at most) and have encrusting growth forms. None of them exhibits the typical deep-water aspect mentioned by Wells (1954) for some of the specimens from Marshall Islands. These were bright green in colour, had a partly ramose habit and calices with well developed paliform lobes widely separated by a spinous peritheca.

Distribution

Widely distributed in the Indo-Pacific, from the Red Sea to Society Island (Tahiti) and from Inhaca (26°S) to Honshu (35°05′N).

Bathymetric range

0–54m, 0–12m (present study).

Figs. 47–49 *Stylocoeniella guentheri*

Fig. 47 From Fantome Island, Palm Islands, collecting station 43, (× 0.6).
Fig. 48 From Dewar Island, Murray Islands, collecting station 28, (× 0.6).
Fig. 49 From Great Palm Island (× 1.0).

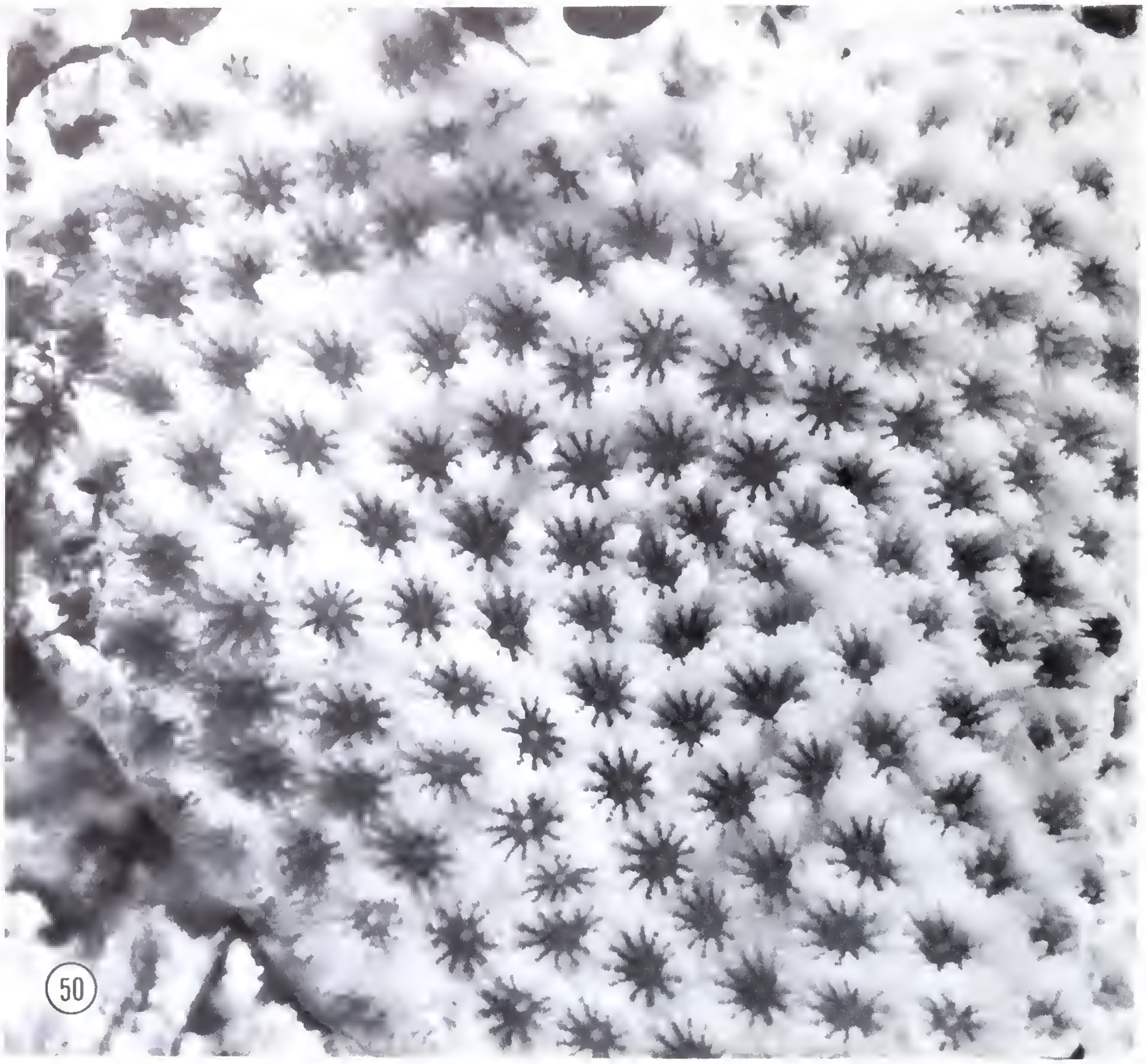


Fig. 50 *Stylocoeniella armata* from Great Detached Reef (× 5.5).

IX
Family Pocilloporidae Gray, 1842

Characters of the family (partly after Wells, 1956)

Colonies are plocoid, generally ramose, mostly hermatypic; colony formation is by extratentacular budding. Calices rarely contain more than two cycles of septa; the columella, when present, is usually styliform and is vertically discontinuous.

GENUS *POCILLOPORA* LAMARCK, 1816

Type species *Pocillopora acuta* Lamarck, 1816 (Subsequent designation Edwards & Haime, 1850).

Characters of the genus

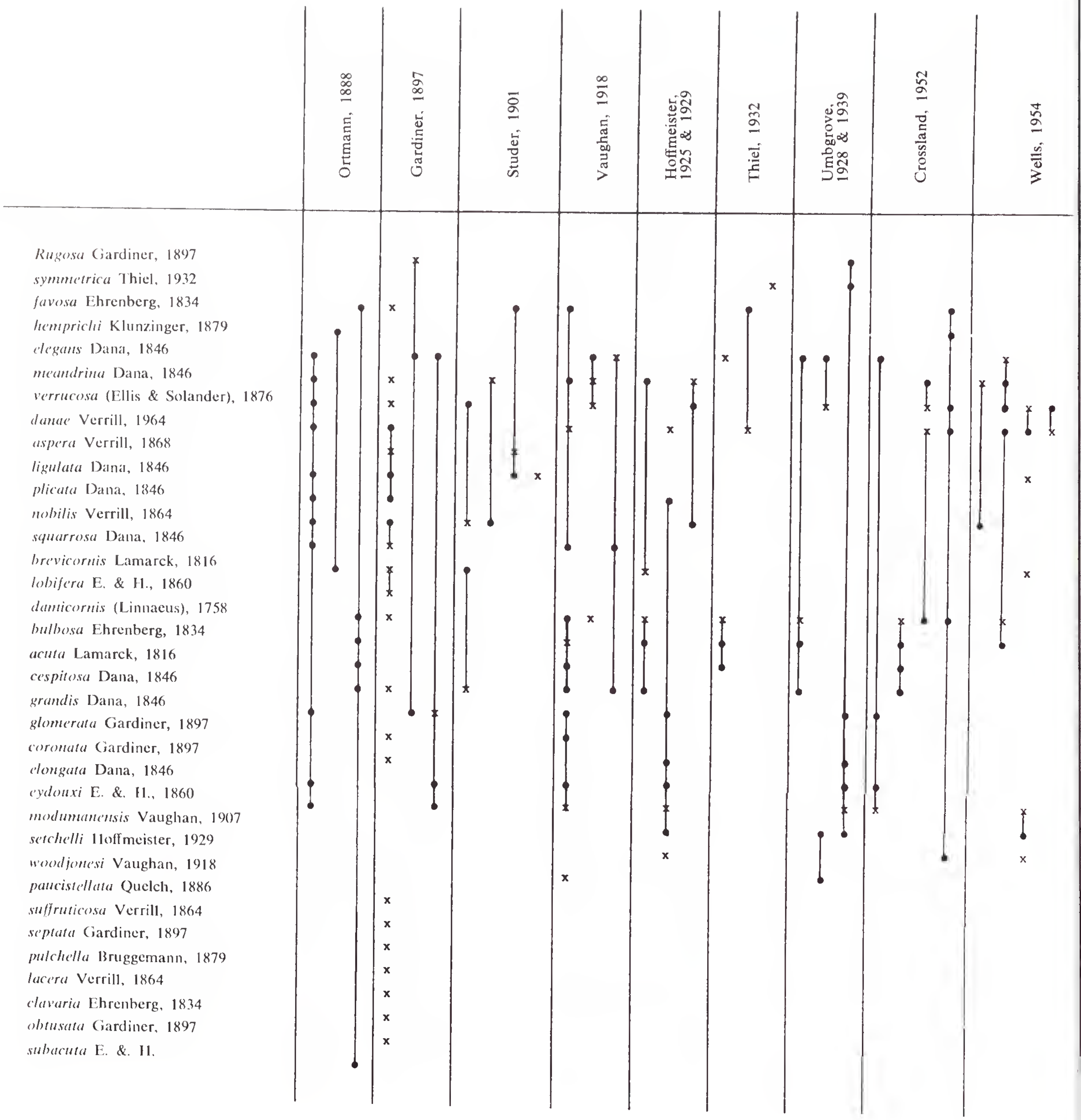
Colonies are ramose, rarely massive or encrusting. Calices are commonly borne on short protuberances (verrucae) from the branches. The septa and columella are usually poorly developed in most species.

Taxonomic history

This is a common genus with a world wide tropical and warm-temperate distribution. Species recorded from the south-west Pacific are listed in Fig. 51, included here primarily to illustrate the complexity of nomenclature created by early taxonomists. As early as 1888, Ortmann wrote (p. 164) 'haben wir hier ein Chaos von Formen' and was unable to decide to which of the described species most of his specimens could be attributed. Later, Gardiner (1897, p. 942) wrote: 'In the collection there are over 50 specimens . . . and in addition I have examined a very large number in the British Museum . . . and I am doubtful whether all these so-called species should not rather be described as varieties of one species, the characters of which would be the characters of the whole genus.'

Crossland (1952) gives the most useful recent account of the Pocilloporidae. He concluded (p. 109) that 'The variations in the species, especially of *Pocillopora,* is enormous . . . and the clue to it has not yet been discovered, nor can be without observation and experiment on the reef, as well as in the marine laboratory. It is probable that such work would bring down the number of species in this genus to about six, but if Vaughan's work on *P. caespitosa–bulbosa–damicornis* etc. applies to other species it might be even smaller.' Later, Wells (1972) comments, 'More than 40 species of this common Indo-Pacific coral have been named but so great is intraspecific variation that it is doubtful whether 10 or 15 of these can be maintained.'

In the following account, four species are recognised. In the present collection, one species, *Pocillopora woodjonesi,* is represented by a single specimen; the remaining three species encompass the enormous range of growth forms and fine structures represented by the many specimens collected as well as the growth forms of the many thousands of colonies observed underwater.


Ortmann, 1888
Gardiner, 1897
Studer, 1901
Vaughan, 1918
Hoffmeister, 1925 & 1929
Thiel, 1932
Umbgrove, 1928 & 1939
Crossland, 1952
Wells, 1954
Rugosa Gardiner, 1897
symmetrica Thiel, 1932
favosa Ehrenberg, 1834
hemprichi Klunzinger, 1879
elegans Dana, 1846
meandrina Dana, 1846
verrucosa (Ellis & Solander), 1876
danae Verrill, 1964
aspera Verrill, 1868
ligulata Dana, 1846
plicata Dana, 1846
nobilis Verrill, 1864
squarrosa Dana, 1846
brevicornis Lamarck, 1816
lobifera E. & H., 1860
damicornis (Linnaeus), 1758
bulbosa Ehrenberg, 1834
acuta Lamarck, 1816
cespitosa Dana, 1846
grandis Dana, 1846
glomerata Gardiner, 1897
coronata Gardiner, 1897
elongata Dana, 1846
eydouxi E. & H., 1860
modumanensis Vaughan, 1907
setchelli Hoffmeister, 1929
woodjonesi Vaughan, 1918
paucistellata Quelch, 1886
suffruticosa Verrill, 1864
septata Gardiner, 1897
pulchella Bruggemann, 1879
lacera Verrill, 1864
clavaria Ehrenberg, 1834
obtusata Gardiner, 1897
subacuta E. & H.

Pocillopora damicornis (Linnaeus, 1758)

Synonymy

Because of its complex taxonomic history, a full synonymy of this species has not been determined. Principal species descriptions include:

Millipora damicornis Linnaeus, 1758
Pocillopora acuta Lamarck, 1816
Pocillopora brevicornis Lamarck, 1816
Pocillopora bulbosa Ehrenberg, 1834
Pocillopora caespitosa Dana, 1846
Pocillopora damicornis (Linnaeus, 1758)

Taxonomic History

This species was originally described by Linnaeus (1758) as *Millepora damicornis*, then placed in the genus *Madrepora* by Pallas in 1766, who described a number of varieties which were illustrated by Esper (1797), and later separated into different species. When Lamarck (1816) created the genus *Pocillopora*, he referred his type species, *P. acuta*, to one of Esper's illustrations of Pallas's varieties. Ehrenberg gave the name *P. bulbosa* to another. Dana (1846) and Edwards & Haime (1860) subsequently differed from each other and from Lamarck as to which of Esper's illustrations the names *damicornis* and *bulbosa* properly refer. The complexities of nomenclature that have resulted are discussed by Vaughan (1918) and Hoffmeister (1925). They are not considered here because these species are clearly synonymous.

Material studied

Barrier reef NE of **Murray Islands**, **Yorke Island**, **Great Detached Reef** (21 specimens), **Tijou Reef** (14 specimens), **Bewick Island** (5 specimens), **Houghton Island** (3 specimens), **Lizard Island**, **Low Isles** (8 specimens), **Hope Island** (5 specimens), **Michaelmas Cay**[4] (3 specimens), **Palm Islands** (29 specimens), **Bowl Reef** (8 specimens), **Yankee Reef** (3 specimens), **Keeper Reef** (5 specimens), **Wheeler Reef**, **Gould Reef** (2 specimens), **Hayman Island**[4], **Broughton Island**[4], **One Tree Island**[4], **Diamond Islet**[4], **North-west Islet**[4], **Minnie Waters**[4], **Solitary Islands** (8 specimens), **Lord Howe Island** (13 specimens), **Maroubra**[4] (3 specimens).

These localities include collecting stations 1, 2, 4, 5, 6, 10, 12, 13, 14, 18, 21, 34, 36, 40, 41, 42, 43, 45, 48, 53, 55, 57 and 60.

Previous records from Eastern Australia

Murray Islands (as *P. damicornis* and *P. bulbosa*), Vaughan (1918); **Low Isles** (as *P. damicornis, P. bulbosa* and/or *P. caespitosa*), Yonge (1930, 1940); Marshall & Orr (1931); Stephenson *et al.* (1931); Stephenson (1931); Yonge & Nicholls (1931a, 1931b); Yonge, Yonge & Nicholls (1932); Marshall (1932); Manton (1932, 1935); Stephenson & Stephenson (1933); Marshall & Stephenson (1933); Crossland (1952); Stephenson & Wells (1955); **North-west Islet** (as *P. bulbosa*), Hedley (1927); **Heron Island**, Salter (1954); **Caloundra**, Wells (1955b); **Solitary Islands**, Veron *et al.* (1974); **Lord Howe Island**, Veron (1974); **Sydney**, Wells (1955b).

Fig. 51 Species of *Pocillopora* recorded from the south-west Pacific. Authors who have discussed the synonymy of the genus are indicated above. Species names considered valid by each author are indicated by a cross; other names referred to are indicated by a dot. Vertical lines join species considered by each author to be 'in synonymy' or to be in some form of 'a series'.

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[4] Localities from specimens held at the Australian Museum.

Characters

This species is distinguished from others of the genus by its lack of true verrucae. Main branches are either with cerioid or irregularly covered with undeveloped sub-branches which may resemble verrucae, but which grade into fully developed sub-branches.

Calices (Figs. 52–56) are 0.7 to 1.5mm in diameter. Those on the ends of branches are cellular in appearance and usually lack internal structures, but may have rudiments of 2 cycles of septa which may be finely toothed. The columella is absent or is a low boss.

Growth form variation

This species occupies a variety of habitats which is probably unequalled by any other Great Barrier Reef coral. It is commonly found on the exposed outer face of

Figs. 52–56 *Pocillopora damicornis*

Fig. 52 Tip of a branch of the corallum illustrated in Fig. 64 (× 6.5).
Fig. 53 Tip of a branch of the corallum illustrated in Fig. 61 (× 6.2).
Fig. 54 Tip of a branch of a corallum from Orpheus Island, Palm Islands, collecting station 45, (× 5.0).
Fig. 55 Calices of the sides of a branch of the coralla illustrated in Figs. 52, 64 (× 6.4).
Fig. 56 Calices of the sides of a branch of the corallum illustrated in Fig. 61 (× 6.4).


