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A STUDY OF THE TAXONOMY AND DISTRIBUTION OF HERMATYPIC
CORALS OF THE CHAGOS ARCHIPELAGO, INDIAN OCEAN

being a thesis submitted for the degree of Master of Science of
the University of Durham

by

Zena D. Dinesen B.Sc. (Sussex)

January 1976

All the field work for this study was carried out by members of the Joint Services Expeditions to Egmont in 1972 and to Danger Island and other Islands of the Chagos Bank in 1975. The identification of the Egmont coral collection was carried out by Dr B.R. Rosen of the British Museum (Natural History). Identification of the Chagos Bank collection and all analysis and discussion of the Egmont and Chagos Bank data are entirely my own work. This thesis has not been accepted for any degree, and is not being submitted concurrently in candidature for any other degree.

Fera D. Dinesen

"Full fathom five thy father lies,
Of his bones are coral made."

William Shakespeare : *The Tempest*

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ABSTRACT

This study is based on corals collected during the Joint Services Expedition to Egmont Atoll (in 1972) and to the western part of the Chagos Bank (in 1975). The corals were identified to generic level, and where appropriate to species and species groups. A systematic check-list is presented covering the material from both collections.

Much of the information from Egmont has been lost, especially regarding the locations where specimens were collected. It was hoped however to use the data from the Chagos Bank collection to classify the coral communities in terms of associations, according to the methodology of the Zürich-Montpellier School of Sociology (Braun-Blanquet, 1951). This was attempted with the aid of suitable computer analysis, but owing to the highly variable nature of the data, the approach had to be abandoned.

Nevertheless, some patterns may be observed in the distribution of the corals from Chagos Bank, principally in relation to depth. No definite zones can be delimited, but some of the genera and species are more conspicuous at certain depths. This is most obvious in the shallowest collections (3 - 6m) and the deeper areas (33 - 45m).

The major factors influencing local distribution patterns of hermatypic corals are discussed, and the Chagos Bank data are compared with similar studies in the Indo-Pacific.

At least 55 hermatypic genera have so far been recorded from the Chagos Archipelago. There is a high diversity of coral genera in the western Indian Ocean, which may or may not be continuous with the very rich Indonesian-west Pacific area. The records presented here suggest that the high diversity region in the Southern Maldives may extend south of the equator to include the Chagos reefs.

Few quantitative studies have been carried out on reef corals, and most of the work has been confined to the accessible reef flat, while deeper areas of the reef front have been neglected. Furthermore, sampling methods and the kind of information recorded have varied greatly. It is recommended that a standard sampling procedure is laid down, so that data collected in the course of future studies may be meaningfully compared.

ACKNOWLEDGEMENTS

I am indebted to all members of the Joint Services Expeditions to Egmont and the Chagos Bank who worked so hard to collect the coral specimens. Many thanks are due also to Dr B.R. Rosen for identifying the Egmont Collection, and for his advice on taxonomic problems; to Dr B.D. Wheeler, Mr Diz Diaz and members of the Computer Unit for their advice on computer analysis; and to Mrs R.L. Reed for typing this thesis so rapidly and efficiently. Finally, I should like to thank my supervisor Dr D.J. Bellamy for his guidance and encouragement throughout this study.

NOMENCLATURE

Classification of coral genera is according to Wells (1956).

Classification of species is as indicated in the check-list in Appendix A.

All other terms are defined where necessary in the text.

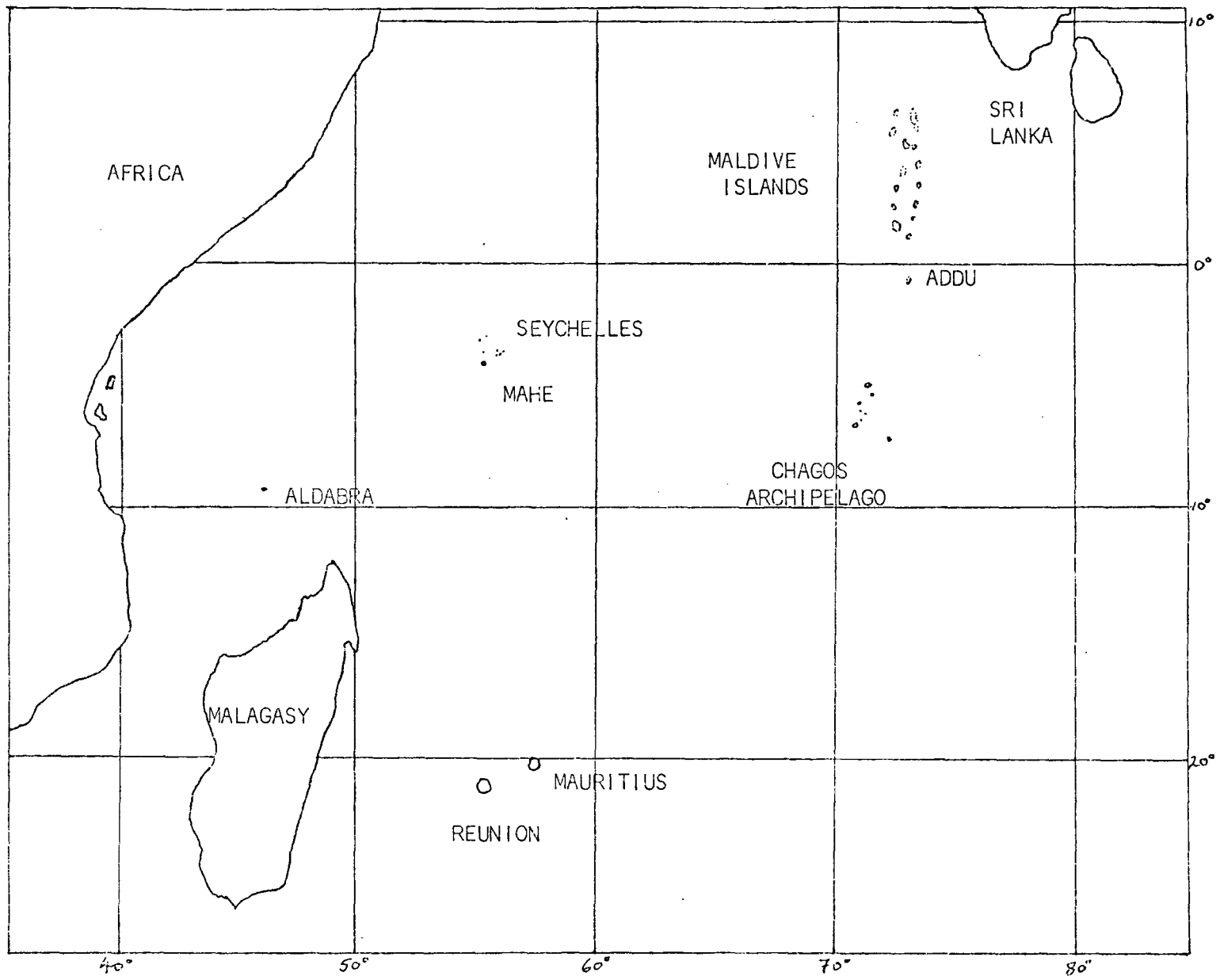


Figure 1 The western Indian Ocean showing the position of the Chagos Archipelago

central Indian Ridge apparently runs north-south, geological, magnetic and bathymetric studies indicate that this region is in fact composed of *en echelon* northwest-southeast spreading centres and northeast-southwest fracture zones.

Just to the east of the central part of the Mid-Ocean Ridge lies the Chagos-Laccadive Ridge; this ridge and the southern part of the Mascarene Plateau are linear volcanic features. Studies on the evolution of the floor of the Indian Ocean suggest that during the Mid-Oligocene the Chagos-Laccadive Ridge was part of the Mascarene Ridge and formed a chain of volcanic islands parallel to the Ninetyeast Ridge.

The climate in the Chagos Archipelago is governed mostly by a zone of equatorial westerly winds which migrate north and south across the region, separating the NE and SE Trades. Where the westerlies and the Trades converge there are shear zones with unsettled and squally weather. During December to March the winds are variable but mostly westerly. Then the westerlies weaken, and throughout June to September the SE Trade winds are dominant. In October and November the winds are again variable but still blow mostly from the south and east. Cyclones are rare in such low latitudes, but calm periods are only occasional and seldom occur during the Trades.

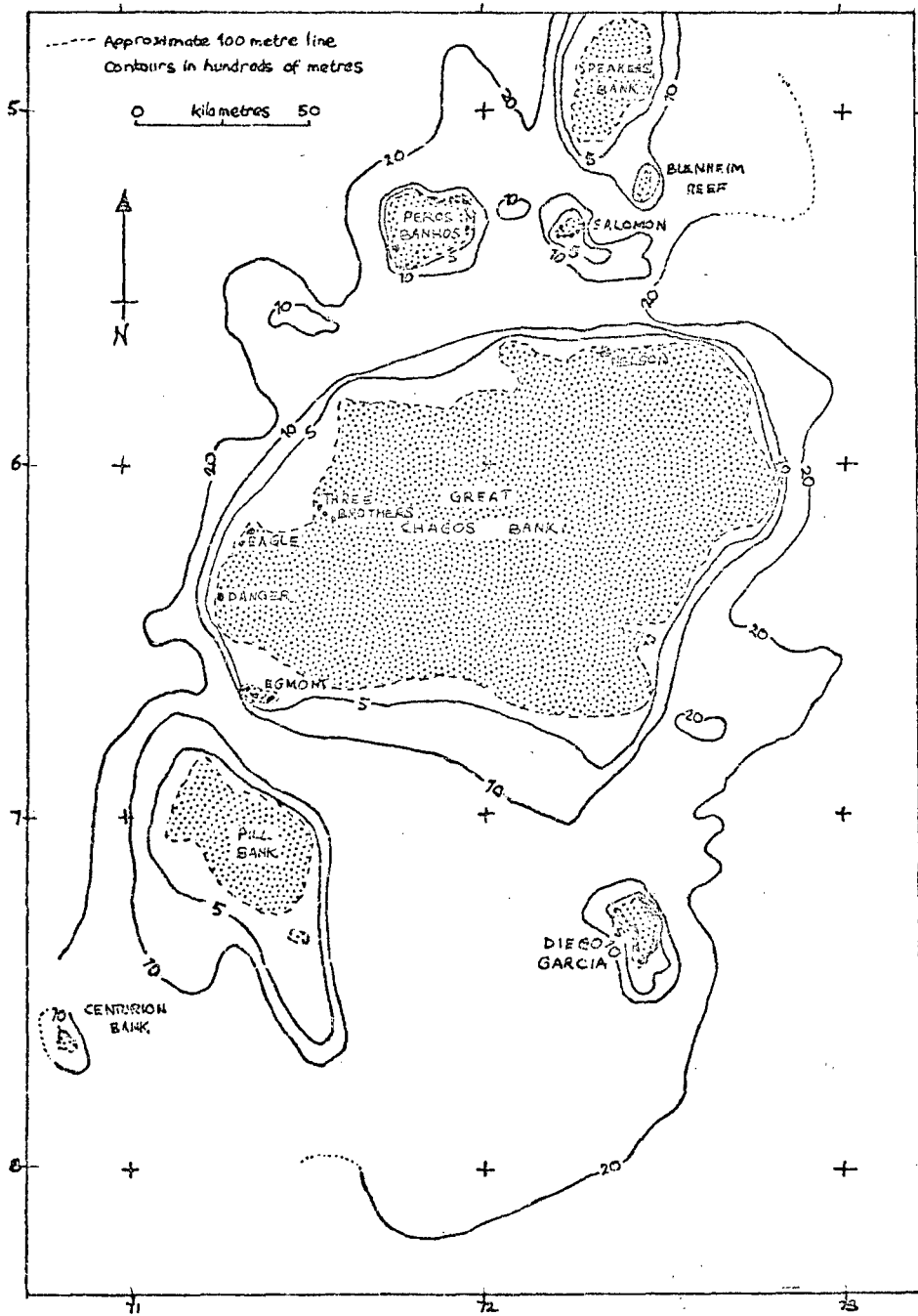
The temperature follows the wind pattern and is lowest during the Trade months. The diurnal variation is less than 10°C , and records (from Diego Garcia) show a mean maximum temperature of over 30° in March, and a mean minimum of almost 24°C in August. The Chagos Islands are the wettest in the Indian Ocean, with an annual mean rainfall of over 3000mm.

The rainfall seems to vary from year to year, and is highest in the north of the archipelago, the annual figure for Peros Banhos being 3999mm. Further south at Diego Garcia and north at Addu Atoll, the annual mean drops by some 500mm.

The tides are semi-diurnal and somewhat greater in amplitude than at the southern Maldives. Records from Diego Garcia show a maximum range at springs of 1.6m and a minimum at neaps of 0.7m.

The Chagos Bank measures some 120km across and 80km north to south. About 17,000 years ago it may have had a dry land area of about 13,500 sq km, and there were presumably other large land areas in the outlying Speakers and Pill Banks. The present structure suggests that it is now a drowned atoll, and the only remaining land areas are a few islands along the western rim and one in the north (Figure 2). The largest of the islands is Eagle (244 hectares), with the much smaller Sea Cow 2km to the south; and some 25km south of Eagle lies Danger Island (66 hectares). The Three Brothers and Resurgent lie along a NW-SE axis 8km long, and together constitute a land area of over 37 hectares. On the northern rim of the Chagos Bank lies Nelson or Legonne Island, with an area of 81 hectares.