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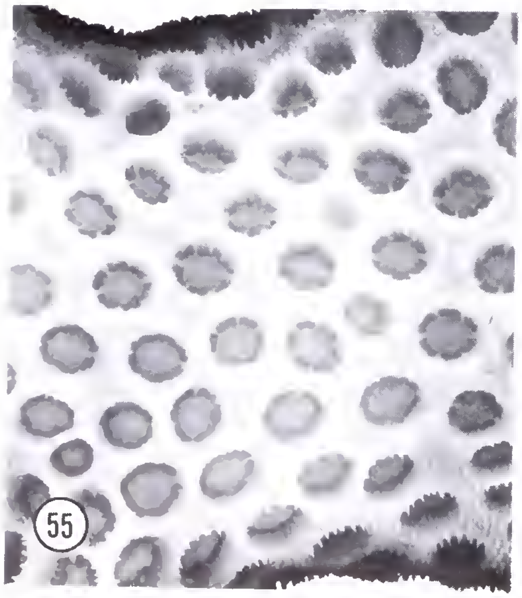
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Fig. 57 *Pocillopora damicornis* colonies from between Orpheus and Fantome Islands, Palm Islands, collecting station 60, see Fig. 62.

ribbon reefs, is common in patch reef lagoons, outer slopes and on the fringing reefs of high and low islands, has been trawled from a 38m deep sandy ocean floor 12km east of Townsville, is common in sheltered, muddy bays of the Palm Islands and has even been found growing on mangrove roots (Stephenson *et al.*, 1931) and on submerged debris. It is the dominant species of the areas of high current around the Palm Islands (Fig. 57). It is also one of the dominant species of South-West Solitary Island (34°S lat.) (Veron *et al.*, 1974) and is known to extend as far south as Sydney Harbour (Wells, 1955b).

Four main intergrading ecomorphs may be recognised:

Pocillopora damicornis from exposed biotopes (ecomorph *brevicornis*) (Figs. 58–60).

This form occurs in areas of strong to extreme wave action. Colonies may be so stunted that outer branches are reduced to simple ridges a few mm high. Main branches

Figs. 58–68 *Pocillopora damicornis* (× 0.5).

Fig. 58	From Bowl Reef, collecting station 3.
Fig. 59	From Great Detached Reef, collecting station 1.
Fig. 60	From Bowl Reef, collecting station 3.
Fig. 61	From Bowl Reef.
Fig. 62	From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.
Fig. 63	From Elk Cliff, Great Palm Island, collecting station 37.
Fig. 64	From Low Isles.
Fig. 65	From Houghton Island, collecting station 40.
Fig. 66	From Gould Reef.
Fig. 67	From Lizard Island, collecting station 11.
Fig. 68	From Wyer Island, Murray Islands, collecting station 30.

are set close together and may be as thick as, or thicker than, they are high (2–4cm). Colonies from slightly less exposed biotopes have masses of close cropped, frequently dividing outer branches 1–3mm thick. Main branches are much thicker and likewise divide at very frequent intervals.

In 16 colonies collected from the outer face of exposed ribbon reefs at 5–15m depth, only an outer zone of 3–6cm was found to be living. Within this zone, expanded polyps occupy almost all the space available between branches and are thus greatly protected from the effects of wave action by the density of branches.

Living colonies are usually pale brown in colour with almost colourless polyps.

Pocillopora damicornis from semi-protected biotopes (Figs. 61–65).

This form occurs in most reef situations which are not exposed to full wave action. The wide range of growth forms commonly attributed to this species is included here. The outermost branches of colonies are usually 2–4mm in diameter, are of irregular length, and do not form distinct heads to main branches as occurs in *P. verrucosa* (Fig. 3). The ends of branches are frequently of greater diameter than their bases, because they are continually in a process of three-dimensional growth. Once a certain diameter is reached, the branch divides into two or more sub-branches. This diameter varies enormously in colonies from different biotopes. In some biotopes, e.g. partly protected reef backs, branching may be regular and almost dichotomous; in others, many sub-branches may grow simultaneously from a single greatly expanded branch end. The latter process produces colonies of very irregular shape and appearance.

Pocillopora damicornis from turbid deep or very protected water (ecomorph *bulbosa*) (Figs. 66–68).

This form differs from the above ecomorph in having thinner, elongated branches. Colonies are frequently infested with a variety of parasites and commensals which contribute to their irregular appearance. These colonies are usually found in calm, turbid waters such as are found in muddy bays on the protected sides of large islands, but may also occur in reef situations where light availability is limited.

Pocillopora damicornis from temperate biotopes.

Colonies from temperate biotopes often have long thick branches which divide relatively infrequently (up to 12 calice diameters between branches, as opposed to 2–4 calice diameters in colonies from northern Queensland).

Living colonies from the Solitary Islands (30°S lat.) are dark brown with deep green polyps (Veron, *et al.* 1974).

Distribution

Widely distributed throughout the Indo-Pacific.

Bathymetric range

0–42m (present study only).

Pocillopora verrucosa (Ellis & Solander, 1786)

Synonymy

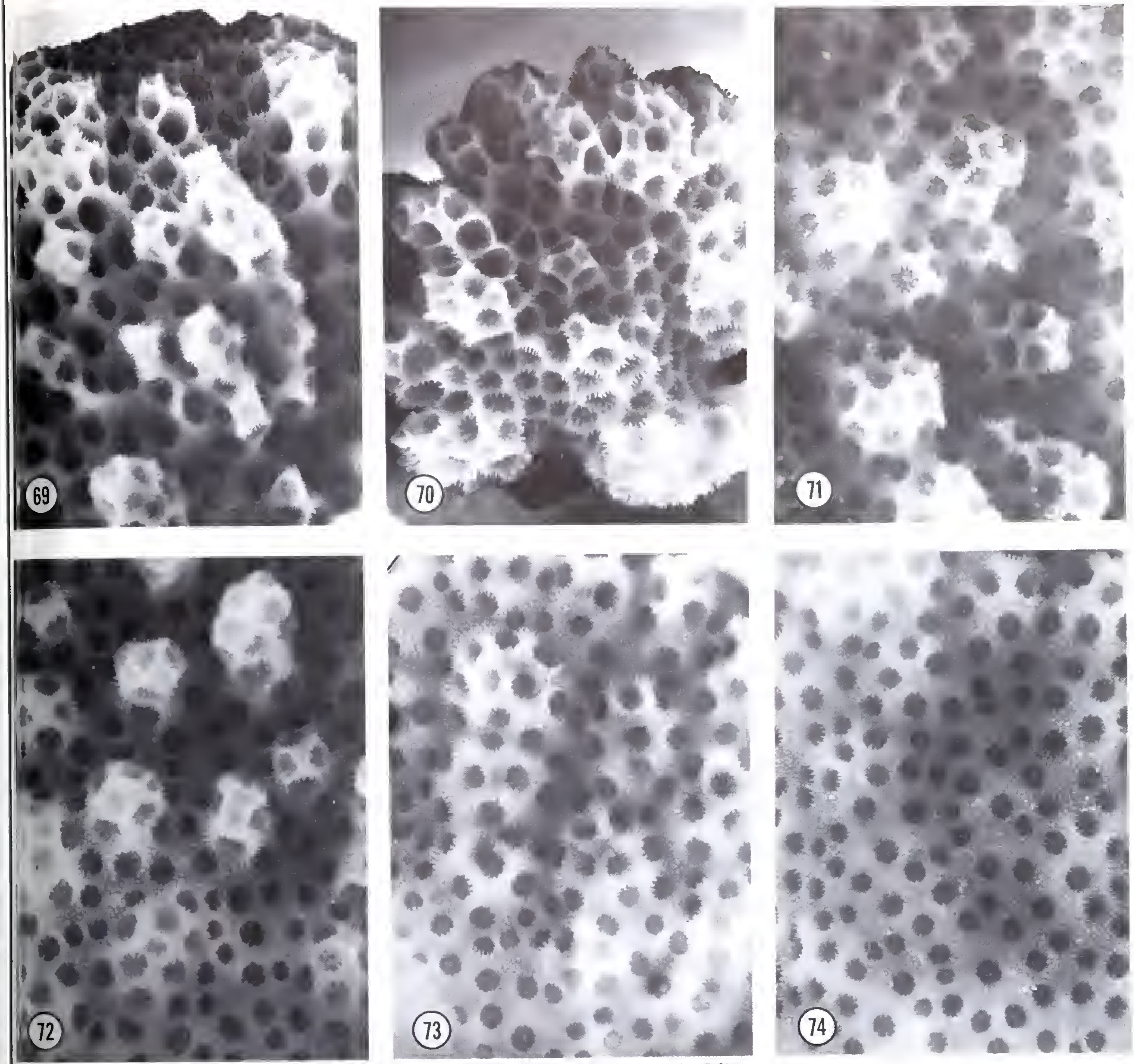
As with the preceding species, a full synonymy has not been determined. Principal species descriptions include:

Pocillopora verrucosa (Ellis & Solander, 1786)

Pocillopora hemprichi Ehrenberg, 1834

?Pocillopora elegans Dana, 1846

Pocillopora meandrina Dana, 1846



Figs. 69–74 *Pocillopora verrucosa* (× 5.0).

Fig. 69 From Tijou Reef, collecting station 2, showing calices near the tip of a branch.
Fig. 70 From Hope island, a well protected biotope showing calices near the tip of a branch.
Fig. 71 From Great Detached Reef, collecting station 1, showing calices 2cm below a branch tip.
Fig. 72 Same specimen as Fig. 69, showing calices 2cm below a branch tip.
Fig. 73 Same corallum as Fig. 69, showing calices midway down a main branch.
Fig. 74 Same corallum as Fig. 69, showing calices at the corallum base.

Pocillopora nobilis Verrill, 1864
Pocillopora meandrina var nobilis Verrill, 1864
?*Pocillopora danae* Verrill, 1864

Material Studied

Murray Islands[5]; **Great Detached Reef** (27 specimens), **Tijou Reef** (20 specimens), **Bewick Island** (2 specimens), **Hope Island** (4 specimens), **Low Isles**

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[5] Localities from specimens held at the Australian Museum.

(5 specimens), **Herald Island**[5], **Palm Islands, Bowl Reef** (9 specimens), **Yankee Reef** (2 specimens), **Keeper Reef, One Tree Island**[5] (4 specimens).

These localities include collecting stations 1, 2, 4, 5, 6, 10, 18, 21, 38, 48 and 53.

Previous records from Eastern Australia

Murray Islands (as *P. danae*), Vaughan (1918), **Low Isles** (as *P. verrucosa* and *P. danae*), Manton (1935); Crossland (1952); (as *P. verrucosa*), Stephenson & Wells (1955).

Characters

Colonies are ramose and verrucate. The minimum diameters of all main branches within a single colony vary less than approximately twice the diameter of the smallest branch.

Calices (Figs. 69–74) are approximately 0.5 to 1.3mm in diameter. Those of main branches (Figs. 73, 74) are circular with vertical walls. Between 8 and 20 approximately equal septa are usually present. They vary from simple vertical ridges covered with fine denticles, with 2–4 poorly defined blunt teeth spaced equally along their inner edge, to vertical rows of sharp spines projecting towards the calice centre. The latter arrangement usually occurs near the tips of branches (Figs. 69–71) and is characteristic of the species. The columella is usually absent or is a low boss; sometimes it is fascicular.

Growth form variation

This study confirms the observation of Manton (1935) and Crossland (1952) that this species is common in exposed areas such as outer reef fronts but is uncommon elsewhere. Growth forms are correspondingly less variable than those of *P. damicornis*.

Pocillopora verrucosa from exposed biotopes (ecomorph *meandrina*) (Fig. 75).

In areas of extreme wave action (e.g. Fig. 6) the growth form of this species converges with that of *P. damicornis* ecomorph *brevicornis* but is distinguished from it by the presence of verrucae rather than sub-branches on the outer surface of colonies, the verrucae always being immediately adjoined to a thick main branch (Fig. 3). Vaughan (1907) and Hoffmeister (1925) were both of the opinion that *P. brevicornis* belonged to the same series as *P. danae* and *P. verrucosa*.

There is little difference between the forms commonly known as *P. meandrina, P. verrucosa* and *P. elegans*. All these forms may occur within the one biotope. As with *P. damicornis*, the ends of branches are frequently of greater diameter than their bases. In some colonies, sub-branches develop after the branch diameter has approximately doubled, producing the characteristic *verrucosa* form; in other colonies, branch ends continually expand in one plane without dividing to produce the characteristic *meandrina* form. Both forms have been observed to occur within the one large colony.

Pocillopora verrucosa from semi-protected biotopes (Figs. 76–79).

Like *P. eydouxi, P. verrucosa* appears to occur only in areas exposed to regular water movement (by wave action or currents) and good illumination. Growth forms characteristic of the most protected areas that the species will tolerate (e.g. the eastern fringing reefs of Great Palm Island) are in all ways similar to *P. danae* which is either a synonym of *P. verrucosa* or else is apparently absent from the Great Barrier Reef. Wells (1954) comments that *P. danae* is 'very close' to *P. verrucosa*. However, Crossland (1952) was of the opinion that *P. danae* is in a series with *P. damicornis*.

Figs. 75–79 *Pocillopora verrucosa* (× 0.5).

Fig. 75 From Bowl Reef, collecting station 4.
Fig. 76 From Bewick Island, collecting station 18.
Fig. 77 From Great Detached Reef, collecting station 5.
Fig. 78 From Yankee Reef, collecting station 52.
Fig. 79 From Low Isles, collecting station 12.

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Two specimens from the Red Sea identified as *P. hemprichi*, one by J. W. Wells (specimen from Tel Aviv University), the other by G. Scheer (specimen from the Australian Museum, number G 14565) are in all ways identical with the *P. verrucosa* of the Great Barrier Reef. *P. hemprichi* is thus placed into synonymy with *P. verrucosa* on the assumption that these specimens correspond to Ehrenberg's 'species'.

Distribution

Widely distributed throughout the Indo-Pacific.

Bathymetric Range

0–20m (present study only).

Pocillopora eydouxi Edwards & Haime, 1860

Synonymy

The synonymy of this species, as discussed by Vaughan (1918), Umbgrove (1939) and Crossland (1952) includes:

Pocillopora grandis Dana, 1846; Gardiner (1897)

Pocillopora elongata Dana, 1846

Pocillopora eydouxi Edwards & Haime, 1860; Vaughan (1907, 1918); Hoffmeister (1925); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939, 1940); Crossland (1952); Wells (1954); Stephenson & Wells (1955); Scheer & Pillai (1974)

?*Pocillopora coronata* Gardiner, 1897

Pocillopora rugosa Gardiner, 1897

?*Pocillopora modumanensis* Vaughan, 1907; Yabe, Sugiyama & Eguchi (1936)

Pocillopora symmetrica Thiel, 1932

Material Studied

Great Detached Reef (3 specimens), **Tijou Reef** (8 specimens), **Palm Islands** (4 specimens), **Bowl Reef**.

These localities include collecting stations 1, 2, 4, 5, 6, 51 and 60.

Previous records from Eastern Australia

Murray Islands Vaughan (1918); **Low Isles** Manton (1935); Crossland (1952).

Characters

Colonies are ramose and verrucate. Branching occurs relatively infrequently and branches are generally much larger in all dimensions than those of other species of the genus (Figs. 80–83). They vary greatly in size and shape within the same colony, major branches being cylindrical (2–4cm in diameter) or broad-ended up to 15cm wide (Crossland records a branch 15.5cm wide). Colonies up to 95cm high have been observed at the Palm Islands.

Calicular structure (Figs. 84, 85) can vary markedly within the one branch. Branch ends are covered with cellular calices devoid of any internal structure. A few centimetres below the ends, calices usually reach their maximum complexity, although well developed calices may be found on other parts of some colonies. They have two unequal cycles of septa, with primary septa extending approximately half-way towards the calice centre. One, or sometimes a pair of directive septa are markedly dominant and are joined to the prominent, pinnacle-like columella. Septal edges are irregularly toothed. The septa and columella may both be covered with fine denticles. Less complex calices may have one cycle or an irregular number of septa with one dominant directive and a columella. Some older calices have no internal structure; calices on verrucae are usually relatively well developed. Thecal walls, especially of calices on verrucae, may support a row of spinules which are usually continuous with spinules or granulations on the coenenchyma.

Fig. 80 *Pocillopora eydouxi* colonies from between Orpheus and Fantome Islands, Palm Islands, collecting station 60, *in situ*, see Fig. 9.

Fig. 81 *Pocillopora eydouxi* from Tijou Reef, collecting station 2, *in situ*.

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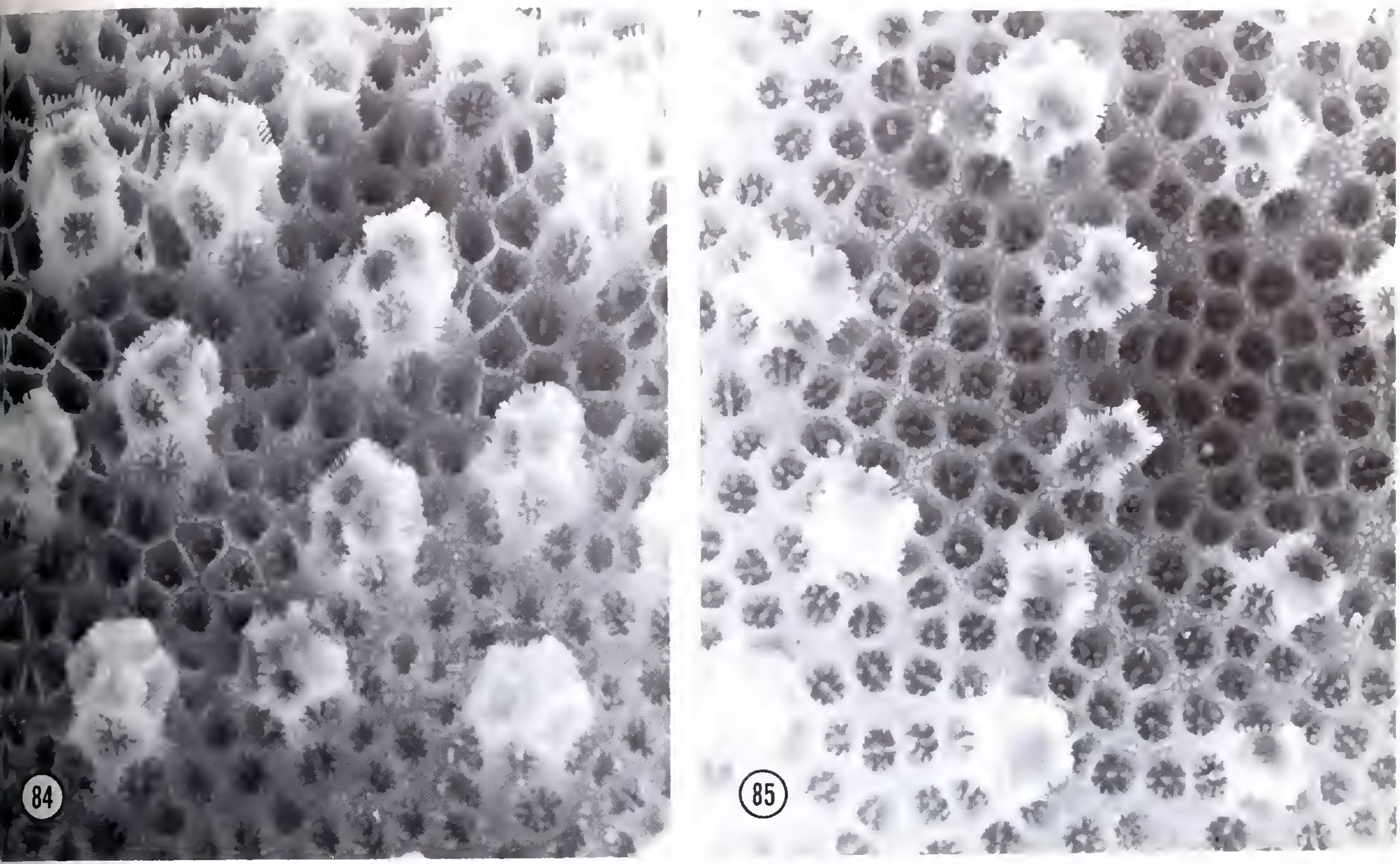


Figs. 84, 85 *Pocillopora eydouxi* (× 7.5).

Fig. 84 Calices near the tip of a branch of the corallum illustrated in Fig. 83.
Fig. 85 Calices on the side of a branch of the corallum illustrated in Fig. 83.

Growth form variation

Crossland (1952) divided his 'three specimens and four fragments' into three 'very distinct' groups to which he attributed distinct calicular characters. The present study shows that the growth form variations are similar to those observed in other species of the genus. Two major ecomorphs may be recognised:

Pocillopora eydouxi from exposed biotopes.

This form is characteristic of shallow reef waters exposed to strong or moderate wave action or to currents. Colonies are frequently hemispherical in shape or may be flattened and are composed of regular, radiating, relatively frequently dividing branches. Sub-branches develop after branch ends approximately double in width (about 6cm). In areas of strong wave action, colonies may be flattened so that branches are mostly horizontal. The colour of branch ends varies from pale brown to pale pink, blue and purple.

Pocillopora eydouxi from semi-protected biotopes.

This species is rarely found in turbid waters. Where it does occur, colonies may be very variable in appearance, having a few elongated arms of variable shape and size. No specimens have been observed in very turbid biotopes.

Distribution

Widely distributed throughout the Indo-Pacific from south Mozambique (Boschoff,

Figs. 82, 83 *Pocillopora eydouxi* (× 0.8).

Fig. 82 From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.
Fig. 83 From Tijou Reef, collecting station 2.

1958) and the Red Sea (unpublished) to Hawaii (Vaughan, 1907, under the name of *P. modumanensis*).

Bathymetric Range

0–30m (present study only).

Fig. 86 *Pocillopora woodjonesi* from Tijou Reef, collecting station 2 (× 0.8).

Pocillopora woodjonesi Vaughan, 1918

Synonymy

Pocillopora woodjonesi Vaughan, 1918.

Material Studied

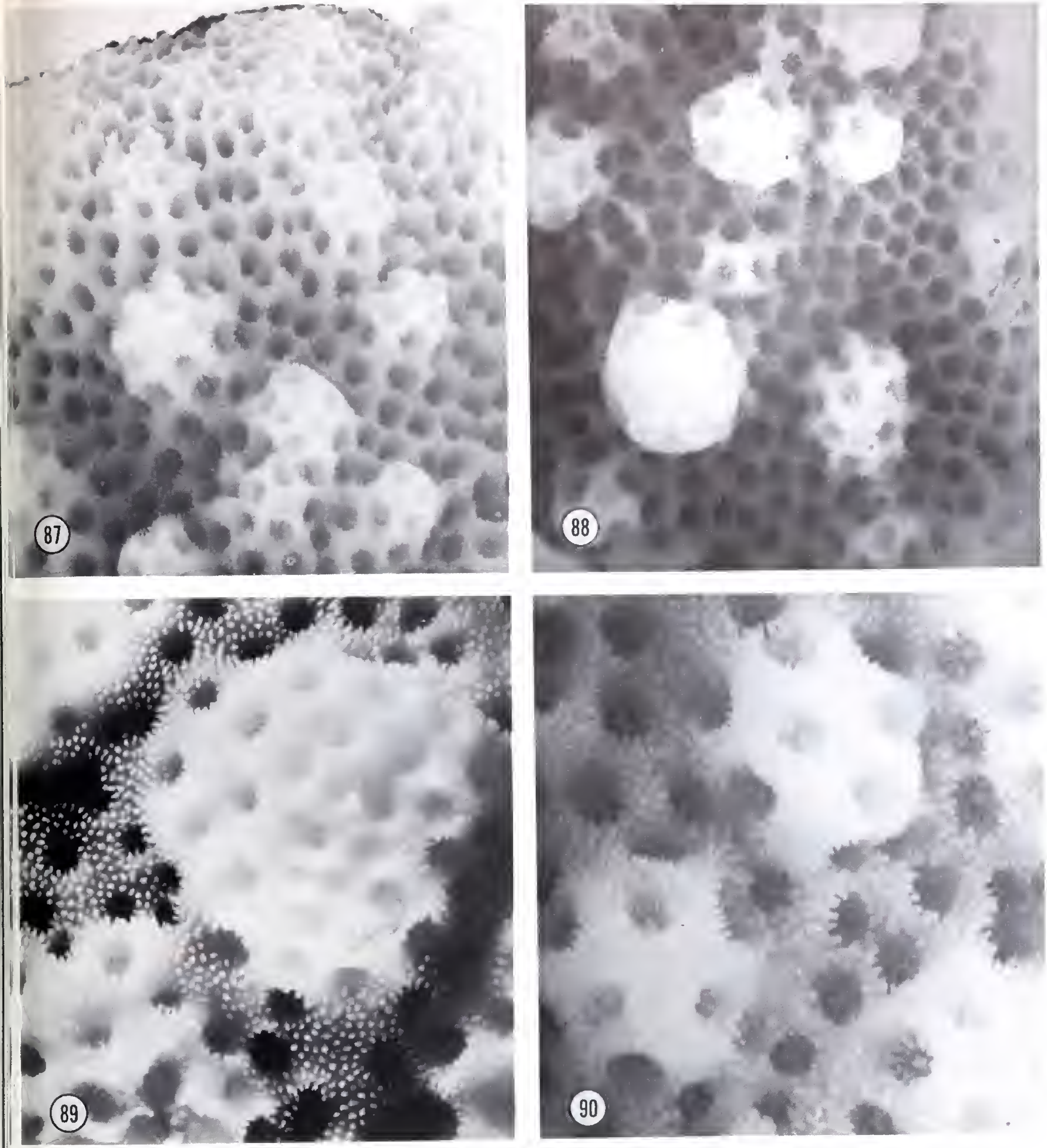
Front, **Tijou Reef**, 10m below reef crest (Fig. 86).

Previous records from Eastern Australia

Not previously recorded.

Characters

'Corallum somewhat similar in growth form to *P. eydouxi,* but the branches tend to be more dwarfed and to become fan-shaped instead of elongate. The branches are short, more or less contorted plates.' (Vaughan, 1918 p. 80). Calices (Figs. 87–90) on branch ends are cellular, approximately 0.7mm in diameter and are devoid of internal structures.



Figs. 87–90 *Pocillopora woodjonesi* (same corallum as Fig. 86).

Fig. 87	Calices near the tip of a branch (× 5.0). .
Fig. 88	Calices on the side of a branch (× 5.0).
Fig. 89	Calices at the base of a branch (× 10.0).
Fig. 90	Calices on the side of a branch (× 6.5).

Calices on branch sides are of equal or slightly greater diameter; the calicular fossa is a rather deep pit. Two equal or sub-equal cycles of septa are situated deep in the calices and extend approximately half way to the pinnacle-like columella. One or a pair of directives are markedly dominant. Septa are usually irregularly toothed and may be covered with fine denticles. ‘Coenenchyma thin; granulations radially compressed, often forming costal striations around the calicular edges, tops truncated, with secondary frosting. The coenenchymal ornamentation is strikingly different from that of *P. eydouxi*.' (Vaughan, 1918 p. 80).

Distribution

This species has been recorded only from the Cocos Keeling Islands (Vaughan, 1918) and from the Great Barrier Reef (present study).

GENUS *SERIATOPORA* LAMARCK, 1816

Type species *Seriatopora subulata* Edwards & Haime, 1850.

A very wide range of growth forms combined with a lack of conservative skeletal characters make the species of this genus particularly difficult to define. The comments of Umbgrove (1939) are appropriate to the 28 'species' that have so far been described:

'I am convinced that the great number of "species" will be reduced considerably. Many *nova* species have been created on one or a few specimens, even on worn-off branches only. . . .' 'For the moment it is hardly possible to make a safe identification. Even when a coral corresponds exactly to an adequately described and figured species, the student has no certainty that the species name is correct. It may be that *hystrix* is a synonym of one of the older species names, of Ehrenberg's or Lamarck's.'

Characters of the genus

Colonies are ramose with anastomosing branches. Corallites are arranged in longitudinal series along branches.

Seriatopora hystrix Dana, 1846

Synonymy

Many, if not most, of the 'species' names attributed to this genus refer to this one extremely polymorphic species. The following synonymy, however, refers only to studies where the names *hystrix* and *angulata* are used.

Seriatopora hystrix Dana, 1846; Edwards & Haime (1860); Brüggemann (1877); Quelch (1886); Studer (1901); Bedot (1907); Vaughan (1918); Yabe & Sugiyama (1932b, 1935b); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939, 1940); Crossland (1952); Wells (1954); Stephenson & Wells (1955); Searle (1956); Nemenzo (1964); Chevalier (1968); Scheer & Pillai (1974).

Seriatopora angulata Klunzinger, 1879; von Marenzeller (1907); Vaughan (1918); Yabe, Sugiyama & Eguchi (1936); Crossland (1952); Wells (1950, 1954); Rossi (1954); Nemenzo (1964); Scheer (1967); Wells & Davies (1966); Scheer & Pillai (1974).

Material Studied

Barrier reef NE of **Murray Islands**, **Sue Island** (2 specimens), **North-west Reef**, **Great Detached Reef** (6 specimens), **Tijou Reef** (13 specimens), **Bewick Island** (2 specimens), **Two Isles** (2 specimens), **Hope Island**, **Low Isles**, **Michaelmas Cay**[6] (2 specimens), **Hedley Reef**[6], **Palm Islands** (51 specimens), **Keeper Reef** (2 specimens), **Lodestone Reef**, **Wheeler Reef** (12 specimens), **Bowl Reef** (14 specimens), **East of Bowl Reef** (5 specimens), **Bowden Reef**, **Hayman Island**[6], **Swain Reefs**[6], **North-west Islet**[6], **Masthead Island**[6], **One Tree Island**[6], **Lord Howe Island** (2 specimens).

These localities include collecting stations 1, 2, 5, 7, 10, 14, 17, 18, 21, 22, 30, 34, 36, 38, 41, 42, 43, 45, 46, 55, 56, 58 and 60.

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[6] Localities from specimens held at the Australian Museum.

Previous records from Eastern Australia

Darnley Island (as *S. subulata*), Tenison-Woods (1879c); **Murray Islands,** Vaughan (1918); **Low Isles,** Yonge (1930); Stephenson *et al.* (1931); Stephenson & Stephenson (1933); Manton (1935); Crossland (1952); Stephenson & Wells (1955); **North-west Islet,** Hedley (1927); **Heron Island,** Salter (1954); **Lord Howe Island,** Veron (1974).

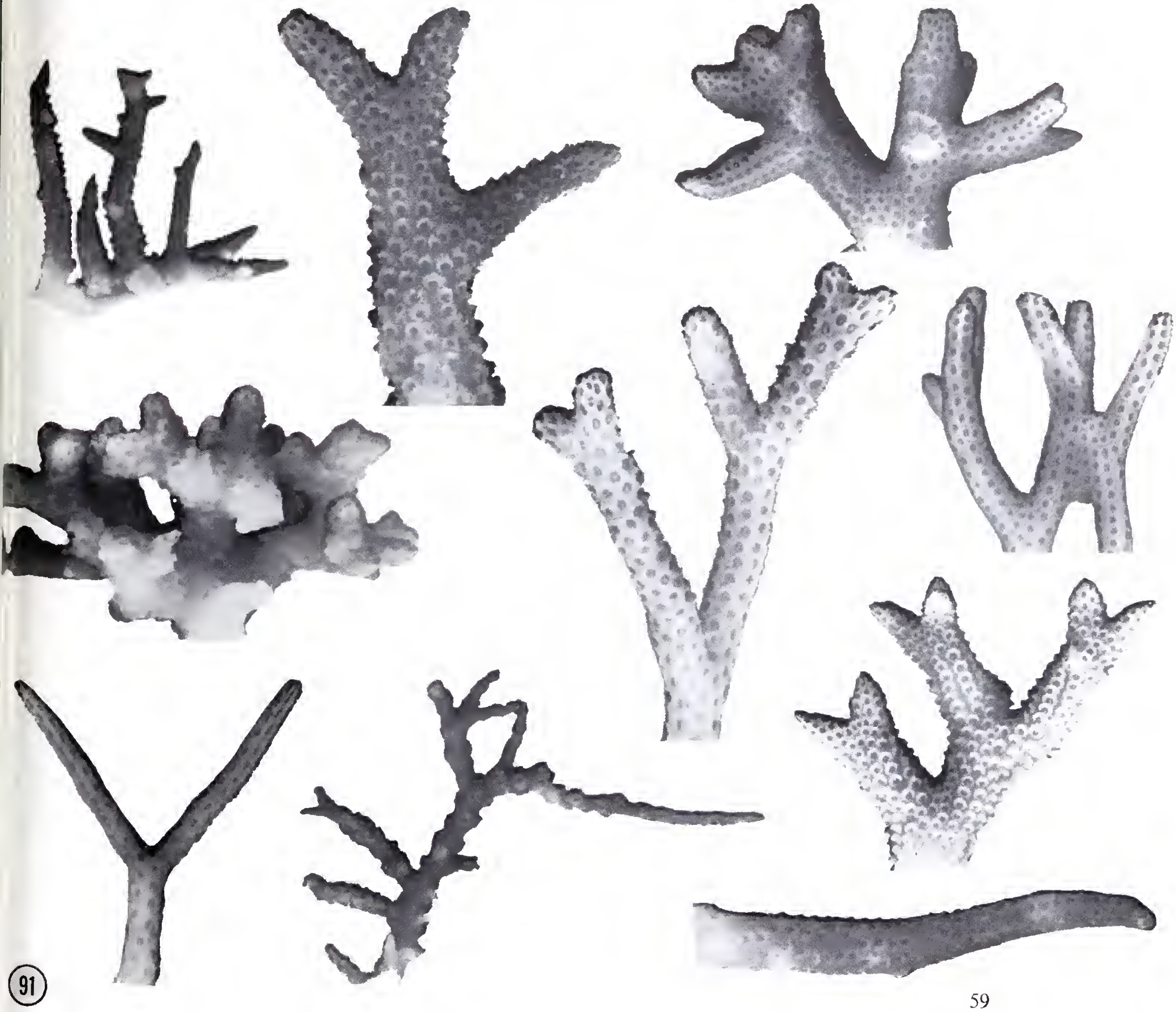
Characters

Colonies are composed of masses of anastomosing branches of very variable shape, size and appearance. Branches are usually circular in transverse section but are sometimes anastomosed into flat basal plates several cm across.

They vary according to the following characteristics:

1. The diameter varies from 1.5 to 4.5mm, 1cm below the tip and 2.5 to 8mm near the base of well developed coralla.
2. Sub-branches may be equal to markedly unequal in size.

Fig. 91 Tips of *Seriatopora hystrix* branches illustrated in Figs. 99–118 (× 2.0).