The greatest land areas are now concentrated in the outlying atolls (Figure 2). Egmont is a small atoll with its axis inclined WNW to ESE, with seven islands scattered around the shallow lagoon to form an oval 9km by 3km. In the west are Rat Island, Lubine and Cipaye (or Sipaille) with an adjacent islet. In the south lie Tatamaka, Carapate and South-East Islands. North of the Bank is the large, almost rectangular Peros Banhos Atoll with some 30 islets (land area 1150 hectares). East of this



Figures 2 a (and 2 b overleaf)

The Chagos Archipelago

1600

2082

2062
crl.m

1972
crl.m. gl. oz

1380
gl. oz

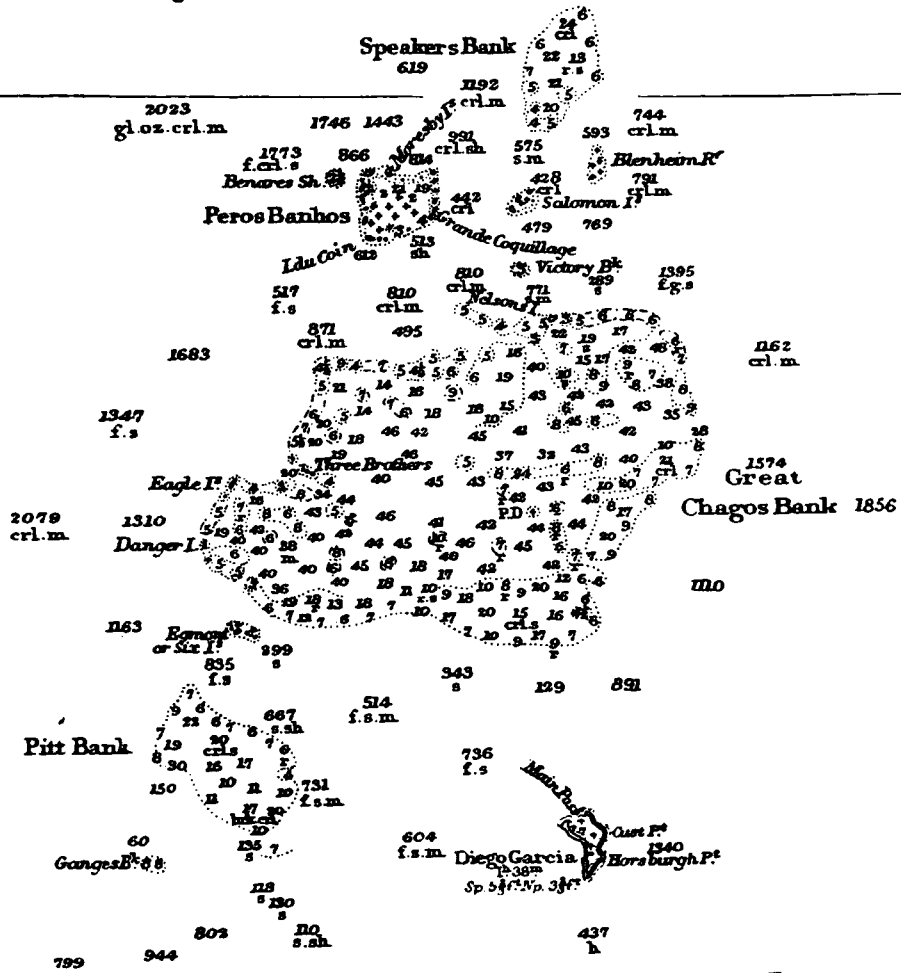


Figure 2b

Iles Salomon, a smaller atoll with eleven islands and a land area of 500 hectares. Some distance to the south of the Bank is Diego Garcia with four islands, the largest one being U-shaped and constituting one of the most continuous land rims found anywhere on an atoll. The total land area is about 3000 hectares, more than one-sixth of the total atoll area.

The Chagos Islands were probably discovered and first named by the Portuguese at the end of the fifteenth century. Although the islands appear in sixteenth century charts, their positions were not well plotted even at the end of the following century. None of the islands was settled until the latter part of the eighteenth century.

The economic importance of Chagos has always been in the coconut trade. Egmont and Eagle were both inhabited by the mid 1800s, and there seem to have been brief settlements on most of the other islands of the Chagos Bank, except Resurgent and possibly Nelson. But the settlements on Egmont were not well managed and the society there seems to have fallen into decay. By the 1930s the inhabitants of both Egmont and Eagle Island were evacuated to Peros Banhos. All the islands in Egmont and the Chagos Bank are now uninhabited. The atolls of Salomon, Peros Banhos and Diego Garcia are however still populated, and they export considerable amounts of copra and coconut oil. They have also been used for other purposes, for example, Diego Garcia was once a coaling station, and was of some importance as a naval base during the world wars.

During the Joint Services expedition to the Chagos Bank in 1975 all the Chagos Bank islands were visited and some surveys of the vegetation were carried out. There are still many coconut palms on the islands,

especially Eagle and Sea Cow, and domestic plants such as paw paw are in evidence. (Resurgent is the only island unaffected by human activity). But it seems that the broad-leaved forests are recovering well, in many cases actively spreading into the coconut areas. Similar observations were made during the earlier expedition to Egmont: the vegetation was found to be chiefly coconut, but there are some broad-leaved areas which are spreading.

All the Egmont Islands are rat-infested, likewise Eagle Island; but the other islands of the Chagos Bank support many thousands of nesting birds, estimated at well over 100,000 breeding pairs. About 15 species of seabirds are represented, including various species of Shearwaters, Boobies, Herons, Frigate Birds and Terns.

During the island surveys other interesting features were recorded. For example, on Eagle there are four barachois systems which are senescent in that they are no longer normally flooded by the sea. Profiles from the barachois were carried out, and the sub-fossil pollen should produce a record of the vegetation prior to the period of coconut farming.

Resurgent Island was marked on Moresby's chart of 1837 as being a shoal drying at low tide. But there is a small piece of land rising to well over 2m above the extreme high water mark. North Brother and Sea Cow also have areas well above the high water mark, and around the former there are pinnacles of coral rock rising well beyond the level of extreme high water. Such features suggest that these three islands may be raised reefs.

The major scientific expeditions to the archipelago include the visit by G.C. Bourne in 1885-1886, the Deutsche Tiefsee-Expedition in the *Valdivia* in 1899, the Percy Sladen Trust Expedition in 1905, and the expedition in H.M.S. *Vidal* in 1967.

General references for Chapter One

Geology and climate Stoddart (1971a; 1971b; 1973); Laughton *et al* (1973).

Geography and Island surveys Bellamy *et al* (1976); Bourne (1971).

History Scott (1961); Bourne (1971); Stoddart (1971c).

CHAPTER TWO

CORAL SAMPLING AT EGMONT AND THE CHAGOS BANK; LABORATORY
WORK AND PRELIMINARY ANALYSIS OF DATASECTION I Coral Sampling at Egmont Atoll

The majority of the corals collected at Egmont were taken from the seaward sides of the atoll. The locations of the major transects are marked in Figure 3a. All underwater work was carried out by divers using SCUBA and the samples from each collection were placed in separate bags.

The most detailed collections were made at the sheltered northwest area of the atoll where there was the greatest living coral cover. Here the Main Transect was laid down, and samples were taken from the reef flat and at depths from 1m to 46m. A total of fifty 2m x 2m quadrats were used, and for each quadrat a specimen of every different coral present was removed. Many random collections (i.e. not from the quadrats) were carried out at various depths in the vicinity of the Main Transect. The purpose of these random collections was to find specimens apparently not represented in the quadrats at that depth, in order to supplement the main collection.

For the Anti-Transect (opposite the Main Transect at the exposed southwestern end of Egmont) several quadrats were sampled at each of five depth intervals from about 8m to 38m.

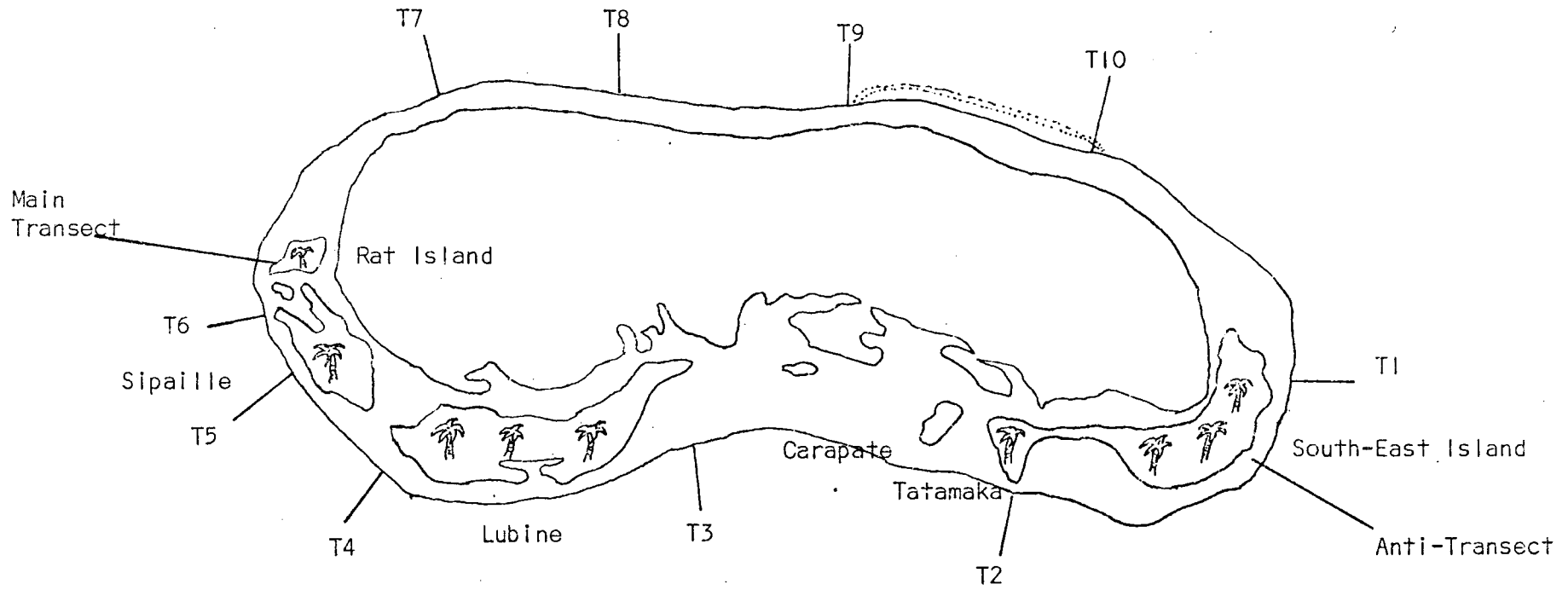


Figure 3a Egmont Atoll showing positions of major transects



Figure 3b. Eumont. Abo4.

In addition, Transects 1 to 10 were set down at intervals around the atoll. For each of these ten transects, divers recorded the major coral growth forms at distances of 10m apart, beginning at a depth of 3m or 6m, usually down as far as 45m. In all cases random collections of corals were made below a depth of 24m to a maximum depth of about 45m. For five of these transects collections were also made on the reef flat, and for Transect 6 also above 9m. Subsequently five further transects were positioned between the transects described above. Specimens (quadrat and random) were collected at a series of depths, usually from 8m down to 38m or 45m. Transect 9.5 (between Transects 9 and 10) was sampled both inside and outside the false ridge (see Figures 3a and 3b).

Finally, there were about ten random collections made in the lagoon at various depths. Random samples were also collected from seven coral banks, and from seven coral heads between 3m and 8m, all in the lagoon.

All specimens were brought back to the expedition camp on South-East Island. A preliminary identification was given and specimens were labelled individually with name and location, this information being recorded in the field log-book. Corals were then laid out to dry, and most of them were packed in boxes just prior to departure for transportation to Durham.

In December, 1974 Dr. B. Rosen of the British Museum (Natural History) kindly examined the collection, and specimens were sorted into genera and species or species groups, as appropriate in the time available. A systematic check-list of the genera

and species is presented in Appendix A, along with the records from the more recent Chagos Bank collection.

On examination of the collection with reference to the field records it appeared that a good number of the specimens must have been lost in transit, including many of those from the valuable Main Transect. Furthermore, many of the labels on the specimens had either come adrift or rotted so that they were illegible. It was hoped that such problems might be overcome to some extent by relying on the data recorded in the field. To check the reliability of the field records, the collection was examined for specimens still bearing labels with the original field identifications. A list was drawn up to compare the field and laboratory identifications. Unfortunately, this revealed that the earlier identifications were often inconsistent, and the names given might apply to a number of different coral types, sometimes to several genera.

As many of the field records could not be relied upon, the remaining possibility was to use information from labels still attached to specimens. Regrettably, it appeared that the only reasonably complete information was for the deeper collections on Transects 2 to 10; plus the growth form profiles for these transects.

Lists of specimens collected from Transects 2 to 10 below 24m, plus the collection above 9m on Transect 6, are given in Appendix B. (The reef flat data for these transects were insufficient in all cases.) There is not a great deal to be learned from these data, but it would appear that even below 24m there is a fairly high diversity of corals, for in these collections alone at least thirty genera are represented. A fuller discussion of coral distribution in relation to depth is given

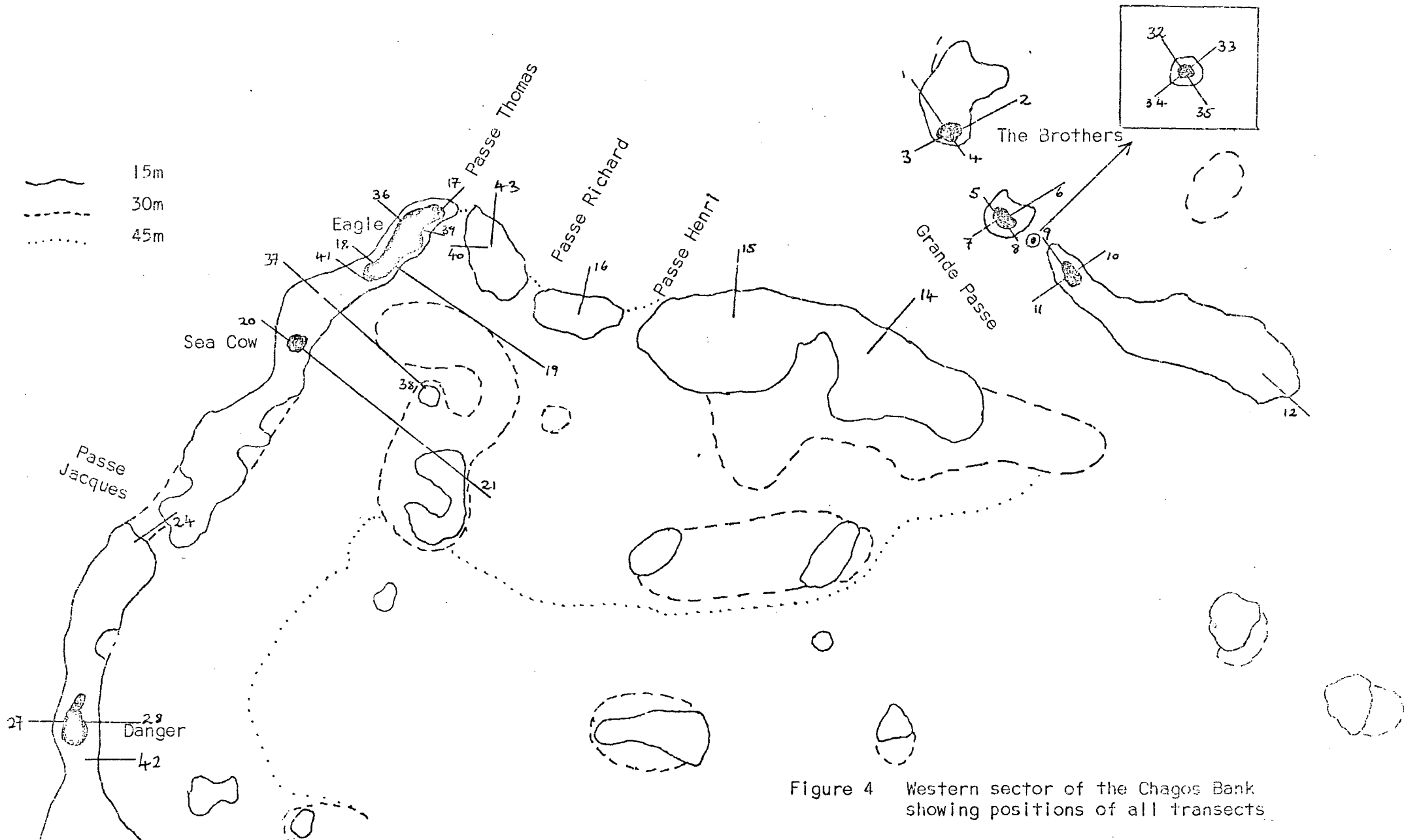
In Chapter 3, with particular reference to the Chagos Bank data. Some of the profiles of the coral growth forms recorded for Transects 1 to 10 are presented in Figure 6, and these are also discussed in Chapter 3.