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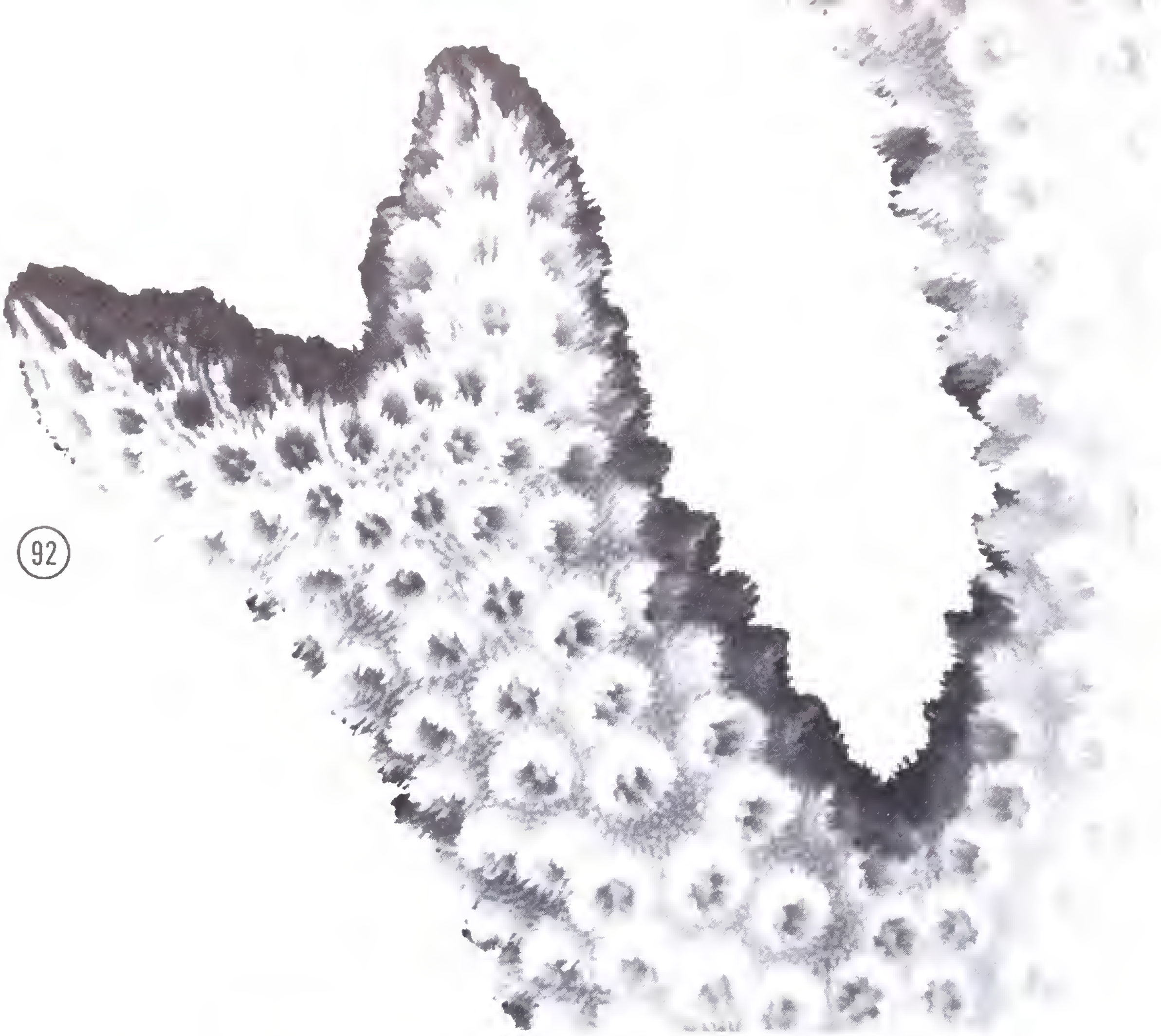
(92)


(93)


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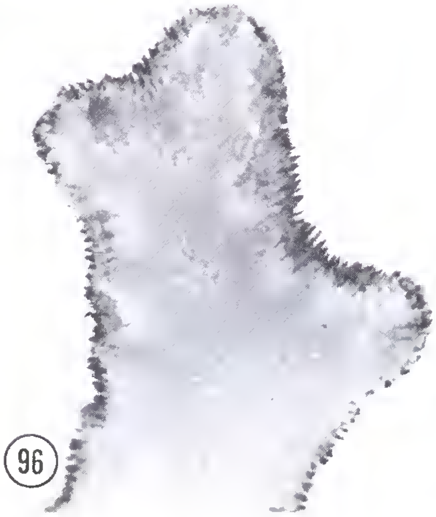
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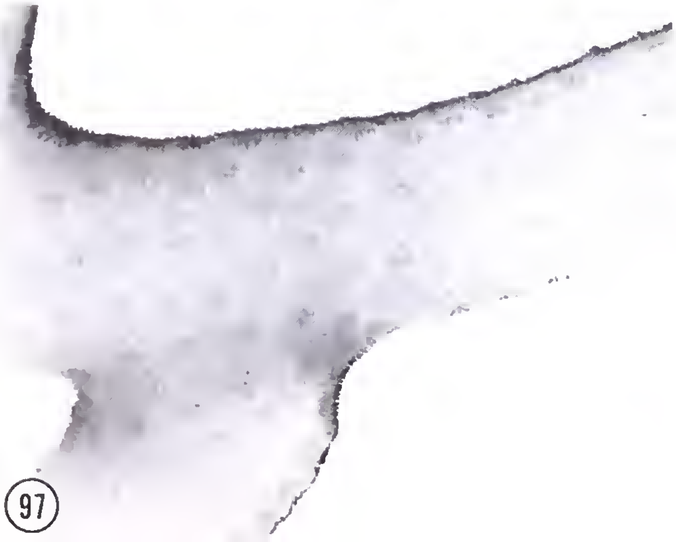
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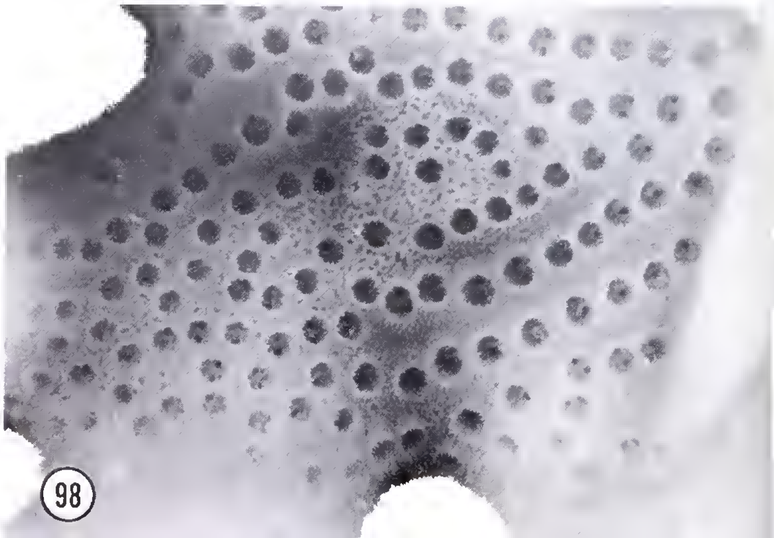
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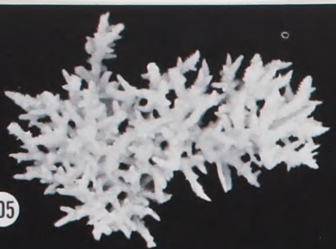
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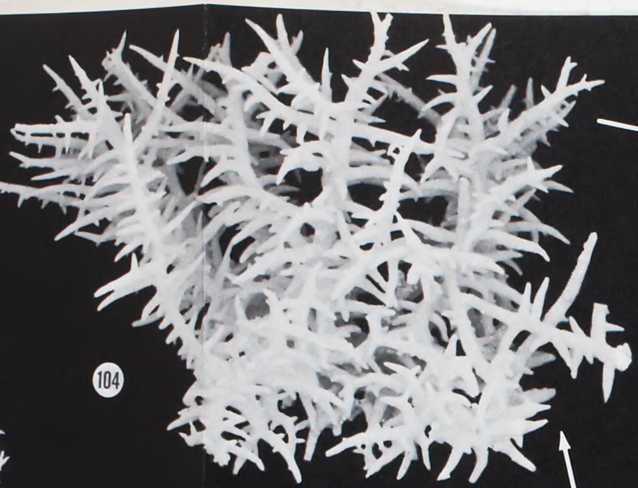
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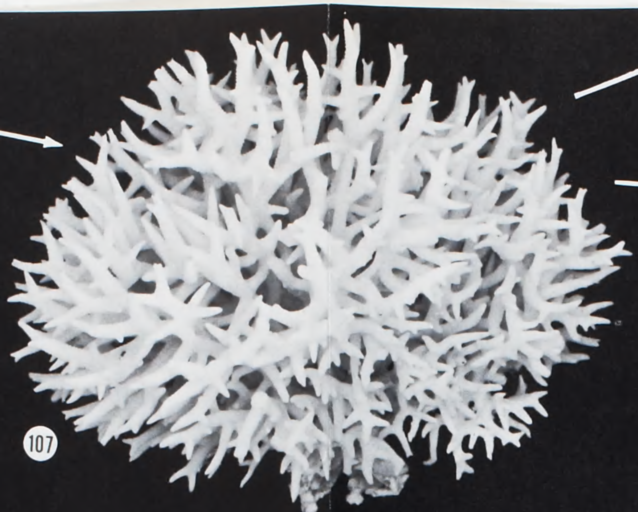
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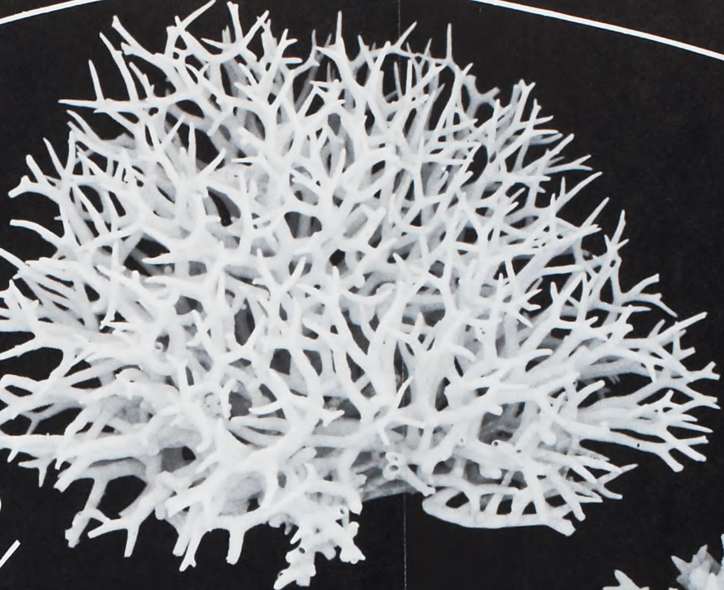
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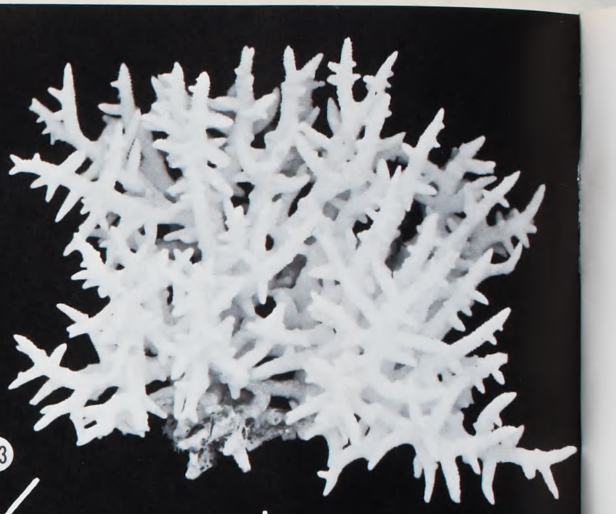
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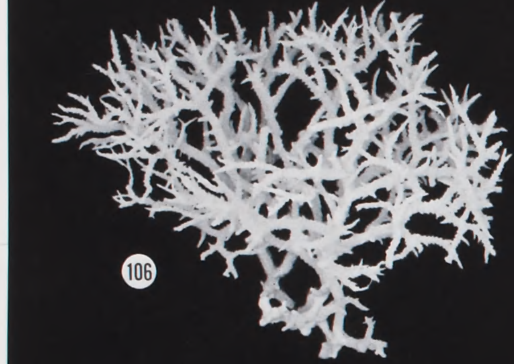
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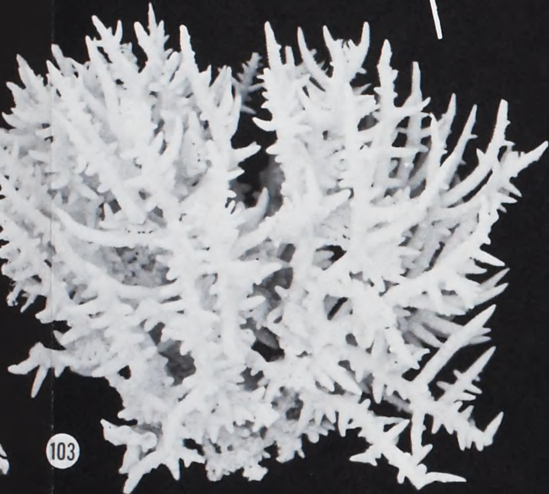
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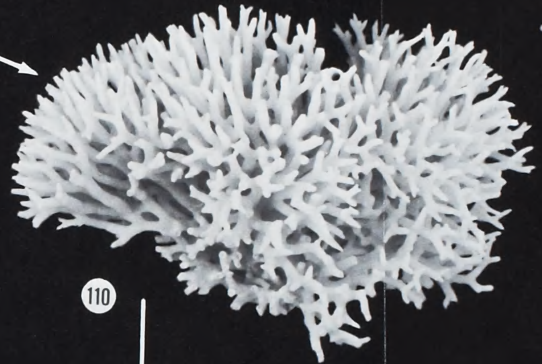
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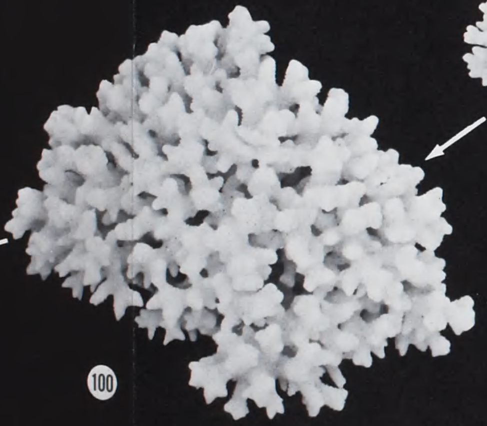
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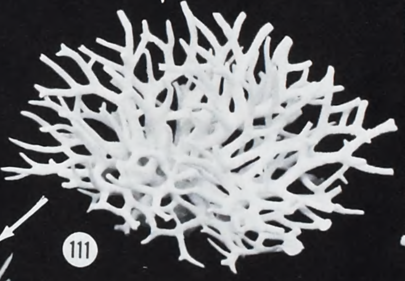
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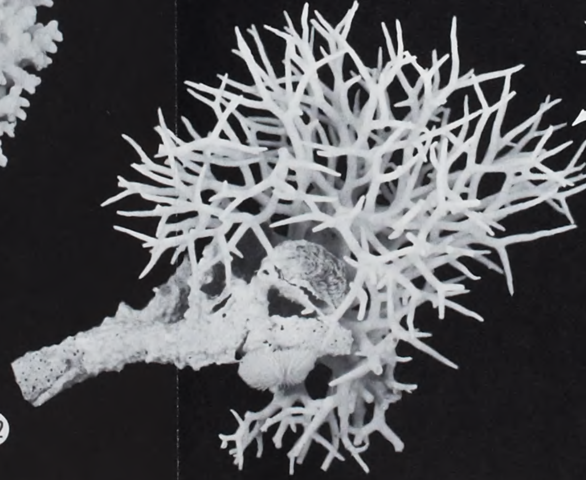
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115


117

3. The angle of branching varies from acute (approximately 30°) to right angles.
4. Branches may taper slowly or abruptly to form sharp points, or may taper little and have blunt, rounded points.

These characteristics appear to vary more or less independently of each other according to major, or sometimes subtle, changes in environmental conditions. The angle of branching is perhaps the most variable characteristic. Large colonies frequently display acute-angle branching at their centres and right-angle branching at their peripheries. In such cases, the acute-angle branches are usually more or less equal and the right-angled branches unequal or very unequal. The nature of the branch tips (i.e. whether or not they are pointed or rounded) is usually uniform within a corallum but varies considerably among colonies within the same biotope, sometimes even among colonies situated immediately adjacent to each other. The diameter of the branches is the most conservative characteristic and appears to be a direct function of exposure to light and turbulence.

As with other Pocilloporidae, the structure of the calices varies greatly according to their position along the branches (Figs. 92–98). Calices at the tips of branches are tightly packed, thin-walled and cellular in appearance. Immediately below the tip, they usually become extremely longitudinally distorted. They develop a plate-like or styliform columella and six small septa high on the theca. The directive septa, particularly the lower one, become markedly dominant and form a ridge or wall extending across the floor of the calice to fuse with the columella in the direction of growth of the branch. A second cycle of septa is occasionally discernible and all septa, as well as the columella, may become irregularly toothed. Older calices on lower branches usually have greatly thickened walls, lower directive septa and columellas. One or both pairs of lateral primary septa usually become thickened also, although they usually remain poorly developed or may become completely obscured. Deep interseptal loculi frequently become very conspicuous.

Figs. 92–98 Calices of *Seriatopora hystrix* illustrated in Figs. 99–117

Fig. 92 Calices of a branch tip (× 10.0).
Figs. 93–96 Calices of branch tips (× 6.0).
Figs. 97–98 Calices of the base of branches (× 10.0).

Figs. 99–117 *Seriatopora hystrix* (× 0.5).

Figs. 99–117 are arranged, as far as possible, into sequences of growth form variation. It is emphasised that these sequences do not necessarily reflect or indicate sequences of biotope variation but rather sequences of micro-environment variation, many of which may occur within the one biotope, or conversely, in widely differing biotopes.

Fig. 99	From Great Detached Reef, collecting station 1.
Fig. 100	From Bowl Reef, collecting station 2.
Fig. 101	From Juno Bay, Palm Islands, collecting station 43.
Fig. 102	From Bowl Reef, collecting station 10.
Fig. 103	From Wheeler Reef, collecting station 22.
Fig. 104	From Wheeler Reef, collecting station 22.
Fig. 105	From Tijou Reef, collecting station 2.
Fig. 106	From Wyer Island, Murray Islands, collecting station 30.
Fig. 107	From Wheeler Reef, collecting station 22.
Fig. 108	From Orpheus Island, Palm Islands, collecting station 45.
Fig. 109	From Fantome Island, Palm Islands, collecting station 43.
Fig. 110	From Sue Island, collecting station 17.
Fig. 111	From Elk Cliff, Great Palm Island, collecting station 37.
Fig. 112	From Orpheus Island, Palm Islands, collecting station 55.
Fig. 113	From Bowl Reef.
Fig. 114	From the barrier reef N E of Murray Islands, collecting station 7.
Fig. 115	From Bowl Reef.
Fig. 116	From Electra Head, Great Palm Island, collecting station 36.
Fig. 117	From Orpheus Island, Palm Islands, collecting station 45.

The thecal rim usually supports a row of tall spinules, as does the coenenchyme, where they frequently form ornate rows along the branches between the calices. The calices always form neat, straight or slightly spiralled rows along branches.

Growth form variation

The growth forms of this species vary enormously according to the many micro-environments in which it grows. Thus a wide range of growth forms may occur within one biotope and often within one colony. Three broad categories may be recognised, but they are by no means mutually exclusive.

Seriatopora hystrix from exposed biotopes.

This form occurs in the same biotopes as *Pocillopora damicornis* (ecomorph *brevicornis*), *Pocillopora verrucosa* (first ecomorph) and *Seriatopora caliendrum* (first ecomorph), i.e. on reef fronts exposed to very strong wave action (collecting stations 1 and 2), and exhibits similar growth form modifications. Colonies are very compact, being composed of masses of frequently dividing, anastomosing branches (e.g. Figs. 99, 100).

Whole colonies or branches of colonies frequently invade the matrix of dead *Acropora* branches which make up much of the substrate of most outer reef fronts. These colonies or branches of colonies are quite unlike those exposed to strong wave action; branches are very delicate and meander through any part of the substrate matrix with sufficient light penetration (e.g. Fig. 105).

Seriatopora hystrix from semi-protected biotopes.

This species may dominate extensive reef areas that are partially protected from strong wave action but which are exposed to current and illumination of widely varying strengths and intensity. In such situations, e.g. on the west side of Wheeler Reef, intrabiotope growth forms may vary so widely as to surpass variation in any other coral species. This variation appears to be partly genotypic, but is primarily phenotypic in origin. Adjacent colonies within the same microhabitat, apparently resulting from separate larval settlement, may show considerable growth form differences (e.g. Figs. 104, 108). However, major growth form variation is frequently seen within very large colonies (up to 6m across) that extend from one microhabitat to another. Thus, most of the growth form variations illustrated in Figs. 102–104, 107–109, 113–117 have been traced *within* a few colonies at Wheeler Reef (collecting station 22) and thus appear to be primarily attributable to variations in micro-environment.

Seriatopora hystrix from turbid or deep water

In conditions of poor illumination, growth form variation in this species is sufficiently reduced to be definable as a relatively uniform 'ecomorph'. Branches are long and thin and divide relatively infrequently. Specimens dredged from a depth of 55m east of

Fig. 118 Tips of branches of *Seriatopora caliendrum* illustrated in Figs. 125–130.

Bowl Reef were found to be almost identical in growth form to those collected from a protected muddy bay in the Palm Islands at a depth of 5m (Fig. 11).

Distribution

Widely distributed throughout the Indo-Pacific.

Bathymetric Range

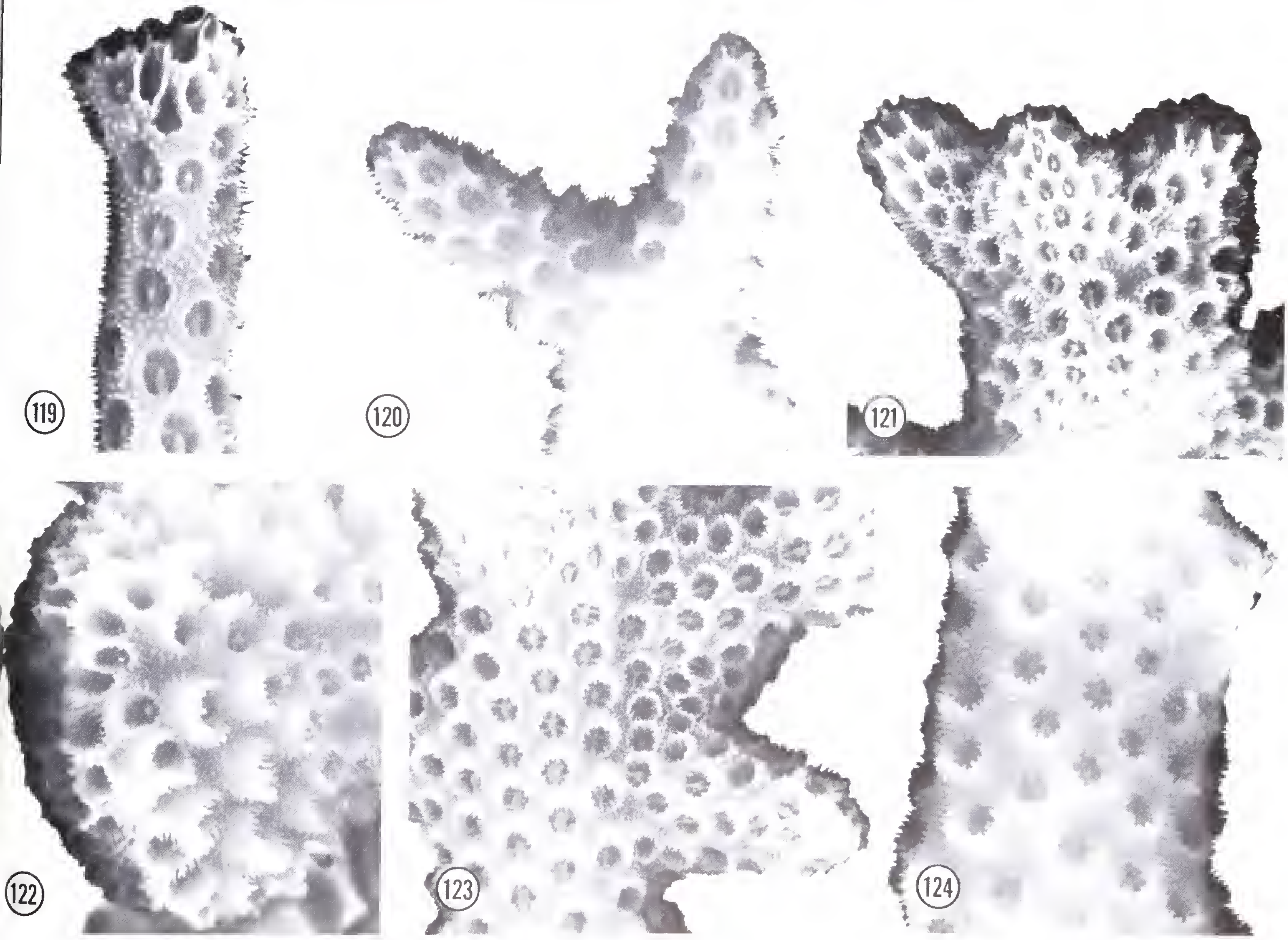
0–55m.

Seriatopora caliendrum Ehrenberg, 1834

Synonymy

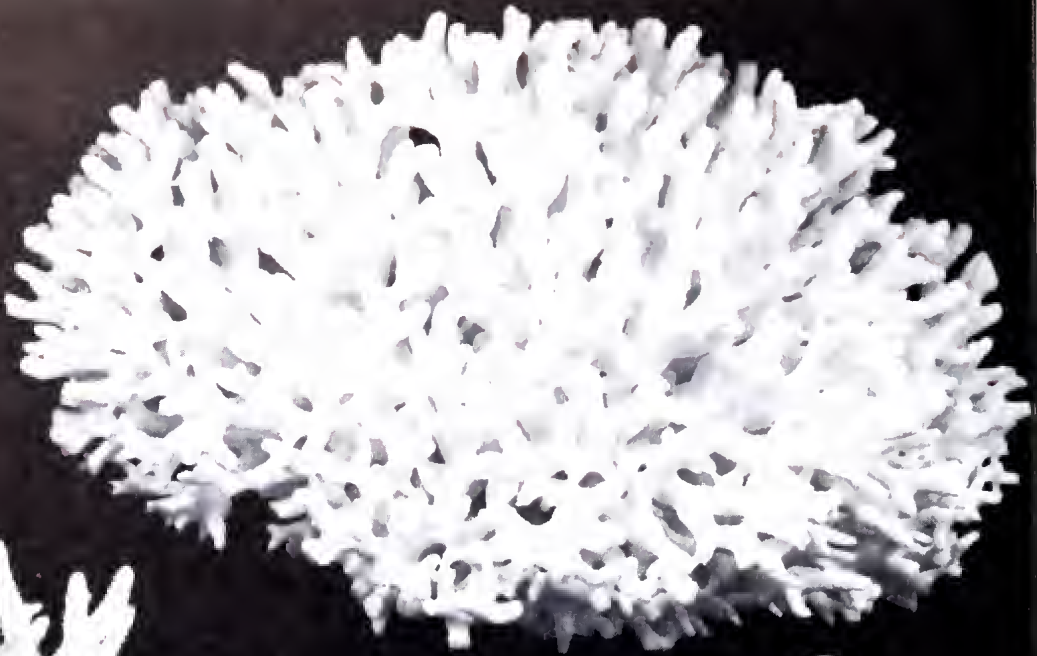
As with *S. hystrix,* various growth forms of this species appear to have been described as separate species. A satisfactory synonymy, however, has yet to be determined.

Seriatopora caliendrum Ehrenberg, 1834; Dana (1846); Edwards & Haime (1860); Klunzinger (1879); Quelch (1886); Ortmann (1888); von Marenzeller (1901, 1907); Gravier (1911); Faustino (1927); Yabe & Sugiyama (1935b); Eguchi (1935); Yabe, Sugiyama & Eguchi (1936); Nemenzo (1964); Scheer (1967); Scheer & Pillai (1974).



Figs. 119–124 Calices of branch tips of *Seriatopora caliendrum* illustrated in Figs. 125–130. Figs. 119–122 are of branch tips, Figs. 123, 124 are of the sides of branches.


125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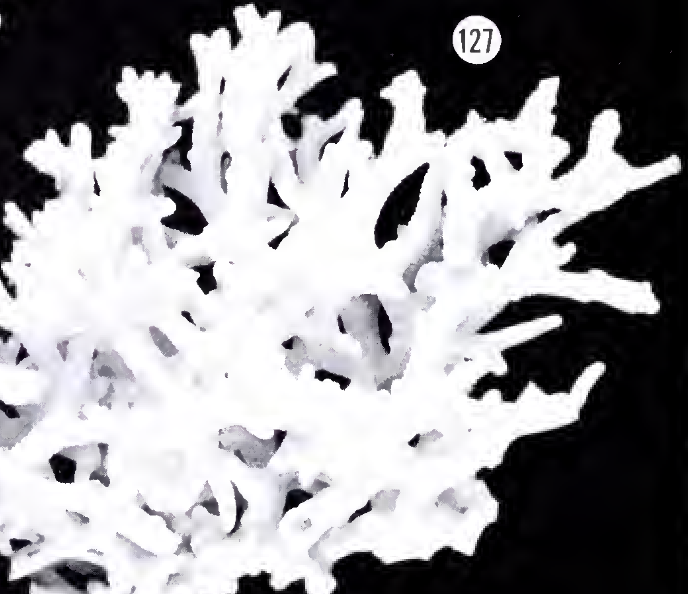
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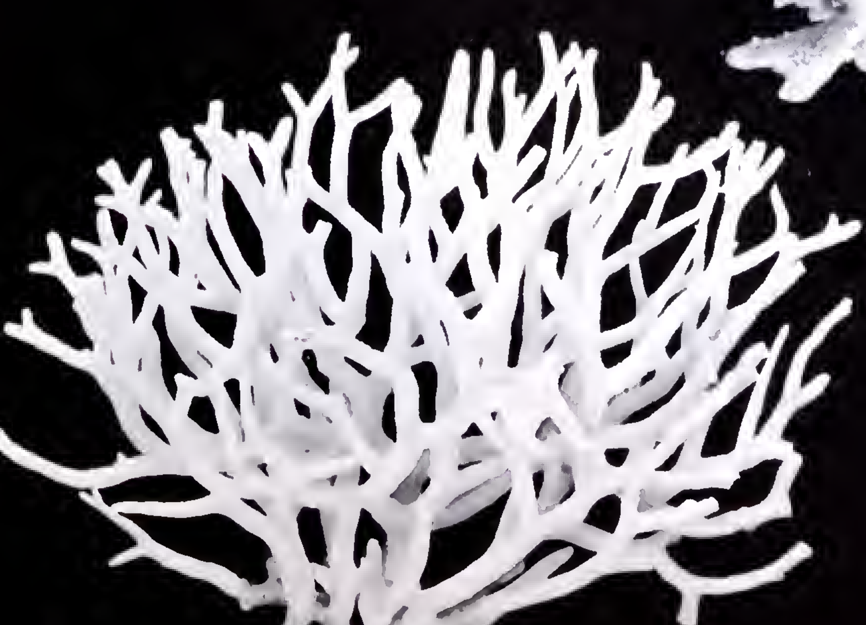
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130

Material collected

Great Detached Reef, Tijou Reef, Bewick Island, Hope Island, Palm Islands (9 specimens), **Bowl Reef** (6 specimens), **Keeper Reef**.

These localities include collecting stations 1, 2, 10, 18, 21, 34, 36, 43, 45 and 55.

Previous records from Eastern Australia

Not previously recorded.

Characters

As with *S. hystrix*, colonies are composed of masses of anastomosing branches. These are usually thicker (3–8mm) than those of *S. hystrix* from the same biotope. The diameters of all sub-branches within a colony are relatively constant. The average angle of branching is approximately 60–80°. The ends of branches are blunt (Fig. 118), rarely bulbous; branches do not taper.

Calices (Figs. 119–124) are similar in structure to those of *S. hystrix*. They differ primarily (1) in usually having distinct, almost *Stylophora*-like hoods, (2) in usually having more than 6 septa (rudimentary though they may be) in the majority of calices (notably older calices) and (3) in frequently having pairs of deep interseptal loculi between the two pairs of lateral septa. It must be emphasised, however, that calicular structures are so variable that they are of very limited taxonomic use.

Growth form variation

The principal growth form variations of this species are similar to those described for *S. hystrix*. However, it is clear that where these two species occur within the same biotope, they are always readily separable on the basis of gross skeletal characters alone.

Seriatopora caliendrum from exposed biotopes (Fig. 125).

As noted for *S. hystrix*, this form occurs on reef fronts exposed to very strong wave action. Colonies are similarly compact and usually have expanded branch ends.

Seriatopora caliendrum from semi-exposed biotopes (Figs. 126–128).

This species seldom forms extensive colonies as does *S. hystrix* and thus little information is available on growth form variation within colonies. However, study of the specimens available indicates that growth form variations are comparatively uniform over a very wide variety of biotopes.

Seriatopora caliendrum from protected biotopes (Figs. 129, 130).

As with *S. hystrix*, branches become long and delicate.

Distribution

Widely distributed throughout the Indo-Pacific.

Bathymetric range

0–20m (present study only).

Figs. 125–130 *Seriatopora caliendrum* (× 0.5).

Fig. 125	From Bewick Island.
Fig. 126	From Hope Island.
Fig. 127	From Elk Cliff, Great Palm Island, collecting station 37.
Fig. 128	From Bowl Reef.
Fig. 129	From Orpheus Island, Palm Islands, collecting station 45.
Fig. 130	From Fantome Island, Palm Islands, collecting station 43.

GENUS *STYLOPHORA* SCHWEIGGER, 1819

Type species *Madrepora pistillaris* Esper, 1797.

Generic synonymy (after Vaughan and Wells, 1943)

Madrepora (pars.) Pallas (1766); *Porites* (pars.) Lamarck (1816); *Sideropora* de Blainville (1830); *Anthropora* Gray (1835); *Enallastrea* d'Orbigny (1849); *Phyllopora* Tenison-Woods (1879c).

Characters of the genus

Colonies are ramose to submassive and are without true verrucae. Corallites are usually hooded. Septa of the first cycle unite with a styliform columella.