It is unfortunate that there is very little useful information available for the Main Transect, for this detailed survey of the richest part of the Egmont reefs might have yielded some interesting results. The loss of data limited the scope of ecological and statistical work which could be carried out by the author.

SECTION 11 Coral Sampling on the Great Chagos Bank

Most of the sampling on the Chagos Bank was carried out on the western side of the Bank on the reefs surrounding the extant islands. Darwin (1842) remarked on the scarcity of living coral on the Great Chagos Bank; and Gardiner (1936) states that "the coral society is not generally either luxuriant or extensive." Observations made during the 1975 expedition suggest that the majority of the Bank is not actively growing at present. But it seems that both seaward and lagoon reefs along the western sector of the Bank between Danger and the Three Brothers (and perhaps further north towards Nelson) have a good coverage of living coral, and could be said to be actively growing (Bellamy *et al*, 1976). The richest coral growth was in the more sheltered areas, as was found at Egmont and at Aldabra (Barnes *et al*, 1971).

Transects were laid down on the seaward and lagoon areas of the western side, on the reefs surrounding the extant islands. The positions of the transects are marked on the map in Figure 4. The survey methods



were similar to those used for the Egmont Main Transect. Collections were made from 2m x 2m quadrats by SCUBA divers, and samples were placed in bags (separate for each collection). Generally a random collection was made near each quadrat, at about the same depth, to collect corals which did not seem to be present in the corresponding quadrat collection. A photograph was taken of every quadrat before removal of any specimens.

In total, 36 transects were surveyed, using 317 quadrat and random collections. The number of quadrats sampled for each transect varied from two to eight, but samples were generally taken from four or five depth intervals. The depths at which sampling was carried out varied, but collecting usually began at 3 or 6m, generally down to over 30m, and frequently as deep as 45m. Divers also made notes on the percentage cover of coral growth forms at various depths along the transects, and these records were photographed when the divers returned to the shore.

In addition, two further sets of specimens were collected, using different survey methods. For the "minimal area" experiment, corals were collected from a depth of 12m off Middle Brother using 7 quadrats, each quadrat being twice the size of the previous one. For the "trammel lines", specimens were collected along 10m line transects at intervals from 9m down to 45m. Finally, there was a collection of "pristine" corals, very fine specimens representing 35 genera (but with no location data).

All specimens were brought back to the expedition camp where they were identified and the information recorded in the field data book. The samples were then laid out to dry, the collections generally being kept

separate. Later, each collection was placed in a separate plastic bag, with a label stating depth and transect number in a separately sealed compartment at the top of each bag. The bags were then stored in crates and transported to Durham.

When the corals arrived in Durham, the specimens were unpacked, each one was washed in running water, and all the "pristine" collection and some problem specimens were soaked in bleach to clean them further. Every specimen was labelled individually according to location and depth. The specimens were then identified (by the author) to genera and species or species groups, as Dr Rosen had done for the Egmont collection, using the following texts :

Wells (1956, 1966); Vaughan and Wells (1943); Pichon (1971);
and with reference to the Egmont collection.

The identification was mostly to generic level only, partly because of the large number of specimens which had to be identified within a few weeks, also because the author's somewhat limited knowledge of coral systematics did not usually go beyond an identification to generic level.

A systematic check-list of the corals so far identified is given in Appendix A, with notes on the identifications and approximate numbers of each genus/species. In all, about 3930 specimens were received in Durham, though this number may be slightly exaggerated because of breakage of fragile specimens such as Pectiniids and delicate *Acropora* specimens. Of this total, over 3850 were Scleractinian corals (the remainder being *Tubipora musica*, *Heliopora coerulea* and hydrozoans). Table I indicates the approximate numbers of corals in the various sub-orders, and their percentage contribution to the total Scleractinian collection.

TABLE 1 PROPORTIONS OF SCLERACTINIAN SUB-ORDERS IN THE CHAGOS

BANK COLLECTION		
Sub-order	Number of specimens	Approximate percentage of Scleractinian collection
ASTROCOENIINA	> 960	25%
FUNGIINA	> 1180	30%
FAVIINA	> 1570	40%
CARYOPHYLLIINA + DENDROPHYLLIINA	> 130	5%

Lists were compiled to show which genera or species/species groups had occurred in the quadrat and random collections along the various transects. The author's lists were then compared with the information initially recorded during the expedition.

In the end, about two-thirds of the data collected were used for further analysis. Table 2 indicates the numbers of transects sampled and collections made in various areas, as compared with the number of quadrat and random collections which could be included in discussion of the data. It turns out that the greatest loss of information is from transects carried out around the Brothers where half of the data have been abandoned. However, all 36 transects have been represented in the collections further considered.

TABLE 2 **NUMBER OF COLLECTIONS MADE IN VARIOUS AREAS ON WESTERN CHAGOS BANK, COMPARED WITH**
AMOUNT OF DATA WHICH COULD BE USED FOR FURTHER ANALYSIS

	Around the Brothers	Grande Passe	Lagoon (Eastern side)	Seaward (Western side)	Passe Jacques	Diego Garcia	Total
Number of transects sampled	16	5	7	6	1	1	36
Number of quadrat and random collections	110	39	74	85	7	2	317
Number of transects used for further analysis	16	5	7	6	1	1	36
Number of collections used for further analysis	55	36	60	63	6	2	222

The loss of one-third of the data was mostly caused by inadequate labelling of the specimens.

SECTION IIIPreliminary analysis of data

In some of the more recent reef studies, attempts have been made to classify coral communities using the methods and concepts of plant sociology. This kind of approach has been adopted in more general terms by Barnes *et al* (1971) and Rosen (1971a) for defining coral zones and assemblages. Jaubert and Vasseur (1974) and Vasseur (1974) have used such methods in the study of various communities in the reef environment, and Scheer has rigorously followed phytosociological procedure for describing coral associations (e.g. Scheer, 1971, 1974; Mergner and Scheer, 1974).

It was hoped that a similar procedure might be adopted in the analysis of the Chagos Bank coral data though these are strictly in terms of the presence or absence of coral types. At Durham University a considerable amount of research has been carried out on plant communities, following the Zürich-Montpellier method (Braun-Blanquet, 1951) with the aid of computer analysis. In particular, Dr Wheeler has used available computer programs in conjunction with ancillary programs which he wrote himself. The Chagos data were computed using some of these programs, and for more details the reader should refer to Dr Wheeler's Ph.D. thesis.

Program SHUFFLE (devised by Wheeler) allows a rapid and error-free means of re-ordering and re-writing the species-sample matrix. This program can also be used to express in tabular form the results of numerical classifications. Various programs for numerical clustering strategies are available in the CLUSTAN 1A package (see Wishart, 1969). Wheeler has linked these with programs of his own to form a continuous system for numerical analysis which can be used to generate dendrograms and species-sample tables according to the classification produced.

Wheeler investigated the many clustering techniques available and compared the results with data sorted according to the traditional Braun-Blanquet table method. He concluded that Information Analysis and Ward's Analysis (see Ward, 1963) are the most satisfactory of the available procedures for the purposes of clustering phytosociological data. Therefore Ward's method was adopted for analysis of the Chagos Bank data. The system is arranged so that normal and inverse Ward's analysis of the same data set can be performed sequentially, so that in the final table outputted both species and samples have been clustered.

The Ward's analysis of the coral data produced a most disappointing final SHUFFLE table, with almost no clustering of the *aufnahmen* (samples) or the genera/species. Dr Wheeler pointed out that computer analysis of highly variable data (such as those from Chagos) would be unlikely to yield very good results. In the end, the attempt to order the data according to the Braun-Blanquet hierarchical classification system had to be abandoned. Scheer (1974) admits that "it is difficult to fix characteristic species and to classify coral communities in associations", but if sufficient data are available, phytosociological methods could be extremely useful for describing and comparing different coral communities.

Most of the subsequent computer analysis was restricted to manual rearrangement of the species/sample table using program SHUFFLE. (In addition, using further programs from the CLUSTAN package, species similarity coefficients were calculated, testing in pairs all the most common genera and species. Preliminary observation suggested that certain coral types tended to occur together, e.g. *Leptoseris* and *Pachyseris*; *Pavona clavus* group and *P. varians* group. For reference, a list of the genera or species with similarity coefficients for the ten nearest neighbours is presented in Table 8, Appendix B.

In manually rearranging the genera/species-sample table, an attempt was made to sort the coral types and *aufnahmen* into groups, though obviously these could only be poorly defined. An attempt was made to arrange the data according to exposure levels, but this was not found to be very fruitful, probably because most of the sites suffer a similar degree of exposure (see Chapter 3). In fact, the fauna seem to be evenly distributed among the different locations sampled, in that all the common genera were found on most of the transects. There are a few exceptions, for example, *Leptoseris* and *Pachyseris* were rarely found on lagoon-facing reefs, but this is probably because they are more frequent in deeper water, and not many deep collections were made on the lagoon side. The same can be said for *Dendrophyllia* which, if found in lagoon collections, occurred mostly in the vicinity of Passe Thomas, where a strong current flows through. (*Dendrophyllia* has often been observed in shallower water in channels; this is attributed to the effects of current and light attenuation.) It was found that the only clear patterns in the distribution of the corals were in relation to depth. If the samples are arranged in increasing order of depth, certain of the genera can be grouped together as being more typical of certain depths. Occasionally, a sample from, for example, 12m might be better grouped with those from 18m, but since the most obvious distribution patterns are according to depth, it was thought best to keep the samples arranged in approximate depth order. The results are given in Table 5 and discussed in conjunction with other studies in the following chapter. (Please note that Table 9 in Appendix B contains, for reference, a full record of the corals collected in every sample considered in analysis of the data.)

Perhaps a fuller identification of the Chagos corals to species level might yield a more fruitful sociological analysis. But some estimates of cover by the different coral genera and species are also required. Photographs were taken of every quadrat, but the use of photographic records in coral studies is fairly limited, chiefly because identification of some coral types from photographs is impossible (see Loya, 1972).

None of the transects studied at Chagos Bank was sampled in as much detail as the Egmont Main Transect, and on some transects collections were made only at two or three depth intervals. Furthermore, data for the full range of depths sampled is available for only a few of the transects. For this reason, and because there were no striking differences between the different stretches of reef sampled, it was thought best to pool the data from all the transects, in order to have as large a data set as possible. Therefore, in the discussion in Chapter 3, Sections III - V, no distinction is drawn between lagoon, lee and seaward reefs, as such distinctions are not really valid for the Chagos Bank. Any conclusions drawn from the depth distribution of the Chagos corals must be taken to apply, in very general terms, to any type of reef; although discussion of the deepest zones may be more applicable to seaward reefs.

CHAPTER THREE

LOCAL DISTRIBUTION PATTERNS OF HERMATYPIC CORALS :
THE CHAGOS DATA COMPARED WITH OTHER STUDIES

SECTION I Factors affecting the distribution of hermatypic corals

Hermatypic corals are restricted to the shallow waters of tropical zones. Before proceeding to any discussion of the Chagos corals data, some mention of the environmental factors which may affect coral distribution is relevant. The principal factors are light, temperature, salinity, water turbulence and related effects of sedimentation, nutrient supply, and oxygen and carbon dioxide levels.

Temperature Temperature seems mostly to govern the geographical distribution of hermatypic corals, which will be considered in Chapter 4. Wells (1967) states that the minimum temperatures for reproduction are about 16°C, and 18°C for significant growth and reef development. The upper limit tolerated can be as high as 40°C. Temperature is generally not important in controlling local distribution patterns, for temperature ranges are usually well within the limits for good growth. Regarding temperature change with depth, Wells (e.g. 1954, 1967) has shown that even at 120m, beyond the range of most hermatypes, the temperature in the tropics is usually around 24°C, well within their tolerance range.

Light This seems to be a major factor controlling the depth distribution of hermatypic corals, as they are generally restricted to shallower, illuminated water. Table 3 shows the decline

in light intensity with depth, and very broadly speaking, coral species diversity drops off accordingly (Wells, 1954, 1957) (but see discussion in Section V).

TABLE 3 DECLINE IN LIGHT INTENSITY WITH DEPTH IN CLEAR TROPICAL WATER (after Wells, 1967)

Depth (m)	Percentage surface illumination
20	35
40	20
60	13
100	5

All hermatypic corals contain within their tissues unicellular flagellate algae called zooxanthellae. Many of the experiments carried out on the dependence of corals on their zooxanthellae have produced rather contradictory results. (For a review of nutrition in corals, see Muscatine, 1973.) The zooxanthellae are active primary producers; some of their metabolic products are transferred to the host polyps. This may be more important in the case of small colonial polyps with high metabolic rates. Zooxanthellae also act as nutrient conservers in that they accumulate host waste material (see below). But corals also benefit from their carnivorous habits. Goreau *et al* (1971) emphasise the heterotrophic nutritional activities of reef corals, as indicated by their specialised carnivorous feeding, primarily on zooplankton (facilitated by ciliated currents and mucus and by direct transfer of prey by tentacles to the mouth), by their unspecialised detritus feeding, and by direction utilisation of dissolved or colloidal organic matter. Drew (1973) suggests that corals are adaptable organisms which may use the sources of nutrition available in their particular area, "efficiently carnivorous where the water is turbid and relatively rich in zooplankton, but autotrophic on clear water reefs with little plankton".