Stylophora pistillata Esper, 1797

Synonymy (partly after Thiel, 1932)

Madrepora pistillaris Esper, 1797

Porites subdigitata Lamarck, 1816

Stylophora pistillaris (Esper, 1797); Schweigger (1819); de Blainville (1830)

Sideropora subdigitata (Lamarck, 1816); de Blainville (1830); Dana (1846)

Stylophora palmata de Blainville, 1830; Edwards & Haime (1857); Brüggemann (1879); Klunzinger (1879); Quelch (1886); Ortmann (1888); Gardiner (1897)

Porites pistillata (Esper, 1797); Ehrenberg (1834)

Sideropora mordax Dana, 1846

Sideropora pistillata (Esper, 1797); Dana (1846)

Stylophora digitata (Pallas, 1766); Edwards & Haime (1857); Verrill (1864); Klunzinger (1879); Studer (1881); Quelch (1886); Bassett-Smith (1890); Gardiner (1898); Whitelegge (1898); Bedot (1907)

Stylophora pistillata (Esper, 1797); Edwards & Haime (1857); Klunzinger (1879); Ortmann (1888, 1892); Bassett-Smith (1890); Gardiner (1898); von Marenzeller (1901, 1907); Gravier (1911); Vaughan (1918); Mayer (1918); Faustino (1927); Thiel (1932); Yabe & Sugiyama (1932b, 1935b); Eguchi (1935); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939, 1940); Crossland (1952); Wells (1954, 1955b); Rossi (1954); Nemenzo (1964); Scheer (1964, 1967); Eguchi (1968); Chevalier (1968)

Stylophora stellata Verrill, 1864; Ortmann (1888)

Stylophora sinaitica Brüggemann, 1877

Stylophora prostrata Klunzinger, 1879; Quelch (1886); Bassett-Smith (1890)

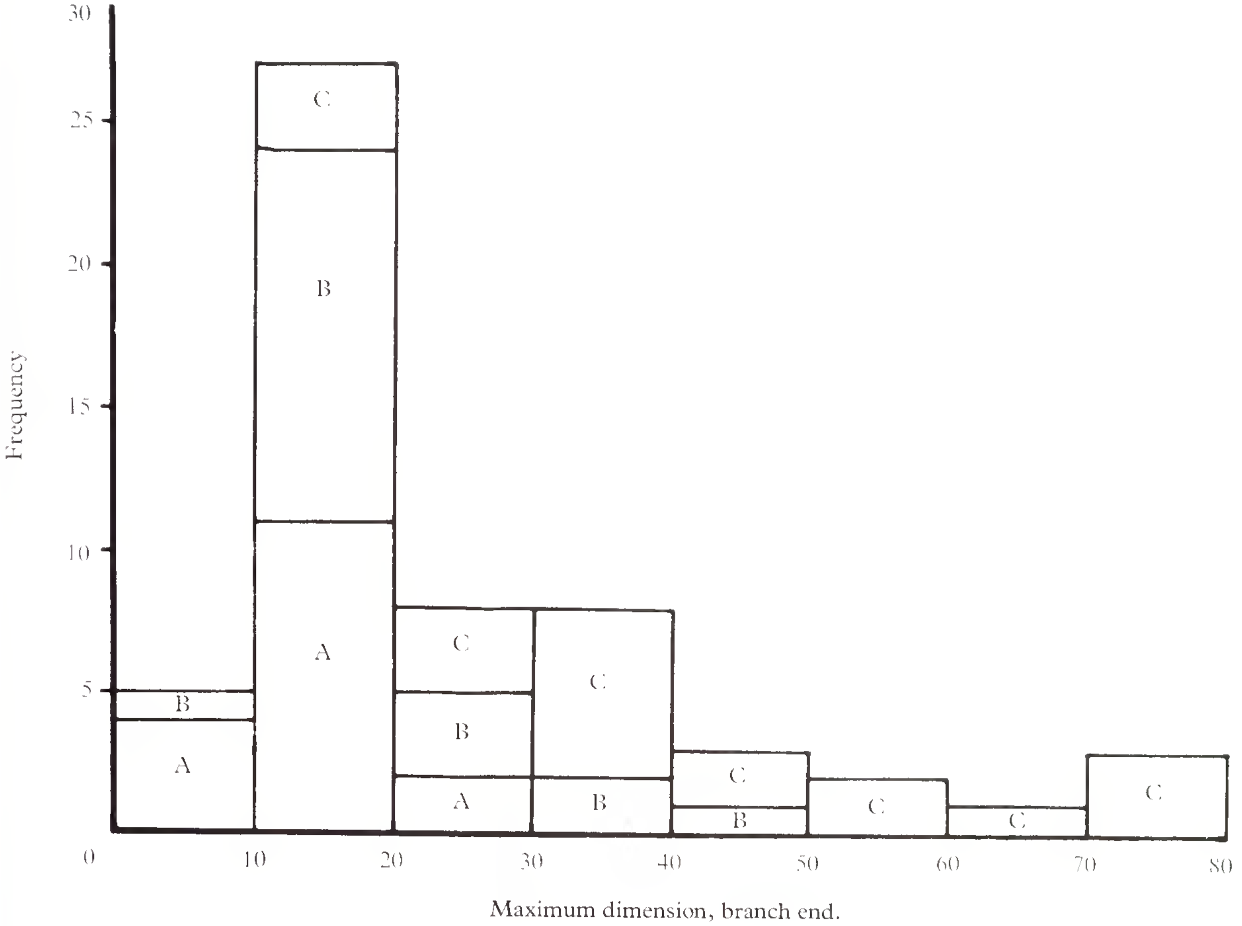
Stylophora cellulosa Quelch, 1886; Faustino (1927)

Stylophora septata Gardiner, 1898; Crossland (1952)

Stylophora mordax (Dana, 1846); Vaughan (1918); Yabe & Sugiyama (1935b); Eguchi (1935); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939); Vaughan & Wells (1943); Wells (1954); Scheer & Pillai (1974)

Fig. 131 Frequency distribution of the maximum diameter of the largest branch end per corallum of *Stylophora pistillata* coralla from localities characterised by:— protected, turbid water A, protected, clear water B, and exposed, very clear water C.

Fig. 132 Frequency distribution of the mean distance, per corallum, between the branch ends of *Stylophora pistillata* coralla. A, B, and C indicate coralla having maximum diameters of branch ends of 20mm, 20–40mm and 40mm respectively.


Frequency
0
5
10
15
20
25
30
0
10
20
30
40
50
60
70
80
A
B
A
B
C
A
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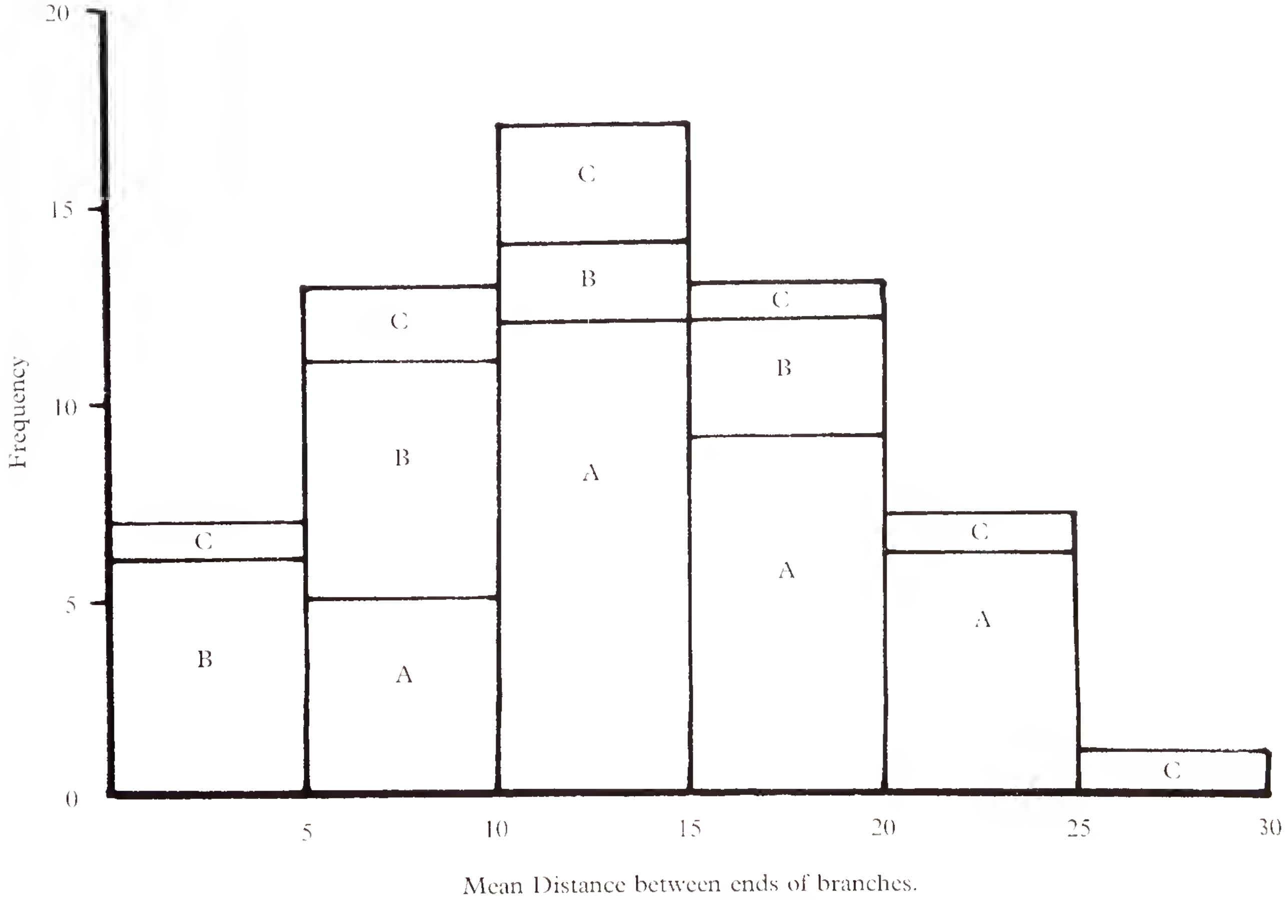
C
B
C
B
C
C
C
C
Maximum dimension, branch end.


Frequency
0
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20
5
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15
20
25
30
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A
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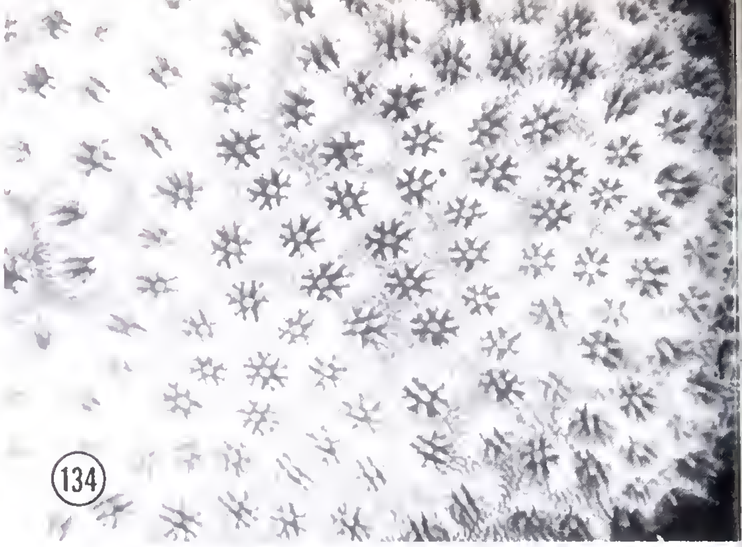
B
C
A
C
C
Mean Distance between ends of branches.


133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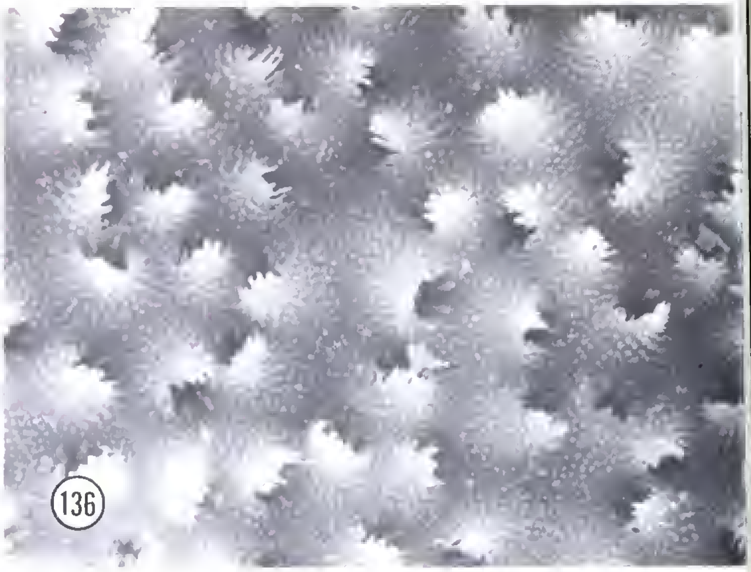
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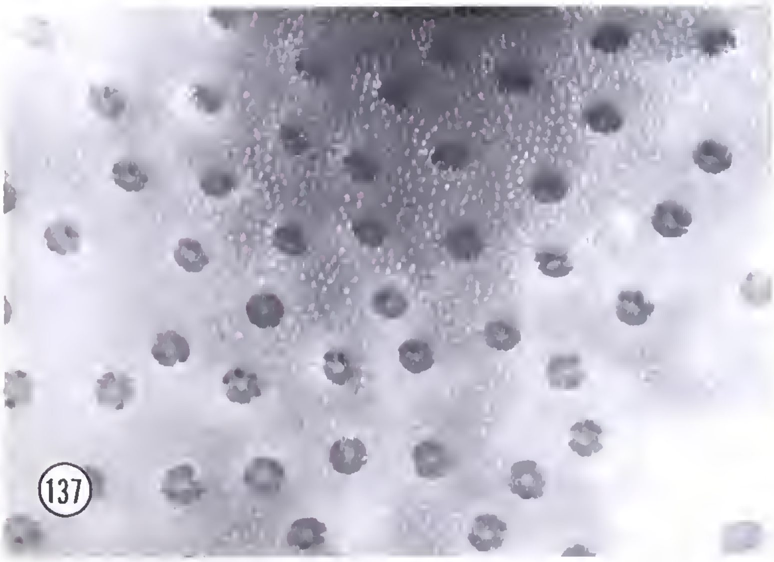
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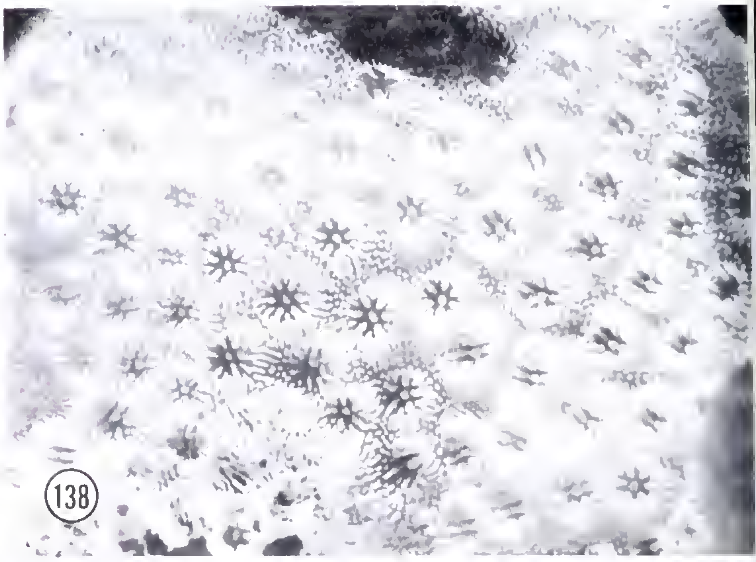
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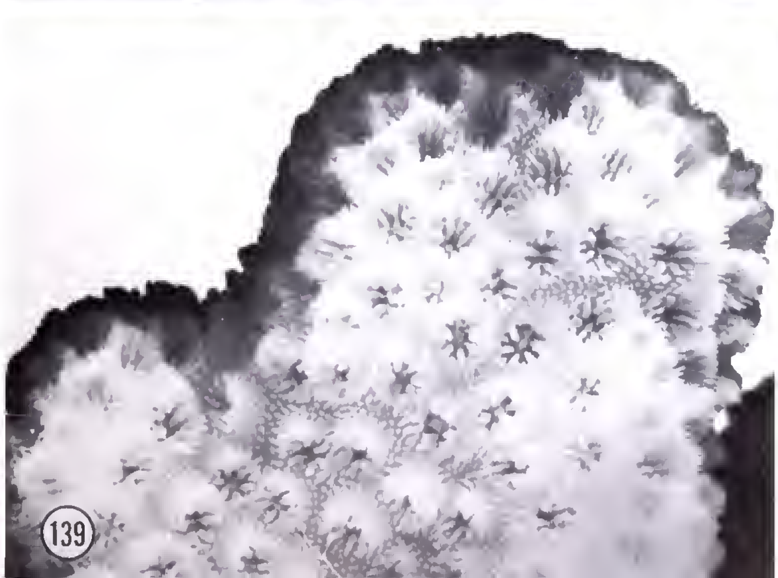
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140

Material studied

Murray Islands (6 specimens), barrier reef NE of **Murray Islands, Sue Island** (6 specimens), **North-west Reef** (3 specimens), **Thursday Island, Great Detached Reef** (20 specimens), **Tijou Reef** (17 specimens), **Bewick Island** (6 specimens), **Low Isles** (3 specimens), **Hope Island, Michaelmas Cay**[7] (2 specimens), **Holmes Reef**[7], **Palm Islands** (48 specimens), **Bowl Reef** (7 specimens), **Wheeler Reef** (6 specimens), **Keeper Reef, Gould Reef, Diamond Islet**[7], **North-west Islet**[7] (2 specimens), **Masthead Island**[7], **One Tree Island**[7] (5 specimens), **Solitary Islands** (3 specimens), **Lord Howe Island** (7 specimens), the *Stylophora septata* of Crossland (1952).

These localities include collecting stations 1, 2, 4, 5, 6, 8, 10, 14, 17, 18, 22, 27, 28, 29, 30, 34, 35, 36, 38, 41, 42, 43, 45, 46, 51, 54, 55, 57, 58 and 60.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918); **Low Isles**, Yonge (1930); Stephenson *et al.* (1931); Manton (1935); Yonge (1940); (as *S. pistillata* and *S. septata*), Crossland (1952); (as *S. pistillata* and *S. mordax*), Stephenson & Wells (1955); **North-west Islet**, Hedley (1927); **Heron Island**, Salter (1954); **Solitary Islands**, Veron *et al.* (1974); **Lord Howe Island,** Veron (1974); 8 localities south to **Heron Island,** Wells (1955a).

Characters

The long synonymy of this species is a reflection of the extent of its growth form variation. In this study, the two forms widely known as *S. pistillata* and *S. mordax* are synonymised to form this single, distinct, polymorphic species. The continuity of this series, which is readily observable underwater, is illustrated in Figs. 131 and 132, which show that both the mean distance between branch ends as well as the maximum dimension of branches have a uni-modal distribution, that these characters are not themselves correlated, but that the latter character is broadly associated with environmental variation.

The synonymy of *S. septata* with this species was established only after study of Gardiner's type specimen and the specimen referred to *S. septata* by Crossland (1952). The calicular characters on which *S. septata* is based were found to occur in restricted areas of several colonies which also exhibited a full range of 'normal' *S. pistillata* calices (compare Figs. 139 with 134 and 138).

Calice structures (Figs. 133–138) vary greatly within most colonies but this variation is remarkably uniform throughout the full range of growth forms. Calices on branch ends are deep, 1–1.5mm in diameter, are thin-walled and have 6 thin, smooth septa which extend horizontally to join the fine pinnacle-like columella (Fig. 133). They are surrounded by a delicately ornamented coenenchyme bearing compact rows of tall, fine spinules. Calices extending down the sides of branches are of similar diameter but become increasingly shallow and have increasingly thickened internal structures.

Figs. 133–140 *Stylophora pistillata* (× 6.0).

Fig. 133 A branch tip showing calices typical of most coralla.
Fig. 134 A branch tip showing extreme *S. septata*-like development of the columella and second cycle of septa.
Fig. 135 A branch side showing calices typical of most coralla.
Fig. 136 Showing the appearances of calices sometimes found on horizontal branches.
Fig. 137 The base of a corallum showing typical calices.
Fig. 138 A branch base showing extreme *S. septata*-like development.
Fig. 139 Holotype of *Stylophora septata* showing the calices of branch ends.
Fig. 140 Holotype of *Stylophora septata* showing the calices of the corallum base.

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[7] Localities from specimens held at the Australian Museum.

Thickened septa extend inwards usually 1/2–2/3 the calice radius, then drop vertically or near vertically to join the usually prominent, peg-like columella near the base (Fig. 135). A second, sometimes incomplete cycle of septa may be present (Fig. 138). Occasionally, two cycles of septa are equally developed. One or a pair of directive septa may be dominant to very dominant. The septa and columella are frequently covered with fine granules. Calices near the base of colonies may be very thickened and shallow, containing a boss-like columella and 6 broad radiating septal ridges (Fig. 137). The coenenchyme is irregularly covered with short spinules or granules.

Most calices have a delicately ornamental hood arching over their upper edge. In some colonies these hoods may be very prominent.

Growth form variation

This species is conveniently divided into two intergrading ecomorphs:

Stylophora pistillata from exposed biotopes (ecomorph *mordax*) (Figs. 141–143).

This form is characteristic of outer reef fronts (see Fig. 6). In general, the greater the exposure to wave action, the more massive and less ramose the colony.

Stylophora pistillata from semi-protected and well-protected biotopes (Figs. 144–150).

This arbitrarily distinguished ecomorph is very widespread and abundant. It occurs in almost all reef situations except in more exposed areas, where it grades into the '*mordax*' form. Growth form variation within partly exposed biotopes may be very wide, each colony apparently being a product of its own restricted microhabitat.

Colonies exposed to strong currents frequently have flattened prostrate branches (Figs. 149, 150). Calices on such branches are usually disarrayed with hoods pointing in different directions (Fig. 136).

Most colonies are a uniform pale brown with paler branch ends. Colonies exposed to full sunlight may be a pale or sometimes deep purple, pink or mauve, usually with whitish branch ends.

Distribution

Widely distributed throughout the Indo-Pacific.

Bathymetric range

0–40m (present study only).

GENUS *PALAUASTREA* YABE & SUGIYAMA, 1941

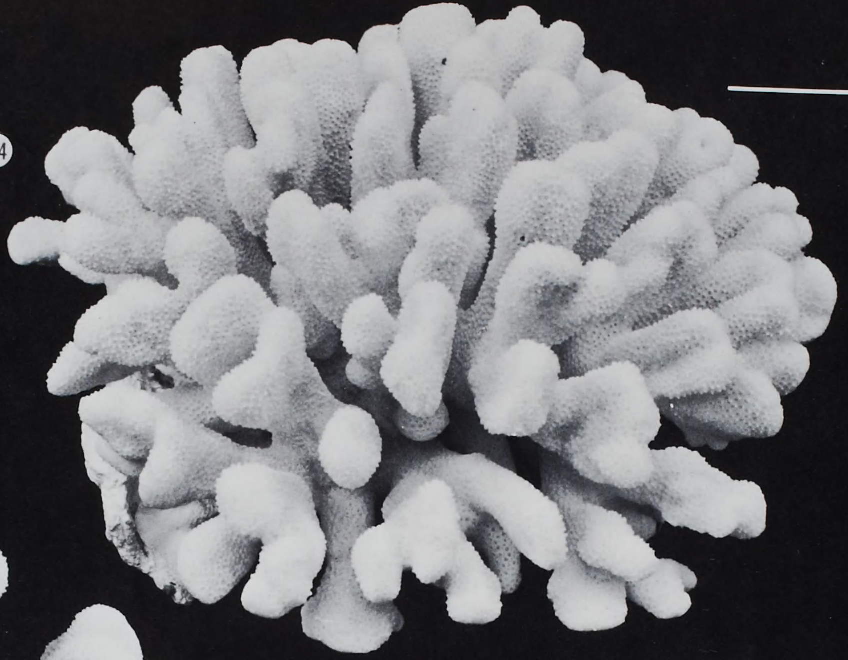
Type species *Palauastrea ramosa* Yabe & Sugiyama, 1941

Characters

The genus *Palauastrea* was established by Yabe & Sugiyama for a small series of specimens from Iwayama Bay (Koror, Palau). The authors placed the new genus in

Figs. 141–150 *stylophora pistillata* (× 0.5).

Fig. 141	From Great Detached Reef, collecting station 1.
Fig. 142	From Bowl Reef, collecting station 4.
Fig. 143	From Tijou Reef, collecting station 51.
Fig. 144	From Elk Cliff, Great Palm Island, collecting station 37.
Fig. 145	From Dewar Island, Murray Islands, collecting station 29.
Fig. 146	From Sue Island, collecting station 17.
Fig. 147	From North-West Reef, collecting station 14.
Fig. 148	From Thursday Island, collecting station 54.
Fig. 149	From Dewar Island, collecting station 29.
Fig. 150	From Tijou Reef, collecting station 8.



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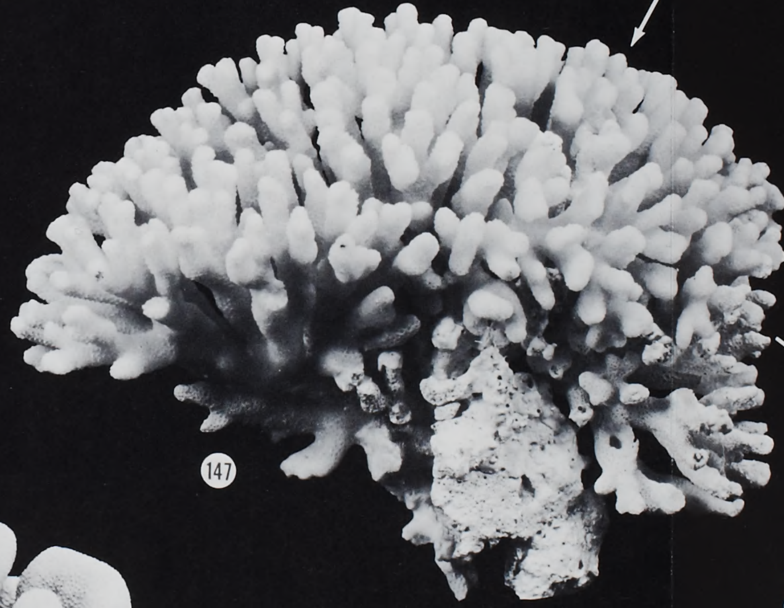

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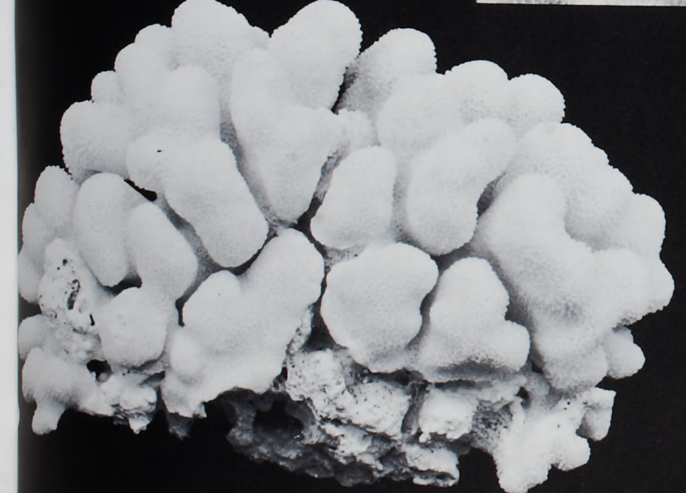

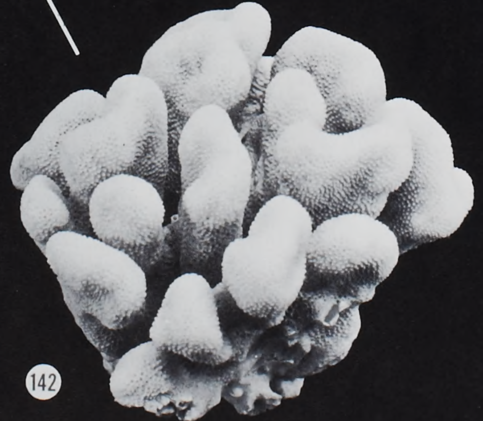

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the family Seriatoporidae Edwards & Haime, 1849 (= Pocilloporidae Gray, 1842), and although they did not fully discuss its relationships and affinities, they nevertheless mentioned some differences from *Stylophora* and *Madracis*. Subsequently, Wells (1956) considered *Palauastrea* as a synonym of *Stylophora*, but did not put forward any evidence to support this opinion.

The specimens from the Great Barrier Reef show a considerable degree of similarity to those of the type series in the following characters: colonies are branching and plocoid, the corallites are small, never hooded and have well developed septa in two cycles. The septal margin is beaded. The columella is styliform and well developed; the coenosteum is spinose and well developed. These characters are sufficiently distinctive to justify considering *Palauastrea* as a valid genus, which is revived here.

Palauastrea is certainly related to *Stylophora*, but differs in its growth form, absence of corallite hoods and septal arrangement and structure (first cycle being slightly exert, the septa granulated), the latter being more like that of *Stylocoeniella*. Except for the growth form and the lack of intercorallite pillars (or styliform protrusions from one of the primary septa), *Palauastrea* also comes close to *Stylocoeniella*. In particular, the only known species, *Palauastrea ramosa*, shares with *Stylocoeniella guentheri* a spinose coenosteum (a character which is basically typical of *Stylophora*). Although there is no well defined bounding ridge of granules at the margin of the calices of *Palauastrea*, as noted by Yabe & Sugiyama, there is a tendency for these granules (laterally compressed and flattened) to be in a circular row, at least in some specimens. This character is best developed in *Madracis*, where a fusion of the granules is observed. We therefore consider that this character of the calicinal margin is a feature relating the two genera rather than separating them.

Palauastrea ramosa Yabe & Sugiyama, 1941

Synonymy

Palauastrea ramosa Yabe & Sugiyama, 1941
Palauastrea ramosa iwayamaensis Yabe & Sugiyama, 1941

Material studied

Palm Islands (20 specimens), **Mourilyan Harbour**.
These localities include collecting stations 41, 45 and 59.

Previous records from Eastern Australia

Not previously recorded.

Characters

All the colonies examined have a distinctive growth form (Figs. 151–155): they are up to 30cm tall, ramose, with branches which taper towards their extremities, averaging 1–1.2cm in diameter. Terminal branches are rather short and blunt or have a rounded, knob-like extremity. In some colonies, the branches are anastomosed, a feature which is also frequently found in the genus *Seriatopora*.

Calices are superficial (Figs. 156, 157), the septa are in two unequal cycles; only the six thick septa of the first cycle reach the columella. Primary septa are sometimes recognisable, but are never greatly differentiated from other septa. The columella is well developed, styliform or pyramidal, with a broad base (half the diameter of the calice). It is sometimes neatly exert above the level of the coenenchyme and pointed at the top, very similar to that of *Madracis*. The antero-superior extremities of the septa of the first cycle are slightly exert above the calice margin. Septal margins slope gently to meet the columella, with one or sometimes two granular proliferations. The

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Fig. 155 *Palauastrea ramosa* from Eclipse Island, Palm Islands, collecting station 59 (× 1.0).

coenenchyme is solid and spinulose. Calices are about 1mm apart on average, but are more crowded on the tips of branches and on concave areas.

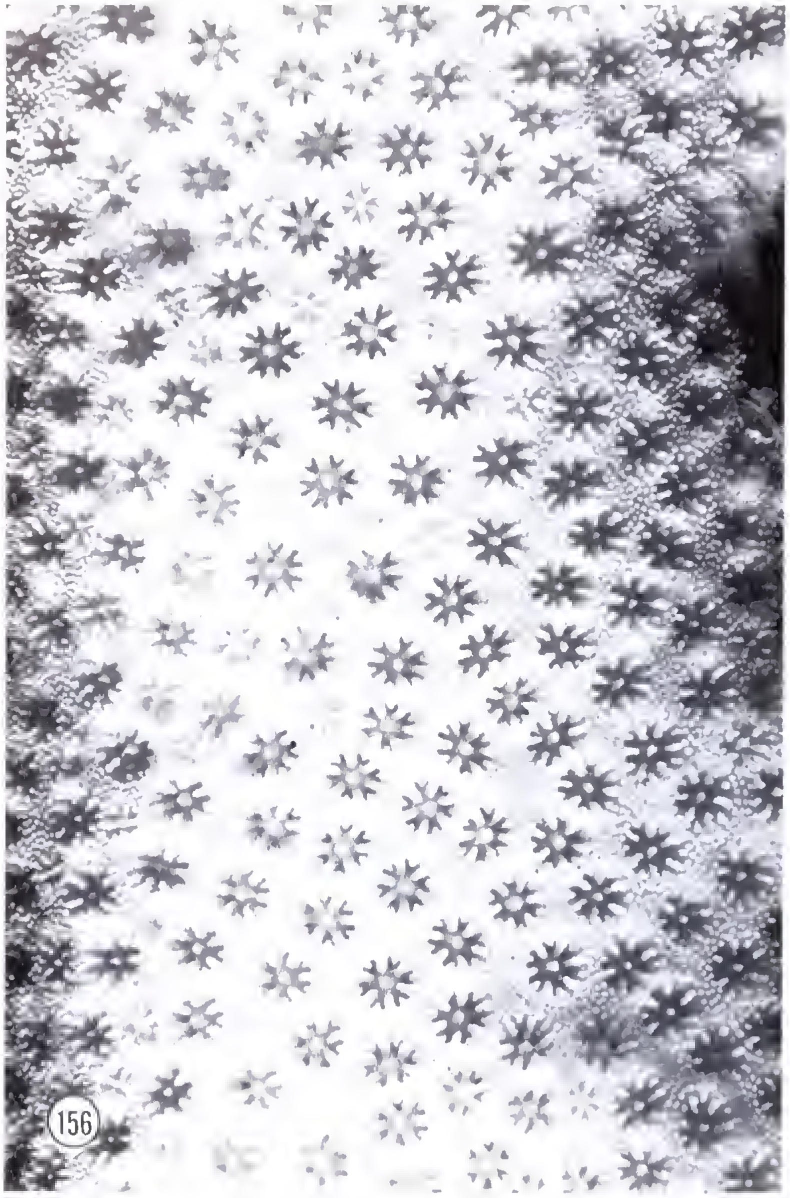
The coenenchyme is amber or light brown in colour with a touch of pink. The oral disc is pale yellow. There are twelve conical yellow to light brown-pink tentacles with brown extremities and one to three brown bands on the distal half when fully expanded (Fig. 158).