It does seem clear that zooxanthellae are very important in causing corals to calcify at accelerated rates in the light, and the work of Goreau has contributed greatly to knowledge in this field. Goreau and Goreau (1959) used Ca^{45} to measure calcium uptake in thirteen hermatypic scleractinian species and two species of *Millepora*. Experiments were carried out underwater on shallow reefs off Jamaica, in conditions as similar as possible to the natural environment. They found that in all cases, light intensity had a profound effect on coral growth rate. All corals deposited calcium fastest in sunlight, less rapidly in cloudy weather, and deposition was slowest in darkness. Bleached colonies (lacking zooxanthellae) deposited calcium more slowly in the light than normal specimens (with zooxanthellae) in the dark.

Several mechanisms linking photosynthesis and calcification have been proposed. Probably the most acceptable hypothesis is that calcification is enhanced through the removal of carbon dioxide from the calcification site by photosynthesis and/or carbonic anhydrase (see, for example, Goreau, 1961). However, the exact reactions and the part played by zooxanthellae are not fully understood, and Drew (1973) points out that the relationship between photosynthesis and calcification is not straightforward, since the reduction in the rate of calcification with depth is not as great as the reduction in photosynthesis and light intensity.

That zooxanthellae enhance calcification by removing metabolic waste (here CO_2) remains an attractive theory, and Weber (1974) suggests that in this way, zooxanthellae have allowed the high degree of phenetic variability displayed by reef-building corals. His arguments are based on studies of stable isotope ratio measurements of carbon and oxygen contained in the skeletal carbonate of a range of corals, the skeletal

carbonate being derived either from seawater bicarbonate ions or from carbon dioxide produced in respiration. Ahermatypes, he suggests, are restricted to relatively simple forms because of the difficulties in metabolic excretion of CO_2 (by diffusion) they would encounter with a more complex geometry. Hermatypes, however, are not so confined, as "zooxanthellae, by removing metabolic waste products in situ, liberate the reef-building corals from restrictions on the range of corallum configurations that their physiological status would otherwise impose".

Salinity

The salinity tolerance of hermatypic corals probably lies between 30 and 48 p.p.t. (Kinsman, 1964). In the open ocean salinity levels should be well within this range, and corals are unlikely to experience severe fluctuations in salinity (except in rare cases where heavy rainfall coincides with an unusually low tide, thus lowering the salinity on the reef flat).

Water turbulence

Water turbulence seems to have a marked effect on coral distribution (see Section II). The extremes will be the most harmful, for example, mechanical stress caused by strong surf or storms. In very still water, there may be accumulation of sediment, which in extreme cases will deprive many types of coral of a suitable substrate for attachment. Corals may also be subject to burial by sediment; branching forms may be less likely to suffer from this by virtue of their shape. Some massive forms seem to be fairly sediment-tolerant, e.g. *Porites*; and *Platygyra lamellina* (see Loya, 1972). Massive species resistant to sedimentation have apparently evolved some cleaning mechanism, perhaps mucus and ciliary cleaning, as discussed by Marshall and Orr (1931). Poor water circulation, especially in very enclosed lagoons, may have adverse effects on corals. This is probably more important for the removal of carbon dioxide than for replenishing the nutrient and oxygen supply (Stoddart, 1969).

SECTION II Distribution patterns of hermatypic corals in shallow
water environments (above 5 - 10m in depth)

The majority of the studies carried out in the Indo-Pacific have been confined to the reef flats or very shallow reef areas. Some of these studies are reviewed by Stoddart (1969, 1973).

There is very little information on the shallower reef environment (above 3m) at the Chagos Bank or Egmont. From preliminary observations at Chagos Bank, it appears that the reef flats usually have very poor coverage of living coral, generally < 5%. The reasons for this are not known. It could be that at very low tide the reef flat may dry out, especially during hot weather. Further, it is possible that if heavy rainfall (frequent in the Chagos area) coincides with low tide the salinity on the reef flat might be reduced to a critical level. In both cases, physiological damage to colonies on the reef flat could occur. (See Stoddart, 1969). Loya (1972) has recorded poor species diversity and living coral coverage at Eilat, where the reef flat environment is severe and unpredictable. Fishelson (1973) has noted at Eilat that massive species are more tolerant of desiccation than bush-shaped colonies.

Figure 5 shows a typical profile of the reef flat and upper reef slope at Chagos Bank. The algal ridge varies in its degree of development, and there are no groove-spur systems. No marine grass beds were observed although *Cymodocea* (= *Thalassodendron*) has been found at Diego Garcia (Stoddart, 1971a). Significant coral growth usually begins at a depth of 2 - 3m in more sheltered areas, and at about 5m on a more exposed reef. The pattern is very similar for the Egmont seaward reefs,

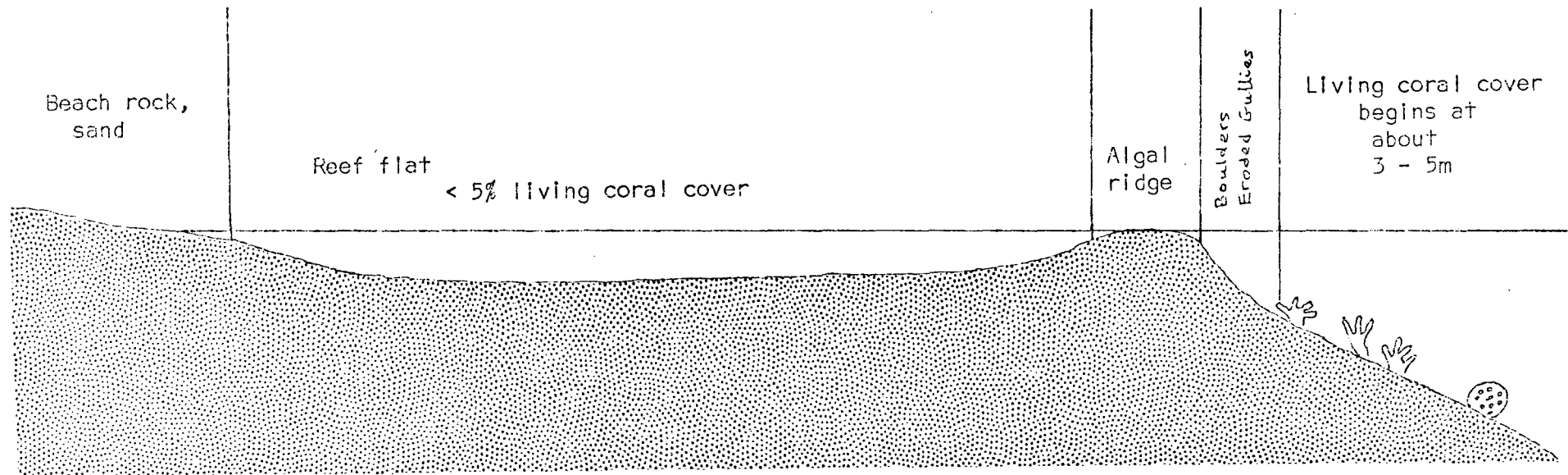


Figure 5 Profile of reef flat and upper reef slope at Chagos Bank

except that in sheltered sites the reef flat and upper few metres of the reef slope have a better living coral growth.

Differences between windward, lee and lagoon reefs have often been observed, both in terms of their morphology and the biota. However, no striking differences were apparent between the various reef areas studied at Chagos Bank, probably because they all suffer a fairly similar degree of exposure. Reefs on the western side of the section studied are exposed to the open ocean, but the westerly winds are not as severe as the Trades. Lagoon facing reefs are also fairly exposed, because the lagoon is so large and not enclosed, and therefore does not offer a great deal of protection from the Trade winds. (The only exception is the area just east of Danger Island. Here on Transects 28 and 42 shallow areas (< 12m deep), entirely dominated by species of *Acropora*, extended for several kilometres from the shore.)

Little can be said about the distribution of coral fauna at Chagos Bank in the very shallow water since most of the data were collected below 3 or 6m. Therefore the shallow environment will not be considered in great detail here, but some discussion is nonetheless relevant.

Water turbulence is probably the most important factor affecting coral distribution in shallower areas. As stated above, most of the coral reef studies in the Indo-Pacific have concentrated on shallow environments; but until recently many of the records have been of a qualitative nature, and the approach taken by workers has varied greatly, especially regarding the features they have used to describe different reef areas. This has made it rather difficult to draw comparisons between the various reefs so far investigated.

Rosen (1971a) describes a pattern for the distribution of coral assemblages in shallow reefs around Mahé, Seychelles, and this is further developed in a subsequent paper (1975) as a tentative scheme for the Indo-Pacific as a whole. The associations are named after the most conspicuous genus or family in each case, plus the calcareous algal ridge. They are distributed in response to a gradient in water movement in three directions: vertically; horizontally in terms of the aspect (i.e. whether the windward or lee side of the reef); and horizontally in relation to the line of the reef edge (see Rosen, 1975, Figure 3). The calcareous algal ridge occurs in the most turbulent area, and there is a progression in the three directions through the *Pocillopora*, *Acropora*, and Faviid (+ Mussid) assemblages, to the *Porites* assemblage in the stillest water. The assemblages may intergrade; and the full range might not be present within a single reef or reef area, due, for example, to insufficient space or variety of conditions for them to develop.

Although the scheme is related to the strength of water movement, several factors may be involved, though there are not many experimental data which might help to clarify the reasons for such a distribution. Mechanical stress is probably most important in the region of the algal ridge, and the *Pocillopora*, and perhaps the *Acropora* assemblages. At the other extreme, *Porites* probably flourishes because it is a highly tolerant genus, able to withstand such effects as sedimentation, poor nutrient supply etc, which may be associated with poor water circulation. In the intermediate areas there is probably much competition for space, especially between the branching forms and the Faviids and Mussids.

Although Rosen's scheme is a very general one, for which there may be many exceptions, this kind of approach is very useful. In the past too many studies have been carried out in isolation, with little attempt to link observations with findings in other areas.

There is little information from the Chagos Bank or Egmont which might be compared with the above pattern (except possibly for the lower end of Rosen's vertical component). But in the absence of any contradictory evidence, it seems fair to assume that the scheme may apply at least in part, though the full range of water movement conditions is unlikely to be present.

SECTION III Coral Distribution patterns in the deeper water environment (mostly below 5m in depth)

(Terms such as "shallow" and "deep" are relative! In Sections III and IV of this chapter the following definitions are applied for convenience :

Shallow = 3 - 12m; Intermediate = 12m - 27m; Deep = below 27m)

As stated in Section III of the preceding chapter, the most obvious parameter to which one can relate any patterns in the distribution of the Chagos corals is depth. Table 4 presents a SHUFFLE with the *aufnahmen* (both quadrat and random) ordered in six depth classes from 3m to 45m. It is immediately clear from the SHUFFLE that practically no genus is restricted to only one or two depth classes, and most can be found over a wide range of depths. However, a fair number of the genera and species do seem to occur more frequently at certain depths. The pattern is

TABLE 4 SHUFFLE WITH SAMPLES ORDERED IN SIX DEPTH CLASSES
FROM 3m - 45m

Top half of table : corals exhibiting some zonation with depth

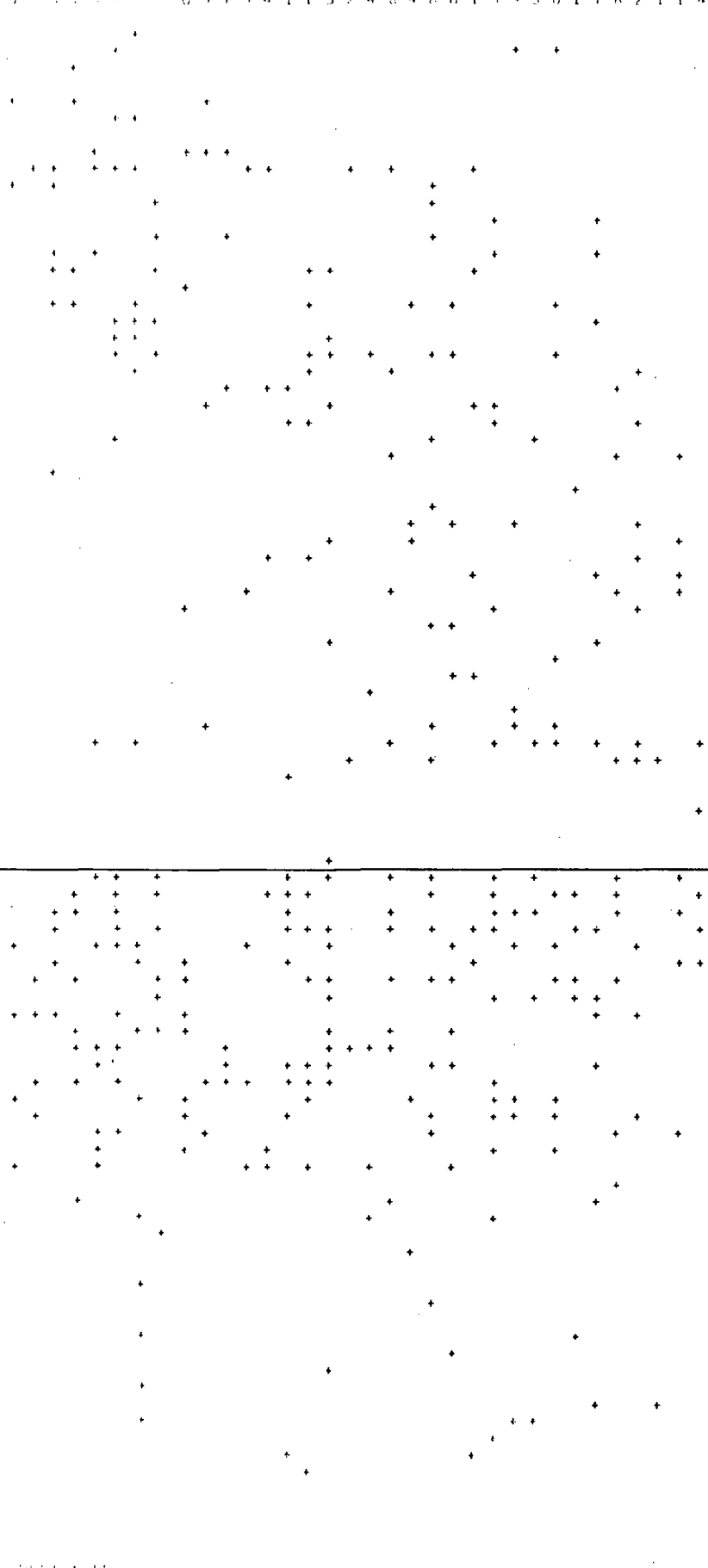
Below : corals apparently showing no zonation, and corals which
are too rare to place.

21-25m

0 0 1 1 1 0 0 1 0 0 2 1 0 1 2 0 0 0 1 0 1 7 2 0 1 1 1 0 0 1 0
 1 5 0 0 0 7 7 7 4 2 1 1 6 1 8 0 4 0 2 4 4 4 1 0 9 0 5 5 3 7 8 5
 2 5 1 1 1 1 1 1 0 0 7 5 4 1 1 3 2 4 8 5 8 6 1 5 9 3 0 1 7 6 2 1 1 5

- 18 ACRO CNF
- 68 LEAF SPP
- 104 HELL CNF
- 103 TONE MICE
- 105 HYDR VAR I
- 3 STYL MORD
- 7 STYL SPP
- 13 ACRO PALL
- 76 PALA FASC
- 11 POCI YOUN
- 15 ACRO TWI
- 56 FAVI STEI
- 57 FAVI CE S
- 73 POCI GEMM
- 78 CTEN SP
- 93 SYMP SPP
- 84 ?SYM SPP
- 70 HYDM SPP
- 4 STYL PIST
- 8 SERI SEP
- 20 ACAR SPP
- 72 CYPH SPP
- 51 FVIT SPP
- 62 BULD SPP
- 102 ?PSA EXSH
- 64 GCNA PECT
- 34 HGFA SPP
- 35 CF H CERI
- 41 FUNG FUNG
- 110 ?FUN FUNG
- 36 CYCL SPP
- 47 PCDA SPP
- 6 STYL DEEP
- 99 TUBA SPP
- 98 BEND SPP
- 101 BEND YOUN
- 86 EPHY SPP
- 87 ?EPH SPP
- 88 OXYP SPP
- 89 NYCE SPP
- 90 ?MYC SPP
- 91 PECT SPP
- 92 PECT FRAG
- 30 PACH SPP
- 28 LEPT NYCE
- 29 CF L NYCE
- 27 LEPT ONE
- 26 LEPT SEP
- 31 CCSC SPP
- 32 CF C SPP
- 33 CF C CONV

- 16 MONT SPP
- 55 FAVI PALL
- 59 FVIT PENT
- 67 PLAT SPP
- 2 PLES SPP
- 50 POCI MASS
- 21 PAVO CLAV
- 51 POCI NYEM
- 71 LSTR SPP
- 17 ACRO SPP
- 37 PLEU SPP
- 90 ACAN SPP
- 18 ASTA SPP
- 60 FVIT VIRE
- 22 PAVO VAR I
- 48 GCNI SPP
- 16 ACRO THRE
- 63 GCNA PALA
- 85 MISS FRAG
- 100 TJFR SPP
- 12 POCI SPP
- 42 FUNG YOUN
- 109 SYNA SPP
- 25 PAVO SPP
- 53 POCI FRAG
- 5 STYL ONE
- 23 PELY SPP
- 24 PSEU SPP
- 54 ALVA SPP
- 66 GCNA SEP
- 77 GALA SMAL
- 81 LEPO SPP
- 82 ZILO SPP
- 5 POCI GAMB
- 38 VERA SEP
- 76 LEPI LAME
- 10 POCI HAMA
- 52 POCI LITH
- 58 FAVI SPP
- 109 ?VIR SPP
- 5 POCI K. EV



clearest for the shallowest (3 - 6m) and the deepest areas (33 - 45m), where a more limited range of coral types tends to be found. Of the corals which seem to exhibit some zonation with depth, those types frequently occurring in the shallowest water seem to be rare or absent in the deepest areas, and vice versa. At depths of 9 or 12m to about 30m there does appear to be some transition, with the shallow types gradually becoming less frequent and apparently giving way to the intermediate and finally to the deeper water corals. But the pattern is not distinct and at all these intermediate depths a broad range of coral types is represented.

Any conclusions which might be drawn about the depth distribution of the corals at Chagos must be based solely on the numbers of occurrences of corals at various depths. Moreover, the author wishes to emphasise that while corals may exhibit zonation with respect to depth, the actual depths at which such zones may occur will vary according to local conditions, principally light.

To clarify any trends emerging in Table 4 some of the data have been re-arranged in Table 5. In creating this table only the data from quadrat collections have been used. The random samples have not been included because for these, collections were only made of those corals not appearing in the corresponding quadrat, hence many specimens were deliberately omitted. In Table 5 a species or genus is only marked where it occurs in at least 15% of the quadrats in that depth class. It is also indicated if a coral type occurred in 25 - 50%, or in more than 50% of the quadrat samples at that depth.

The limitations of the table should be mentioned. There is a bias against less common genera or species if they happen to occur more in the random than in the quadrat samples, e.g. *Hydnophora*; and the shallowest occurrences of *Symphyllia*. Also, a coral will not be included if it occurs only now and again at various depths, but is not prominent in any one depth class. The table does help to improve the pattern suggested by the SHUFFLE by omitting odd occurrences of corals outside their usual depth classes; and excluding, of course, the very rare ones.

It is again clear (from Table 5) that many genera are widely distributed in relation to depth, and some are very common through several depth classes. But from the degree of shading it is more readily apparent which genera or species groups are the most abundant within certain depth classes. It is hard to pick out any genera as being definite "markers" for certain depths. However, the distribution of *Acropora* spp. type 1, *Leptoria*, *Heliopora coerulea* and *Stylophora* cf. *mordax* (+ *Stylophora* spp) is certainly concentrated in water not deeper than 12m. Genera such as *Cycloseris*, *Leptoseris*, and *Coscinaraea* are common only below about 27m; and though *Pachyseris*, *Leptoseris?* *mycetoseroides* group and the Pectiniids are often present at lesser depths, they are clearly most important in the deepest collections. Several genera occur mostly at intermediate depths, e.g. "*Agariciella*", *Goniopora*, *Cyphastrea* and *Oulophyllia*.

A more detailed identification of the material from Chagos might well improve the depth zonation patterns suggested. Regrettably, it was quite impossible to identify such a large number of specimens to species level in the course of this short study.

Unfortunately, there are few studies of depth distribution in the Indian Ocean with which the Chagos data might be compared. The best records seem to be from the Red Sea (Loya and Slobodkin, 1971), Aldabra (Barnes *et al.*, 1971), and the Maldives (Wells and Davies, 1966). The usual depth distributions of a number of genera and species as observed in the four localities are compared in Table 6. It should be borne in mind that the level of identification is not always the same; that different types of reef are being compared; that sampling methods were not always the same; and that the Aldabra data are based on one detailed transect only, while Chagos data are from many transects.

The depth data from the four studies are in some cases in agreement, in others rather discordant. In all cases *Stylophora mordax* and *Leptoria/Leptoria phrygia* are shallow water species. Species with some range, but occurring mostly in shallow or shallow and medium areas, include *Galaxea fascicularis*, *Pocillopora eydouxi*, *Echinopora gemmacea* and *Favia stelligera*. The genus *Acropora* occurs over a wide depth range but mostly commonly in shallower water. *Montipora* and *Porites* are found from shallow through to fairly deep water, likewise *Platygyra/Platygyra lamellina* (except for the Maldives record). *Leptoseris* spp., *Leptoseris? mycetoseroides* group and *Coccolinaraea* do occur at intermediate depths, but particularly in deep water.

The most striking anomaly in Table 6 concerns the depth at which "*Agariciella*" *ponderosa* is likely to be found. At Aldabra the records suggest that it is a deep water species, but its optimum depth range in the Elliot study was found to be above 6m. Chagos records for the genus "*Agariciella*" are mostly from intermediate depths. While at Chagos *Paohyseris* and the Pectiniids do occur at intermediate depths, they are

TABLE 6

COMPARISON OF THE DEPTH RANGES OF SOME GENERA AND SPECIES FROM FOUR LOCALITIES

(In this table shallow = 0 - 12m; medium = 12 - 27m; deep = 27 - 50m)

GENUS OR SPECIES	RED SEA Fringing reef at Ellat	ALDABRA Sheltered reef front of elevated atoll	MALDIVES At Gan, Addu Atoll Mostly lagoon but some seaward collections	CHAGOS BANK IDENTIFICATION	CHAGOS BANK Seaward and Lagoon reefs of partially drowned atoll
<i>Stylophora mordax</i>	-	Shallow	Shallow	<i>S. of mordax</i> and similar <i>Stylophora</i> spp	Mostly shallow, some medium
<i>Pocillopora eydouxi</i>	-	Shallow and medium	Shallow	<i>P. of eydouxi</i>	Shallow and medium
<i>Acropora</i>	8 spp : 2 prominent shallow to 50m; rest shallow only	4 spp, all shallow	18 spp : some medium, most shallow	<i>Acropora</i>	Some range; mostly shallow and medium
<i>Astreopora</i>	Shallow	Range to 35m, but mostly shallow	Shallow and medium	<i>Astreopora</i>	Wide range, but mostly medium
<i>Montipora</i>	Range varies for individual spp, but genus present from shallow to deep	As for Red Sea	From shallow to 27m	<i>Montipora</i>	Abundant to fairly deep water
<i>Favona varians</i>	Shallow	Medium and fairly deep	Shallow and medium	<i>P. varians</i> group	Wide range, especially medium and fairly deep
<i>Favona clavus</i>	Shallow	-	Shallow and medium	<i>P. clavus</i> group	As <i>P. varians</i> group
<i>Leptoseris</i>	25 - 50m	-	Medium and fairly deep	<i>Leptoseris</i>	Deep
<i>Leptoseris? mycetoseroides</i>	-	Fairly deep		<i>L.? mycetoseroides</i> group	Wide range, mostly medium and deep
" <i>Agariciella</i> " <i>ponderosa</i>	Shallow	Deep	-	" <i>Agariciella</i> "	Medium
<i>Pachyseris</i>	10 - 30m	Mostly medium, some fairly deep	Shallow and medium	<i>Pachyseris</i>	Medium and especially deep
<i>Coscinaraea</i>	Medium and deep	-	Medium	<i>Coscinaraea</i>	Deep
<i>Porites</i>	Shallow to deep	Mostly shallow and medium	Shallow to deep	<i>Porites</i>	Abundant shallow to deep

TABLE 6 (Continued)

GENUS OR SPECIES	RED SEA Fringing reef at Ellat	ALDABRA Sheltered reef front of elevated atoll	MALDIVES At Gan, Addu Atoll. Mostly lagoon but some seaward collections	CHAGOS BANK IDENTIFICATION	CHAGOS BANK Seaward and Lagoon reefs of partially drowned atoll
<i>Favia fava</i>	Shallow	-	Shallow	} <i>Favia</i> <i>pallida/fava</i> group	Shallow to quite deep
<i>Favia pallida</i>	-	Shallow to fairly deep	Shallow		
<i>Favia stelligera</i>	Shallow	-	Shallow		
<i>Favites pentagona</i>	Deep	-	Medium	<i>F. pentagona</i> group	Wide range, especially shallow and medium
<i>Favites abdita</i>	Shallow to deep	Shallow and medium	Shallow and medium	} <i>Favites</i> <i>virens/abdita</i> group	Shallow and medium
<i>Favites virens</i>	Shallow	-	-		
<i>Platygyra lamellina</i>	From shallow to deep	Shallow to fairly deep	Shallow	<i>Platygyra</i>	Shallow to fairly deep
<i>Leptoria phrygia</i>	Shallow	Shallow	Shallow	<i>Leptoria</i>	Shallow
<i>Leptastrea</i>	Shallow to deep	Shallow to deep, mostly medium	Shallow	<i>Leptastrea</i>	Wide range, shallow to deep
<i>Echinopora gemmacea</i>	Shallow	Mostly shallow and medium	-	<i>E.cf. gemmacea</i>	Shallow and medium
<i>Galaxea fascicularis</i>	Shallow	Mostly shallow and medium	Shallow	<i>G.cf. fascicularis</i>	Shallow and some medium
<i>Acanthastrea echinata</i>	Shallow to deep	Lower part of medium range, and to 33m	Medium	<i>Acanthastrea</i>	Shallow and medium
<i>Symphyllia</i>	-	Medium	Shallow and medium	<i>Symphyllia</i>	Wide range, mostly medium
<i>Echinophyllia aspera</i>	Lower part of shallow range	Medium	Shallow and medium	Pectiniids, mostly <i>Echinophyllia</i> and <i>Mycedium</i>	Medium and especially deep
<i>Mycedium tubifex</i>	Medium and deep	Both spp medium	Medium		
<i>Mycedium tenuicostatum</i>	-	to fairly deep	-		

most important in deeper water; the records for their distribution at the other sites are rather variable. No explanation can be offered at this stage for the differences in the optimum depth range of some of the genera and species at the four localities. Some of the differences might be due to insufficient sampling or different methods used, or there may be genuine variations due to local environmental conditions and the relative abundance of genera and species in different places.

Wells (1954) presents a detailed account of the distribution of corals at Bikini Atoll. This study provides data from greater depths than those referred to above (but no dredging was carried out on the seaward slope above 18m). Wells defines three broad zones; the *Echinophyllia* zone from 18 - 91m; the *Leptoseris* zone from 91 - 146m; and below this the *Sclerhelia-Dendrophyllia* zone. In the upper part of the *Echinophyllia* zone are several species also occurring on the surface reefs. Not recorded in surface collections, but abundant in this zone, are *Echinophyllia aspera* and *Oxypora lacera*. Other species peculiar to this zone include *Pachyseris spectosa*, *Cycloseris vaughani*, and certain species of *Acropora*, *Montipora*, *Porites*, *Favia* and *Psammocora* (*Plesioseris*). The *Leptoseris* zone is clearly beyond the range of optimum growth of hermatypes. In this zone are found a few stragglers from the zone above, but the most common coral is *Leptoseris* (not found on surface reefs), of which several species are represented. Other species recorded only in this zone include *Montipora granulosa* and *Coscinaraea ostreaeformis*. The *Sclerhelia-Dendrophyllia* zone seems to be ahermatypic.