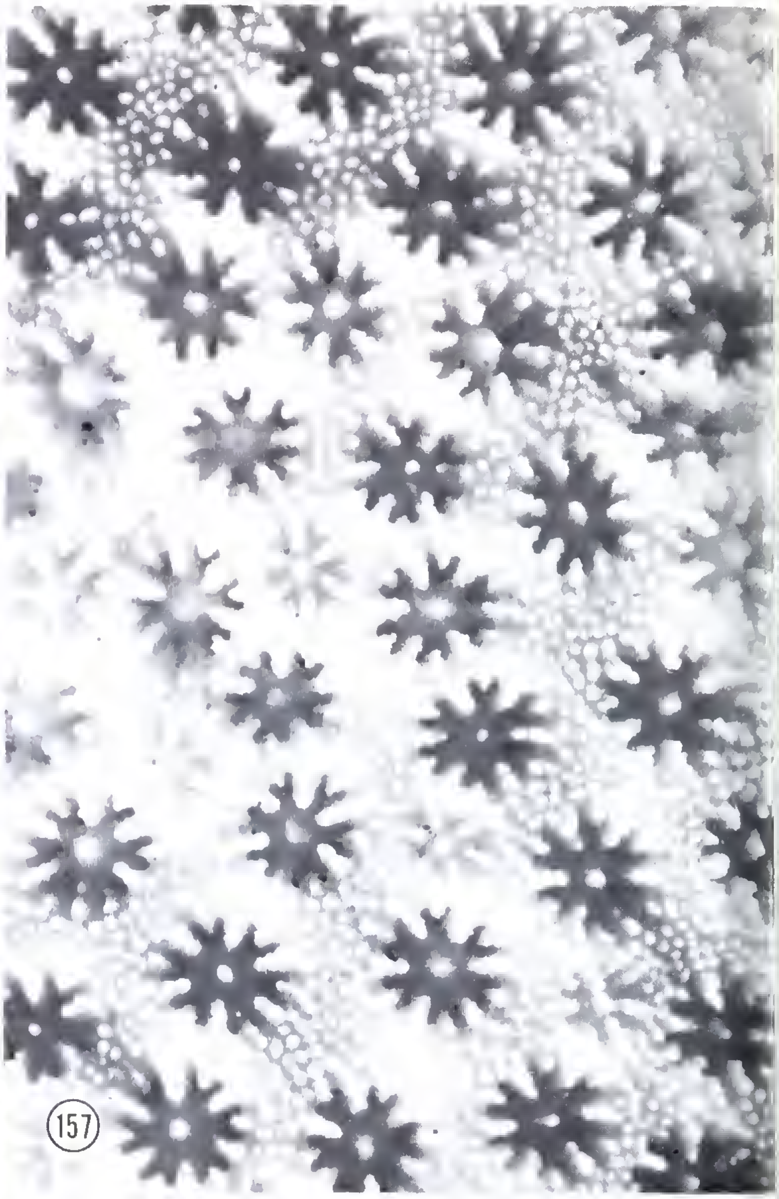
Variations

There is some degree of variation in the skeletal characters of the specimens which we collected, in particular in the degree of development of the secondary cycle of septa. Although it is almost always present, and generally distinctly marked, it may be inconspicuous in some specimens, particularly at the tops of branches. In that respect, it appears that the subspecies *iwayamaensis* described by Yabe & Sugiyama (with a well developed second cycle) is the more widespread, the type subspecies, *P. ramosa ramosa,* being exceptional (only one specimen collected in Palau). Since in our series the development of secondary septa varies continuously from very reduced to well developed, the creation of a subspecies on this basis does not seem justified, especially as the other characters noted by Yabe & Sugiyama (mode of branching, the shape of the branches and the size of the corallites) are also highly variable and are even more regulated by external factors than are calicular structures.

Figs. 151–154 *Palauastrea ramosa* (× 0.5).

Figs. 151, 152 From Eclipse Island, Palm Islands, collecting station 59.
Fig. 153 From Orpheus Island, Palm Islands, collecting station 45.
Fig. 154 From Barber Island, Palm Islands.





Figs. 156, 157 *Palauastrea ramosa*

Figs. 156, 157 Same corallum as Fig. 155 (× 10.0, × 20.0 respectively).

Occurrence

Palauastrea ramosa occurs in relatively shallow water on sheltered coral reef slopes, where mud or sandy mud deposits are abundant. Colonies are frequently unattached to a solid substratum (Fig. 154). In one locality (Barber Island, south of Great Palm Island), numerous colonies of *Palauastrea ramosa* have been observed (depth 8–12m) on a substrate of coral rubble coated with a thin layer of fine sediment.

All our specimens are infested with a burrowing bivalve *(?Lithophaga)* almost completely entrapped within the skeleton, except for a small aperture at the surface of the corallum. The type specimen (registered as no. 41996, according to Yabe & Sugiyama, and actually no. 64324) also harbours this commensal.

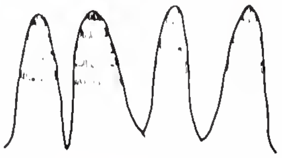


Fig. 158 Expanded tentacles of *Palauastrea ramosa.*

Distribution

Palau and the Great Barrier Reef.

Bathymetric range

1.5–10m.

GENUS *MADRACIS* EDWARDS & HAIME, 1849

Type species *Madracis asperula* Edwards & Haime, 1850

Generic Synonymy

Axhelia Edwards & Haime, 1849
? *Axohelia* Edwards & Haime, 1857
Reussia Michelotti, 1860
Pentalophora Saville-Kent, 1871

Characters

Colonies are ramose, encrusting or submassive, plocoid or plococerioid. Septa are in octameral or more frequently decameral arrangement. The septal margin is smooth. The columella is styliform and well developed.

Characters of the corallum (especially growth form and development of coenosteum) are variable, but the structure of the corallites, and in particular the non-hexameral disposition of the septa, remain conspicuous and typical of the genus.

Madracis is widely distributed throughout the Indo-Pacific but is nowhere abundant. It is seldom found on reefs.

Madracis kirbyi n.sp.

Material studied

Lizard Island, Barnard Island, Chicken Reef, Palm Islands (10 specimens), **West of Bowl Reef.**

These localities include collecting stations 34, 42 and 57.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are primarily explanate (Figs. 159, 161–163), laminar or encrusting, with low (up to 2cm high) knob-like expansions or nodular protuberances. One colony, 125 x 10cm, was encrusted on both sides of a piece of limestone including recently dead lamellibranchs. Another colony was subramose, with a basal stem 10–13mm in diameter and 6 principal terminal branchlets 10 to 25mm long, with rounded, inflated extremities (Fig. 160).

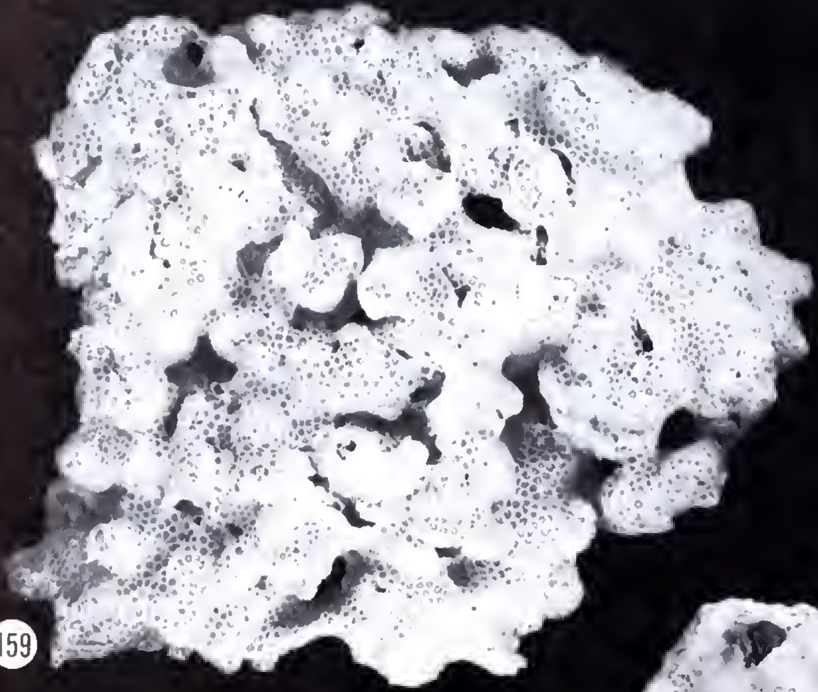
Colonies are plocoid or plococerioid. The calices are generally close to each other (0.5mm apart) and never more than 2mm apart.

Calices (Figs. 164, 165) average 2mm in diameter with a maximum diameter of 3mm. Each corallite is circumscribed by a polygonal ridge of spines or granules which are laterally compressed and flattened but are sometimes fused together into a thin lamina with a wavy upper margin (Fig. 164). These bounding ridges of granules are shared by adjacent corallites. Peritheca are almost invariably reduced, or absent. Where present, the peritheca is generally vesicular, with a few short granules or spines on its surface.

Septal arrangement is basically decameral. Smaller corallites, particularly in concave areas, only have eight septa. Larger corallites have 18–20 septa, all reaching the columella. Septa are narrow and laminar; one upper lobe is generally prominent, and in some corallites a lesser developed inner paliform lobe occurs close to the columella. Occasionally, a weakly developed, rarely complete, second cycle of septa is present. This may be reduced to a ridge of the wall or to a few projecting spines in the space between two primaries.

Fig. 159–163 *Madracis kirbyi* (× 0.5).

Fig. 159 From Barnard Island, paratype.
Fig. 160 From Chicken Reef, paratype.
Fig. 161 From Fantome Island, Palm Islands.
Figs. 162, 163 From Esk Island, Palm Islands, collecting station 42.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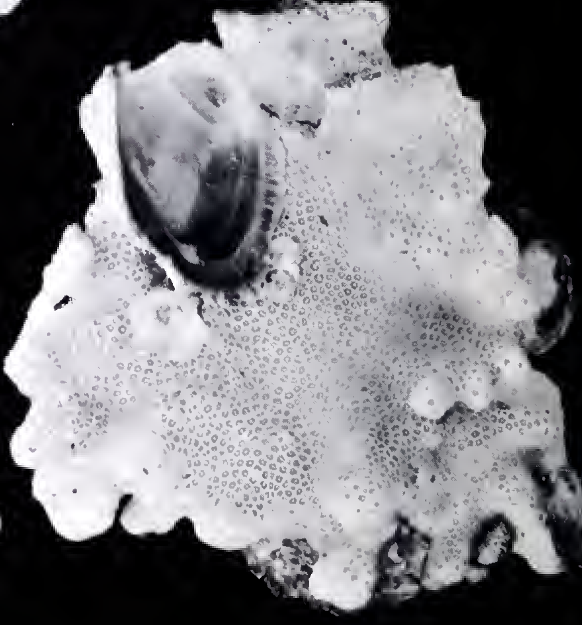
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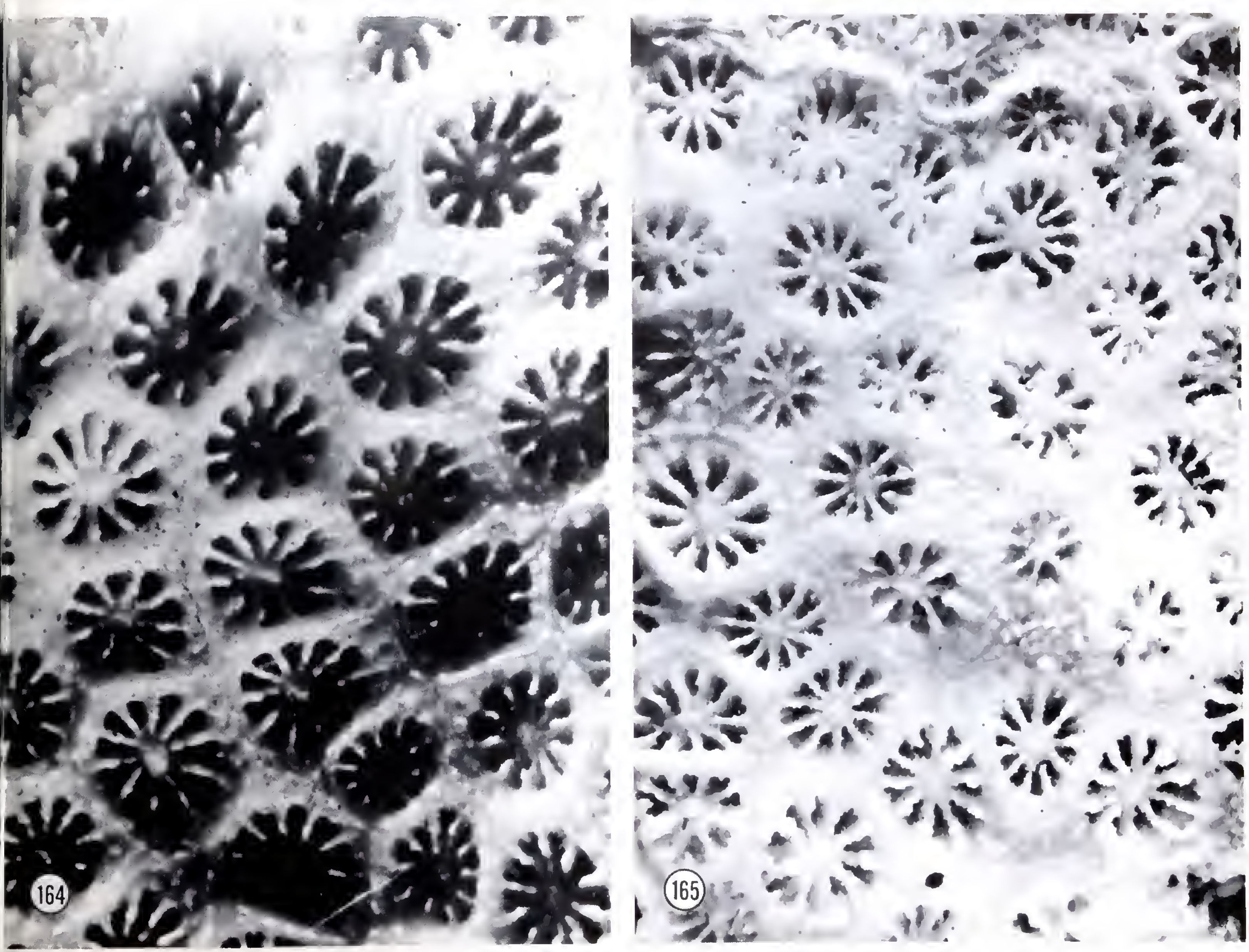
The columella is short and conical.

The oral disc of living specimens is bright green, the coenenchyme is brown, tending to pink in shaded areas. There are about twenty tentacles (Fig. 166) in two rows; these are conical in shape, thick at the base and yellow-brown in colour, terminating in a whitish knob-like expansion.

Figs. 164, 165 *Madracis kirbyi* (× 11.0).

Fig. 164 Calices of the specimen illustrated in Fig. 159, showing extreme reduction of the coenenchyme.
Fig. 165 Calices of the specimen illustrated in Fig. 161, showing spinose coenenchyme and traces of the second cycle of septa.



Variations

Although this small series of specimens is fairly homogeneous, some degree of variation is to be observed, even from one part of a colony to another, on the following characters: (1) thickness of the septa and shape of the septal margin, (2) thickness of the thecal structure, (3) development of the secondaries. In one specimen in particular, a weak secondary cycle is noticeable.

Fig. 166 Expanded tentacles of *Madracis kirbyi.*

Discussion

This genus badly needs revision on a world-wide scale, in the light of extensive and reliable ecological data. As it now appears, our series of specimens seems related to *Madracis pharensis* (Heller), originally described from the Mediterranean. By courtesy of Dr Zibrowius, we have examined a series of specimens of *M. pharensis* from various localities in the Mediterranean and the Atlantic. This comparison shows that our specimens have a much reduced second cycle compared with that of the Mediterranean specimens. This characteristic places our east Australian *Madracis* close to *Madracis decactis* (Lyman), although it should be noted that some specimens of *M. pharensis* from the Azores which we examined also sometimes have a reduced second cycle. Indeed, when considering the calicular structure, our specimens represent an intermediate between *M. pharensis* and *M. decactis* (the latter being hermatypic). Another species concerned here is *M. singularis* Rehberg from Fiji, which is considered by Gardiner (1939) as a synonym of *M. decactis.* It is difficult to draw conclusions from Rehberg's description and figure, which applies to only one specimen, but Gardiner's specimen is certainly different from *Madracis kirbyi.*

This new species is characterised by large-sized corallites, with a conspicuous polygonal outline, by the extreme reduction of the peritheca, giving a plococerioid condition, and by the extreme reduction of the second cycle of septa.

Etymology

Named after the James Cook University research vessel *James Kirby.*

Holotype

Figs. 162 and 163.

–*Dimensions* 12.5 × 10 × 5.5cm.

–*Locality* Palm Islands, SE side of Esk Island.

–*Depth* From sampling between 1 and 22m (J. Veron coll.).

–*Holotype* British Museum (Natural History).

Paratypes

Fig. 161. Fantome Island (Palm Islands), 20–24m.

West of Bowl Reef, 55m (Queensland Museum G8980).

Falcon Island (Palm Islands), 5–10m.

Fig. 159. Barnard Island, 6–12m.

Fig. 160. Chicken Reef, 12m.

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