Rosen (1971b) discusses the distribution of coral genera in the Indian Ocean. In addition to a table presenting records for total fauna (irrespective of depth), he gives records for 18 - 91m, 91 - 146m, and

below 146m, in accordance with Wells' zones for Bikini. Several genera are much more conspicuous in the 18 - 91m zone than in the total fauna, such as *Cycloseris*, *Pachyseris*, *Leptoseris* and *Coscinaraea*. Genera also notably higher in this table than in the total fauna are *Echinophyllia*, *Oxypora* and *Mycedium*. Little information is available for depths below 91m in the Indian Ocean, but occurrences of *Leptoseris*, *Cycloseris*, *Pachyseris* and *Coscinaraea* have been reported.

The Chagos data (collected by SCUBA divers and not by dredging) do not go beyond about 45m. It has already been pointed out that the genera *Leptoseris*, *Cycloseris*, *Coscinaraea*, and Pectiniids (mostly *Echinophyllia* and *Mycedium*) are most abundant between 27m and 45m, and *Leptoseris* and *Coscinaraea* rarely occur at lesser depths. These records are well supported by the data presented by Wells and Rosen, i.e. that such genera are most conspicuous at depths beyond the optimum range of many other hermatypes. Maragos (1973) carried out a detailed transect survey of a Pacific leeward ocean reef at Fanning Island, using a 1m x 100m contiguous transect. He too found that corals such as *Echinophyllia*, *Leptoseris*, *Leptoseris? mycetoseroides* (and certain species of *Pavona*) were among those typical of deeper water, occurring only below a depth of 18m.

At Bikini Wells found that the *Echinophyllia* zone was succeeded by the *Leptoseris* zone and finally by the ahermatypic zone. The Chagos Bank records indicate that Pectiniids, *Pachyseris* and *Leptoseris* are abundant together from 27m downwards, and the ahermatypic *Dendrophyllia* occurs alongside these genera. It seems that here the deeper water genera are not as distinctly zoned as at Bikini, though nothing can be said about their distribution at depths below about 45m.

SECTION IV Discussion

Not a great deal can be added about the depth distribution of the corals at Chagos. Other studies, for example those mentioned above at Aldabra (Barnes *et al.*, 1971) and at Ellat (Loya and Slobodkin, 1971; Loya, 1972) and Pichon's work at Madagascar (1964), suggest that there is a succession of more or less distinct zones down the reef front, typified by certain marker species (not necessarily the same marker types in different localities). From the Chagos data in Table 5, and the preceding discussion, it appears that some genera or species groups occur more frequently at certain depths. Beyond this, however, it is not possible to describe very definite zones with marker species. A fuller identification to species level might help; but more data on the abundance and cover of the corals is required. Only limited deductions can be made from records which are purely in terms of the presence or absence of corals.

Some data are available from Egmont on the degree of cover of various coral growth forms down the reef front (Figure 6). There is much intergradation of the zones and some forms (e.g. encrusting) may occur throughout. But very generally there is a progression through branching and brain forms in shallower areas, to bracket forms in deeper water, which where the hermatypic cover declines are replaced by Gorgonians and *Dendrophyllia*. Similar data were collected during the Chagos Bank expedition, and though these were not available in time for inclusion in this report, the same trends seem to emerge (Bellamy *et al.*, 1976). Barnes *et al.* (1971) report the same zonation of growth forms at Aldabra. However, this can only be accepted as a very general scheme, and there are often exceptions (for example, in the studies cited in the previous paragraph).

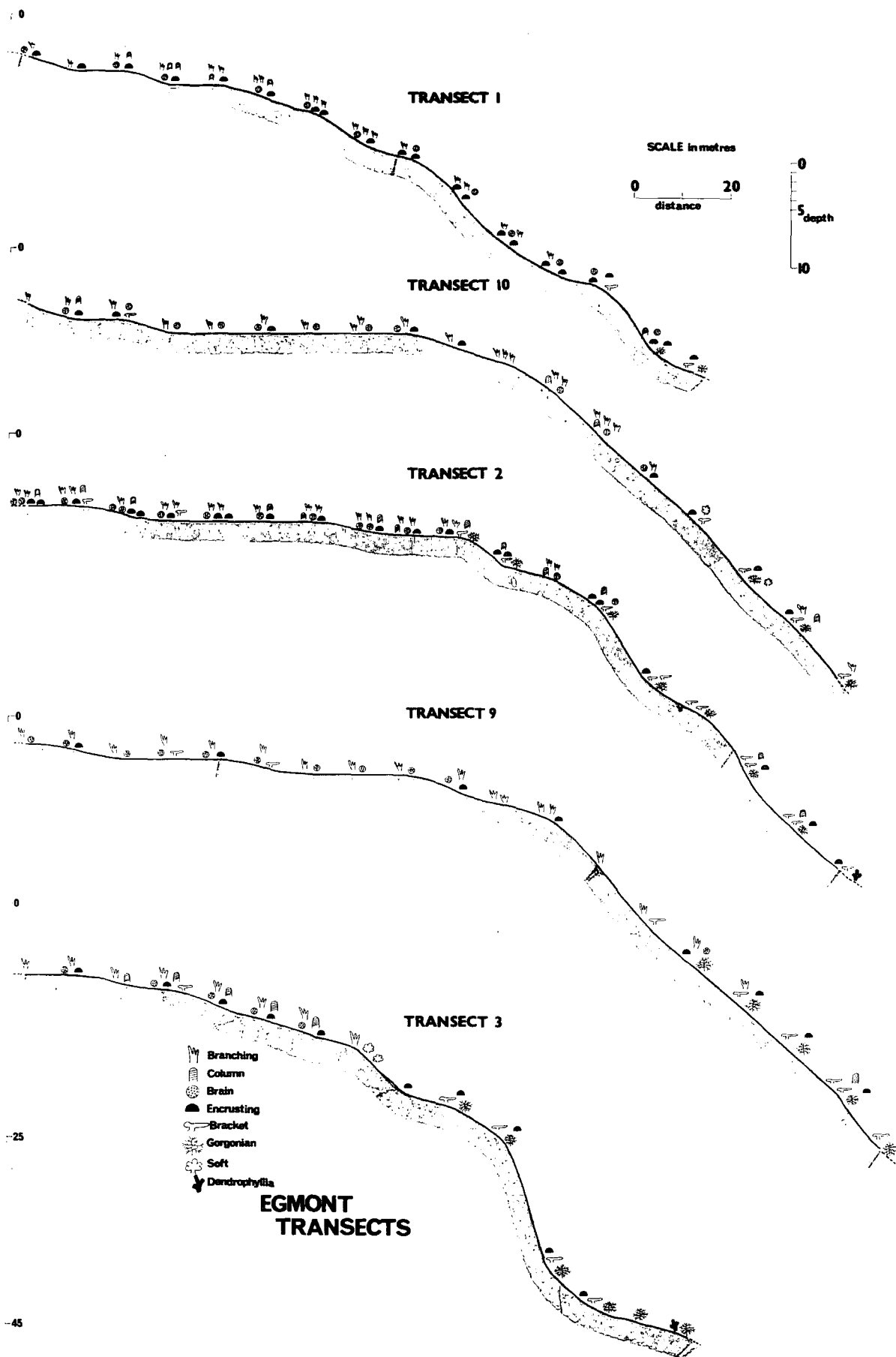


Figure 6

Reasons for zonation of coral growth forms and the distribution of coral genera and species down the reef front can only very tentatively be suggested. Branching forms seem to be dominant in the shallowest water (and are very generally succeeded further down by massive forms). This is probably due to the effects of water turbulence as proposed in Rosen's scheme. The very lowest zone is ahermatypic, presumably because the reduction in radiant energy excludes hermatypes. Corals occurring just above the ahermatypic zone are mostly those with thin, flattened coralla. Because of the reduced calcification rates at greater depths, corals can only produce thin, fragile skeletons; the flattened form will also allow the colony to receive as much as possible of the available light.

Perhaps the coral forms in the very shallow turbulent areas and the poorly irradiated deeper zones are particularly suited to such conditions. But in the intermediate zones the environment should be favourable for many types of coral, and the reasons for any distribution patterns are more obscure. Here Lang's study (1973) of interspecific aggression between corals is relevant. The most aggressive species are slow-growing massive or encrusting members of the Favitina. They use their aggressive interactions as a defence against overgrowth by more rapidly expanding ramose and foliose corals. The stronger aggressors extrude their mesenteral filaments over their weaker neighbours and dissolve those tissues within reach by extracoelenteric forms of digestion. A definite hierarchy exists between different species; some of the weakest aggressors are the foliose Agariciids.

Far more data are required before any very detailed account of the reasons for coral zonation can be given. There seems to be a similar succession of growth forms down the reef front on many reefs. But some of the zones described in terms of definite species or genera do not necessarily correspond; and the species dominant in zones apparently analogous (e.g. in terms of coral forms and depth) may not be the same. The data in Table 6 suggest that there are genuine differences in different areas between the optimum depth ranges of certain genera and species. All such variation cannot be attributed solely to differences in sampling methods. There may be genuine zoogeographical differences; or a range of local differences in reef morphology, and the prevailing environmental conditions may be responsible. Many more studies of zonation patterns in relation to depth are required, with accompanying data on the local environment, before any definite trends in species distribution down the reef front (especially at intermediate depths) can be established, or the reasons for any differences accounted for.

SECTION V Changes in coral diversity with depth

Wells (1967) states that while there is no definite lower bathymetric limit for hermatypic corals, 100m is the lower limit of any significant contribution to reef building. By 50m the number of species has been halved, and at 100m the number of species is about 10% of the surface figure.

As stated above, the reduction of diversity with depth cannot be attributed to change in temperature, for this remains well within the tolerance range of hermatypic corals to well below 100m. Light seems

to be the controlling factor, and Wells (1957) has shown that reduction of coral diversity follows very closely the curves for the decrease in illumination and radiant energy with depth. In his Bikini study (1954) Wells plots of the numbers of both genera and species against depth, distinguishing between surface and non-surface hermatypic corals, and ahermatypic kinds. On the seaward slope the number of species drops very sharply between the surface and 27m, though such a rapid decrease may be due to insufficient sampling between 18 and 75m, as the species diversity changes less rapidly on the lagoon slope.

Sampling methods certainly influence diversity records. For example, Rosen (1975) compares figures for the Southern Maldives where there has been little dredging (but much collecting has been done by SCUBA divers to about 30 or 40m) with the Bikini area where non-surface data have been collected chiefly by dredging. In the former case, the generic diversity is very high above about 30m, but decreases rapidly below this depth. At Bikini, the diversity is much lower in the uppermost 30m, but declines slowly with a long deep-water "tail", so that between about 30 and 180m the diversity is much higher than at the Southern Maldives.

The relationship between light attenuation and coral diversity may not be as simple as Wells' work has suggested. At Ellat, Loya (1972) has found that there is a successive increase in species diversity to around 30m, with about twice as many species recorded at this depth than from very shallow water. (The attenuation of light with depth at Ellat is very similar to that at Bikini.) Loya and Goreau observed a similar pattern on Jamaican reefs (unpublished data, but see Loya, 1972) where the species diversity decreased only below 40m.

that radiant energy and light intensity may have a critical effect on coral diversity only below a certain depth (which may vary from reef to reef according, for example, to turbidity). Loya (1972) found that though species diversity at Eilat increased with depth, the average colony size of many species decreased, this curve following the same pattern as the light intensity curve (except on the reef flat). Clearly, further study is required of the effects of light (especially the different wavelengths) on corals and their zooxanthellae, before the distribution of corals with light and depth can be explained.

CHAPTER FOUR

CORAL DISTRIBUTION AND DIVERSITY PATTERNS IN THE INDO-PACIFIC;
AND DIVERSITY ON CHAGOS REEFSSECTION I Coral Diversity in the Indo-Pacific

The coral fauna of the Indo-Pacific is remarkably homogeneous, at least in terms of its generic composition. In this chapter, reference will be made to generic distribution only, because the confusion surrounding coral systematics at species level does not allow a meaningful discussion of species distribution. Wells (1954) plotted diversity contours for the Indo-Pacific region, and found that these corresponded quite well with isocrymes, i.e. lines of equal minimum surface water temperature. The greatest number of genera occurs within the 25°C isotherm, and especially in the 28°C areas. The diversity declines radially from the rich central strip in a fairly regular pattern, and "In all the peripheral areas the same genera drop out in the same manner, and the remaining peripheral faunas are [with few exceptions] of the same composition and include only genera also found more centrally There is no generic difference between a fauna from one extreme geographical situation and one from another within the same temperature range."

Further confirmation of temperature-related diversity patterns has been provided in subsequent papers, e.g. Stehli and Wells (1971) for the Indo-Pacific and Atlantic, and Rosen (1971b) for the Indian Ocean. Rosen also plotted generic diversity against minimum prevailing surface water temperature, and there is some suggestion of a smooth-

curve relationship with a peak around 28° - 30° C. Temperature controls distribution chiefly in terms of the minimum temperature required for reproduction (Yonge, 1940). There are few data available, but the lowest tolerated for reproduction seems to be about 16° C (Wells, 1967). Presumably, the minimum temperature requirements vary, and genera occurring in the peripheral regions are more tolerant than those restricted to central, warmer areas.

From the maps of Stehli and Wells there seem to be three high diversity centres, situated in the western part of each ocean : the Caribbean and the Indonesian-western Pacific foci, and the western Indian Ocean focus (which may be superficial, see below). As is well-known, the fauna of the Atlantic and the Indo-Pacific regions are quite distinct; they have only five genera in common, and only *Acropora* and *Porites* are abundant in both areas. The highest diversity in the Indo-Pacific is at least 50% higher than that in the Atlantic. It is of interest that the high diversity centres seem to occur just north of the equator, as the thermal equator (in terms of the mean annual sea surface temperatures) lies well to the north of the geographic equator. This suggests that temperature is a more important factor in the geographical distribution of corals than the availability of light for the zooxanthellae, which should be optimal at the equator (Stehli and Wells, 1971).

The thermal gradient latitudinally across the oceans is relatively small, and the higher diversity in the westerly regions of the oceans is attributed to the action of oceanic currents which flow predominantly from east to west. Thus, the spread of coral planulae in an easterly

direction is inhibited. But the lack of islands and shallow areas in the eastern parts of the oceans must also influence coral distribution, since here there will be a smaller area of habitat favourable for coral growth (Stehli and Wells, 1971).

Diversities differing from those predicted by the general model may be due to insufficient sampling in some areas. But some of the anomalies require other explanations. For example, Wells (1954) draws attention to the northerly shift of a high diversity contour from the Philippines towards Japan, well into the 15°C isotherm. This he attributes to the effect of the strong Kuroshio Current, carrying the planulae of genera usually found only in warmer areas. The Agulhas Current may have a similar, though less marked, effect in the South African area (Rosen, 1971b). The higher salinity and temperatures, and greater temperature range, in areas such as the Persian Gulf and the Red Sea, may together act to reduce diversity (Rosen, 1971b).

Stehli and Wells (1971) also determined the "average generic age" of a number of stations, an "old" area being defined as one with a high proportion of genera with a long geological record, and *vice versa* for a "young" region. Their youngest areas correspond with the two main high diversity centres, and they conclude "that evolution is proceeding rapidly in regions of high diversity and that newly evolved genera extend their ranges over a considerable period of time into peripheral regions." The youngest average generic age found in the Pacific is half that of the youngest Atlantic region, and they suggest that evolution has been proceeding twice as fast in the Indo-Pacific as in the Atlantic.

Rosen (1975) has pointed out that the evolutionary centres defined by Stehli and Wells coincide with areas of crustal instability, though data on the distribution of past coral faunas are required before any definite relationship can be established.

In general, the model suggested by Wells (1954) of a central high diversity region with a successive radial decrease in diversity away from the focus seems to hold good. There are, in fact, fringe fauna associated with certain regions, and sub-provinces might be defined. There will not be discussed, except to mention that the genera *Siderastrea*, *Anomastrea*, *Ctenella* (and perhaps "*Agariciella*" and *Gyrosmitia*) are confined to the western part of the Indian Ocean. (But *Siderastrea* also occurs in the Atlantic.) Whether there is a true high diversity centre in the western Indian Ocean has yet to be confirmed. The number of genera found in this region now approaches that recorded in the Indonesian - west Pacific focus, and there may be a continuous high diversity belt across the Indian Ocean. But little sampling has been carried out in the eastern Indian Ocean, and until more data are available from this region the problem must remain unsolved.

SECTION II

Diversity on Chagos Reefs

Rosen (1971c) has presented a check-list of corals from the Chagos Archipelago, based on three collections : the collection of G.C. Bourne from Diego Garcia in 1885; that of J.S. Gardiner *et al* made during the Percy Sladen expedition, 1905; and that of J.D. Taylor from Diego Garcia in 1967. Rosen reports a total of 54 genera and sub-genera, of which 42 are hermatypic Scleractinians.

A check-list of corals so far identified from the recent Egmont and Chagos Bank collections may be found in Appendix A. At least 63 Scleractinian genera and sub-genera are represented, including 55 hermatypic genera. The non-Scleractinians *Tubipora musica*, *Heliopora coerulea* and various hydrozoans were also collected.

These recent collections contain many new records (but as the identifications are not complete, discussion will be in terms of genera only). The thirteen hermatypic genera not previously recorded include *Psammocora* (*Plesioseria*), *Coccolanaraea*, *Horastrea*, *Merulina*, *Cycoloseris*, *Physogyra* and four Pectiniid genera. There are also new records for six ahermatypic genera, including *Tubastrea* and *Oulangia*. Several genera were previously known only from sight records; the recent collections now confirm the presence of *Seriatopora*, *Alveopora* and *Euphyllia* on the Chagos reefs.

Only three genera (all sight records) from Rosen's check-list have not been found in the latest collections. These are the ahermatypic *Fungiacyathus* and *Madrepora*, dredged by Gardiner *et al* from deeper water; and *Siderastrea*. It is unfortunate that *Siderastrea* has not been identified from the recent material. This genus is one of the few genera common to both the West Indies and the Indo-Pacific, and its distribution in the Indo-Pacific region is confined to the western Indian Ocean.

Several genera from the Egmont and Chagos Bank collections are particularly noteworthy. The rare genus *Ctenella* has so far been recorded only from Chagos and Saya da Malha. (Pichon's (1964) record of *Ctenella* from Madagascar has turned out to be *Gyrosmitia* (Personal

communication), an obscure genus of limited distribution.) But *Ctenella* is certainly not uncommon in the Chagos area. A good many specimens of "*Agariciella*" were also collected during the recent expeditions. This is an Agariciid closely allied to *Leptoseria* and *Pavona* (*Polyastra*). It certainly deserves generic or subgeneric status and a redescription is urgently required. "*Agariciella*" seems to occur mostly in the western Indian Ocean, but there has been some confusion with *P.* (*Polyastra*). (See Rosen, 1971b; Ma, 1937). Other less common genera found in the Chagos include *Oulophyllia* and *Plerogyra*, and the newly recorded *Pavona* (*Polyastra*), *P.* (*Pseudocolumnastrea*) and *Physogyra*. *Horastrea*, a genus recently described by Pichon (1971) appeared in both the Egmont and Chagos Bank collections. In the past it may have been confused with other Siderastreids such as *Coscinaraea*. Prior to the Chagos record, it has been found only in the southwest Indian Ocean, where it is fairly common.

In generic terms at least, the Egmont and Chagos Bank collections broadly overlap, and over 85% of the total hermatypic genera occur in both collections. Rosen (1971c) gives the numbers of genera and species recorded at different Chagos atolls, with 29 hermatypic genera recorded at Salomon compared with only 16 at Peros Banhos and Egmont. Such differences, and the fact that Rosen's check-list reports far fewer genera than recently recorded, show that the Chagos area was not very thoroughly sampled until the 1970s. Judging from the latest records, it seems fair to assume that all the atolls have a similarly high diversity, with at least 50 hermatypic genera.

From the latest records it appears that the diversity in the Chagos approaches that recorded in the Southern Maldives. Genera found in the Seychelles and/or the S. Maldives, such as *Diploastrea*, *Psammisora* (*Stephanaria*) and *Anacropora*, may well be recorded from Chagos in future collections. Wells (1966) presents a map showing the distribution of the various Fungiids in the Indo-Pacific. All the Fungiids so far recorded in the Chagos fall within the ranges defined by Wells. Wells' map also predicts that *Fungia* (*Ctenactis*) and *Herpetoglossa* could occur in the Chagos area. These genera may well be collected during future expeditions, or found among the Fungiids not fully identified from the Chagos Bank collection.

As stated above, there is a high diversity focus in the western Indian Ocean which may or may not be continuous with the very rich Indonesian-west Pacific centre. It seems to be fairly well established that the high diversity centres in the Atlantic and Indo-Pacific lie slightly north of the equator. But at least 55 hermatypic genera have definitely been recorded from the Chagos Islands, and the true figure may well be over 60 genera. Thus the diversity here, about 5° to 7°S, and the large number of genera reported in the Seychelles, suggest that the high diversity focus may extend some way south of the equator.

CHAPTER FIVE

SUGGESTIONS REGARDING SAMPLING METHODS AND THE AIMS OF FUTURE STUDIES

It is not possible within the scope of this thesis to give a full review of the sampling methods adopted in the various reef studies undertaken so far. And never having taken part in any field studies on reefs, the author is in no position to dictate to others how such work should be carried out. The purpose of this chapter is simply to summarise some of the difficulties encountered in the course of coral reef surveys, and to recommend some standardisation of the recording of data in future studies.

In the past, many of the studies of reefs and reef corals have been of a qualitative nature. Some of the recent surveys have attempted to collect data in a more quantitative way. But the methods of sampling have varied greatly, and in the absence of standard criteria in recording, much of the quantitative information obtained in different areas is not comparable. An example is the size of quadrat chosen by different workers: where numbers of genera or species per quadrat have been recorded, variation in quadrat size has prevented any meaningful comparison of diversity. Stoddart (1969) lists the quadrat sizes used in a number of studies at different locations, and this ranges from 0.8 to 930m²; sometimes the same workers have used different sizes on different reefs. Selection of quadrat size often seems to be arbitrary, and few attempts have been made to relate quadrat size to statistical criteria. But Scheer (e.g. 1974) has plotted species diversity at Radsu Atoll, Maldives, against area, using quadrats from 0.1m² to 100m². For subsequent work he used a quadrat

size of 5m x 5m, as this area, with an average of 28 species, corresponded to about two thirds of the final asymptotic value (100m² with 37 species).

Although many quantitative studies have used continuous quadrats, or sample quadrats at intervals along transects, the type of information recorded from the quadrats has varied. This has included counts of the number of genera or species in a quadrat; subjective or more quantitative estimates of percentage cover by the corals; the recording of coral growth forms. Pichon (1964) discusses some of the problems of using quadrat sampling techniques on the reef flat and front, and the particular problems encountered on steep slopes.

Loya (1972) has grave doubts about the value of many quantitative studies carried out, and states that "In general, most of them have no usable quantitative data." For a study of the coral communities at Eilat from the reef flat down to 30m, Loya and Slobodkin (1971) (see also Loya, 1972) used line transects instead of quadrats. They found this method more satisfactory on reef slopes with a complex bottom topography. Transects 10m in length were placed along depth contours parallel to the shore, and all corals which lay under the line were recorded and measured. Measurements were also taken of corals growing beneath other colonies. It was found that the line transect survey was very efficient in terms of the information recorded per time spent underwater, an important consideration where deeper diving is concerned.

There are many problems associated with recording coral data, and the difficulties are accentuated if the work is being carried out entirely underwater. Firstly, many coral species and even genera cannot be readily identified, and must be removed, cleaned and examined closely.

The use of photographic records has become increasingly popular, but they are useful only as an indication of major coral types and growth forms. Small specimens and those growing beneath other colonies will not show up; and many species cannot be identified from photographs (see Loya, 1972). Drawings (on slates) have been used to record the percentage cover by different species and the relative positions of colonies. Such data are certainly valuable, but there are errors involved in transferring complex three-dimensional distributions to a two-dimensional plane. Difficulties arise also in estimates of colony size and percentage cover. Colony definition is very difficult, especially for branching and encrusting forms. There are problems with scale for corals growing on vertical or overhanging surfaces, though Pichon (1964) suggests methods of recording coral cover on steep slopes.

To collect such detailed information is very time-consuming, and for satisfactory recording a combination of photographic and sketch records is required, followed by collection of the coral material. Some standards are urgently needed, not only for quadrat size, but for colony definition in cover estimates.

There are however disadvantages in detailed quadrat sampling in that this method concentrates attention on a section of the reef which may be unrepresentative. Surveying by direct visual observations will only provide data regarding the more obvious features of the reef and gross zonation patterns. But a much larger area can be covered and a better impression may be gained of the local variation on a reef. Subjective assessments of broad reef features will not provide quantitative data comparable with other localities, but it is important to combine detailed study with general observations. Ideally the positioning of all transects

should be randomised. However, this is not easy in underwater study where adverse environmental conditions may prevent sampling in certain areas. And in order to spend the maximum possible time working underwater, it may be desirable to locate transects in more accessible areas of the reef. Spencer Davies *et al* (1971) discuss the problems of positioning transects, and mention that random sampling was difficult in areas with human activity (e.g. because of jetties).

If divers can make general observations within a larger area, some check can be made that transects do at least cover fairly typical sections of the reef, if positioning of transects cannot be altogether randomly determined. This may appear to be a rather unscientific approach, but even in a strictly conducted terrestrial survey there is always an element of subjectivity, and the problems are far more acute in the marine environment.

In summary, a combination of detailed surveying and broad observation is required in any reef study. A standard procedure for data recording should be laid down to allow a meaningful comparison of data collected on different reefs. An investigation of sampling techniques is urgently required to find those methods which provide the maximum amount of information per time spent underwater. The advance of underwater diving with SCUBA has provided access to areas of the reef which previously could only be sampled by dredging. But very few studies have been carried out on reef areas below a few metres in depth, and future studies should focus attention on the poorly sampled reef slopes. All publications on reef sampling carried out by divers should include a report on the difficulties encountered, and suggestions on how these might be overcome. Any collection of corals should, wherever possible, be accompanied by full details on location, bottom topography, currents, exposure, and so forth.

In addition to sampling by divers, carefully organised dredging of deeper water is also required; the only account of deep water coral zonation (to over 146m) is that provided by Wells (1954).

There are vast problems in the field of coral systematics, and work on corals will remain very difficult until their taxonomy (especially at species level) is better understood. Studies of coral ecology must be combined with laboratory work for remarkably little is known about the behaviour, physiology and life history of the coral polyps.

It has already been stated that much valuable information was lost from the Egmont and Chagos Bank collections, mostly through inadequate labelling of specimens. For any reef coral survey, all specimens should be clearly labelled showing depth, locality and any other information required. To ensure that labels do not decay, the author recommends the use of paper labels sealed in polythene, or non-degradable labels such as plastic "dymo-tape" or metal tags. Careful packing of corals is necessary to avoid breakage, and specimens should be surrounded with plenty of straw or polystyrene chips when packed into crates.

Identification of corals is often very problematic. For detailed surveys it is most helpful, whenever possible, to include in the expedition persons with a good knowledge of the taxonomy. It is further recommended that specimens of adequate size be collected, as some species are very difficult to identify from small specimens.

In Section III of Chapter 2 some discussion was devoted to the use of phytosociological methodology in reef studies. Such an approach, coupled with the setting down of standards for sampling procedure, may prove very valuable for describing and comparing coral communities and improving our understanding of reef coral ecology.

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APPENDIX A PRELIMINARY CHECK LIST OF CORALS COLLECTED AT
EGMONT AND THE CHAGOS BANK

Generic classification is according to Wells (1956). Species are listed in alphabetical order. Notes on identification are given below. Figures in brackets indicate approximate numbers of specimens from Chagos Bank. No figures are available for the Egmont specimens.

Notation : EG = from Egmont Atoll. CB = from Chagos Bank
* new record over Rosen's (1971c) check list (genera only)

phylum COELENTERATA Frey and Leuckart
subphylum CNIDARIA Hatschek
class ANTHOZOA Ehrenberg
subclass ZOANTHARIA de Blainville
order SCLERACTINIA Bourne
suborder ASTROCOENIINA Vaughan and Wells
family ASTROCOENIIDAE Koby
subfamily ASTROCOENIINAE Felix

genus *Stylocoeniella* Yabe and Sugiyama
Stylocoeniella spp. EG

family THAMNASTERIIDAE Vaughan and Wells

genus *Psammocora* Dana
subgenus *Psammocora* Dana
Psammocora (*Psammocora*) spp. EG and CB

* subgenus *Plesioseris* Duncan
Psammocora (*Plesioseris*) spp. EG and CB (163)

family POCILLOPORIDAE Gray

genus *Stylophora* Schweigger
Stylophora mordax (Dana) EG
Stylophora cf. *mordax* (Dana) CB (31)
Stylophora pistillata (Esper) EG
Stylophora cf. *pistillata* (Esper) CB (24)
Stylophora spp. type I CB (6)
Stylophora spp. deep water forms CB (12)
Stylophora spp. EG and CB (41)
? *Stylophora* spp. CB

genus *Seriatopora* Lamarck
Seriatopora spp. EG and CB (20)

genus *Pocillopora* Lamarck
Pocillopora damicornis (Linnaeus) EG
Pocillopora cf. *damicornis* (Linnaeus) CB (4)
Pocillopora danae Verrill EG

Pocillopora eydouxi Milne-Edwards and Haime EG
Pocillopora cf. *eydouxi* (Milne-Edwards and Haime) CB (74)
Pocillopora verrucosa (Ellis and Solander) EG
Pocillopora danae/verrucosa EG and CB (2)
Pocillopora spp. encrusting EG
Pocillopora spp. EG and CB (18)

genus *Acropora* Oken

Acropora cf. *abrotanoides* (Lamarck) EG
Acropora humilis (Dana) EG
Acropora hyacinthus group EG
Acropora palifera (Lamarck) EG and CB (11)
Acropora cf. *patula* (Brook) EG
Acropora cf. *murrayensis* (Vaughan) EG
Acropora cf. *variabilis* (Klunzinger) EG
Acropora spp. type 1 cf. *humilis* (Dana) CB (15)
Acropora spp. type 2 cf. *variabilis* (Klunzinger) CB (48)
Acropora spp. type 3 cf. *hyacinthus* (Dana) CB (39)
Acropora spp. EG and CB (102)

genus *Astreopora* de Blainville

Astreopora spp. EG and CB (65)

genus *Montipora* Quoy and Gaimard

Montipora foveolate group EG
Montipora non-tuberculate group EG
Montipora tuberculate group EG
Montipora verrucosa group EG
Montipora spp. EG and CB (275)

suborder FUNGIINA Verrill

superfamily AGARICIICAE Gray

family AGARICIIDAE Gray

genus "*Agariciella*" Ma

"*Agariciella*" spp. EG and CB (77)

genus *Pavona* Lamarck

subgenus *Pavona* Lamarck

Pavona (Pavona) clavus group EG and CB (131)
Pavona (Pavona) cf. *danae* (Milne-Edwards and Haime) EG
Pavona (Pavona) varians group EG and CB (79)
Pavona (Pavona) spp. "exsert septa" EG
Pavona (Pavona) "unifacial frond" group EG
Pavona (Pavona) spp. EG and CB (14)

* subgenus *Polyastra* Ehrenberg

Pavona (Polyastra) spp. EG and CB

* subgenus *Pseudocolumnastrea* Yabe and Sugiyama

Pavona (Pseudocolumnastrea) spp. EG and CB

genus *Leptoseris* Milne-Edwards and Haime

Leptoseris spp. type 1 CB (11)

Leptoseris spp. EG and CB (66)

genus *Leptoseris?* Milne-Edwards and Haime

Leptoseris? *mycetoseroides* group EG and CB (87)

cf. *Leptoseris?* *mycetoseroides* group CB (15)

genus *Pachyseris* Milne-Edwards and Haime

Pachyseris spp. EG and CB (82)

family SIDERASTREIDAE Vaughan and Wells

*genus *Coscinaraea* Milne-Edwards and Halme*Coscinaraea* spp. EG and CB (20)cf. *Coscinaraea* spp. CB (8)cf. *Coscinaraea* spp. convoluted CB (3)*genus *Horastrea* n. gen.*Horastrea* spp. EG and CB (37)cf. *Horastrea* spp. cerloid CB (8)

superfamily FUNGIICAE Dana

family FUNGIIDAE Dana

*genus *Cycloseris* Milne-Edwards and Halme*Cycloseris* spp. CB (32)? *Cycloseris* spp. EGgenus *Fungia* Lamarcksubgenus *Pleuractis* Verrill*Fungia* (*Pleuractis*) spp. EG and CB (75)*Fungia* (?*Pleuractis*) spp. EGsubgenus *Verrillofungia* Wells*Fungia* (*Verrillofungia*) cf. *granulosa* Klünzinger CB (24)*Fungia* (*Verrillofungia*) spp. EG and CB (7)*Fungia* (?*Verrillofungia*) spp. CB (4)subgenus *Danafungia* Wells*Fungia* (*Danafungia*) spp. EG and CB (1)subgenus *Fungia* Lamarck*Fungia* (*Fungia*) *fungites* (Linnaeus) EG and CB (11)*Fungia* (?*Fungia*) *fungites* (Linnaeus) CB (6)small *Fungia*, subgenera not determined CB (12)genus *Herpolitha* Eschscholtz*Herpolitha limax* (Esper) EG*Herpolitha* spp. CB (7)? *Herpolitha* spp. CB (3)*genus *Podabacia* Milne-Edwards and Halme*Podabacia* spp. EG and CB (11)genus *Halomitra* Dana*Halomitra* sp. CB (1)

superfamily PORITICAE Gray

family PORITIDAE Gray

genus *Goniopora* de Blainville*Goniopora* cf. *stokesi* Milne-Edwards and Halme?*Goniopora* spp. type I CB (3)*Goniopora* spp. EG and CB (70)genus *Porites* Linksubgenus *Porites* Link*Porites andrewsi* group EG*Porites* (*Porites*) *lichen* Dana EG and CB (33)*Porites* (*Porites*) massive group EG and CB (106)*Porites* (*Porites*) massive/encrusting group EG and CB (101)*Porites* (*Porites*) spp. branching CB (13)subgenus *Synaraea* Verrill*Porites* (*Synaraea*) spp. EG and CB (9)genus *Alveopora* de Blainville*Alveopora* spp. CB (4)

suborder FAVIINA Vaughan and Wells
 superfamily FAVIICAE Gregory
 family FAVIIDAE Gregory
 subfamily FAVIINAE Gregory

genus *Plesiaastrea* Milne-Edwards and Haime

Plesiaastrea sp. EG

genus *Favia* Oken

Favia matthai Vaughan EG

Favia pallida/favus group EG and CB (212)

Favia stelligera (Dana) EG and CB (85)

Favia cf. stelligera (Dana) CB (15)

Favia spp. EG and CB (6)

genus *Favites* Link

Favites pentagona group EG and CB (172)

Favites virens/abditia group EG and CB (77)

Favites spp. EG and CB (29)

genus *Oulophyllia* Milne-Edwards and Haime

Oulophyllia spp. EG and CB (22)

genus *Goniastrea* Milne-Edwards and Haime

Goniastrea pectinata/planulata group EG and CB (25)

Goniastrea cf. palauensis EG and CB (51)

Goniastrea retiformis group CB (21)

Goniastrea spp. EG and CB (5)

?*Goniastrea* spp. EG

genus *Platygyra* Ehrenberg

Platygyra spp. EG and CB (128)

genus *Leptoria* Milne-Edwards and Haime

Leptoria spp. EG and CB (19)

genus *Hydnophora* Fischer

Hydnophora spp. EG and CB (42)

subfamily MONTASTREINAE Vaughan and Wells

genus *Leptastrea* Milne-Edwards and Haime

Leptastrea spp. EG and CB (125)

genus *Cyphastrea* Milne-Edwards and Haime

Cyphastrea spp. EG and CB (33)

genus *Echinopora* Lamarck

Echinopora gemmacea (Lamarck) EG

Echinopora cf. gemmacea (Lamarck) CB (52)

Echinopora cf. lamellosa (Esper) CB (8)

family RHIZANGIIDAE d'Orbigny

* genus *Oulongia* Milne-Edwards and Haime

?*Oulongia* sp. EG and CB

family OCULINIDAE Gray

subfamily GALAXEINAE Vaughan and Wells

genus *Galaxea* Oken

Galaxea fascicularis (Lamarck) EG

Galaxea cf. fascicularis (Lamarck) CB (71)

Galaxea sp. type 1 CB (7)

family MEANDRINIDAE Gray
 subfamily MEANDRININAE Gray
 genus *Ctenella* Matthai
Ctenella sp. EG and CB (62)

family MERULINIDAE Verrill
 *genus *Merulina* Ehrenberg
Merulina sp. CB (1)

family MUSSIDAE Ortmann
 genus *Acanthastrea* Milne-Edwards and Haime
Acanthastrea echinata (Dana) EG
Acanthastrea spp. CB (85)
 genus *Lobophyllia* de Blainville
 subgenus *Lobophyllia* de Blainville
Lobophyllia (Lobophyllia) spp. EG and CB (19)
 ?*Lobophyllia (Lobophyllia)* spp. CB (7)
 genus *Symphyllia* Milne-Edwards and Haime
Symphyllia spp. EG and CB (62)
 ?*Symphyllia* spp. CB (9)
 Mussid fragments CB (21)

family PECTINIIDAE Vaughan and Wells
 *genus *Echinophyllia* Klunzinger
Echinophyllia spp. EG and CB (35)
 ?*Echinophyllia* spp. CB (5)
 *genus *Oxypora* Saville-Kent
Oxypora spp. EG and CB (4)
 ?*Oxypora* spp. EG
 *genus *Mycedium* Oken
Mycedium spp. EG and CB (20)
 ?*Mycedium* spp. CB (5)
 *genus *Pectinia* Oken
Pectinia spp. CB (2)
 Pectiniid fragments EG and CB (30)

suborder CARYOPHYLLIINA Vaughan and Wells
 superfamily CARYOPHYLLIICAE Gray
 family CARYOPHYLLIIDAE Gray

subfamily CARYOPHYLLIINAE Gray

*genus *Paracyathus* Milne-Edwards and Haime
 ?*Paracyathus* sp. EG
 *genus *Polycyathus* Duncan
Polycyathus sp. CB (1)

subfamily DESMOPHYLLINAE Vaughan and Wells
 *genus *Desmophyllum* Ehrenberg
Desmophyllum sp. CB (1)

subfamily EUSMILIINAE Milne-Edwards and Haime
 genus *Euphyllia* Dana
Euphyllia spp. EG
 genus *Plerogyra* Milne-Edwards and Haime
Plerogyra spp. EG and CB (1)

- *genus *Physogyra* Quelch
Physogyra spp. EG and CB (1)
 ?*Physogyra* sp. CB (1)

suborder DENDROPHYLLIINA Vaughan and Wells
 family DENDROPHYLLIIDAE Gray

- genus *Balanophyllia* Wood
Balanophyllia spp. CB (1)
 *genus *Cladopsammia* Lacaze-Duthiers
Cladopsammia sp. CB (1)
 genus *Dendrophyllia* de Blainville
Dendrophyllia spp. EG and CB (4)
Dendrophyllia spp. EG
 *genus *Tubastrea* Lesson
Tubastrea spp. EG and CB (35)
 genus *Tubinaria* Oken
Tubinaria spp. EG and CB (24)
 Dendrophyllids CB (16)

subclass OCTOCORALLIA Haeckel
 order STOLONIFERA Hickson
 family TUBIPORIDAE Ehrenberg

- genus *Tubipora* Linnaeus
Tubipora musica (Linnaeus) EG and CB (18)

- order COENOTHECALIA Bourne
 family HELIOPORIDAE Moseley
 genus *Heliopora* de Blainville
Heliopora coerulea Pallas. EG and CB (31)

There were also various hydrozoans *Millepora*, *Distichopora*, etc.
 but most were not fully identified.

Notes on the Identification

The identification of both collections, especially the much larger collection from Chagos Bank, is very preliminary, and a great deal of work still remains to be done.

It has been recorded above whether coral types were collected at Egmont or Chagos Bank. In a few cases, certain genera or species may have been found only in one of these areas. But the identification of the Chagos Bank collection was generally less detailed than that of the Egmont material. Therefore, a species recorded so far only at Egmont may well be contained in the Chagos Bank collection, but has not as yet been identified. For example, *Acropora* cf. *abrotanoides* is indicated as coming only from Egmont, but it might be among the *Acropora* spp. in the Chagos Bank collection.

The identification of almost 4000 specimens from Chagos Bank had to be carried out within a few weeks, and owing to the author's limited knowledge, the classification is very preliminary and may in some cases need revision. Particular difficulty was experienced with tiny fragments where specimens had broken up in transit. However, the author hopes that the majority of the identifications are correct, and that the errors concern only a small percentage of the total collection.

The following points should be borne in mind regarding the Chagos Bank collection. Many of the specimens identified as *Stylophora* spp. are probably *Stylophora mordax*. Likewise, some of the *Pocillopora* spp. may turn out to be *P. eydouxi*. Apart from *Acropora palifera*, the *Acropora*

specimens have been divided rather arbitrarily into groups, mostly according to their growth form. *Acropora* spp. includes any specimens which could not be readily assigned to one of the above groups. Some difficulty was experienced with certain of the Agariciids and Siderastreids, and a few specimens have been recorded as cf. the genus, e.g. c.f. *Coscinaraea*. There were also problems with the subgenera of *Fungia* (except for *F. (Fleuraotis)*, and the identifications given here may need revision. Most of the *Porites* have been divided into massive or massive/encrusting groups, and there is considerable overlap between these two groups. *Platygyra* and *Leptoria* could not easily be distinguished, and there may be some incorrect identification here. Many of the Mussid and Pectiniid specimens were only small fragments, and some of these could only be assigned to the appropriate family. Small pieces of Dendrophylliids are probably *Dendrophyllia* or *Tubastrea*.

The author has previously stated that the identification of the Chagos Bank collection was very preliminary and that some errors were doubtless made. Since this thesis was originally submitted, the following taxonomic points have come to the author's notice, which should be brought to the reader's attention.

The species originally assigned to *Goniastrea* cf. *palauensis* (Yabe, Sugiyama and Eguchi) is in fact *Favites peresi* (Faure and Pichon, in press). Since the previous identification as *G.* cf. *palauensis* was at least consistent, the author has not sought to amend this in the text.

Some specimens identified as *Dendrophyllia* spp. are probably *Tubastrea micrantha* (Ehrenberg).

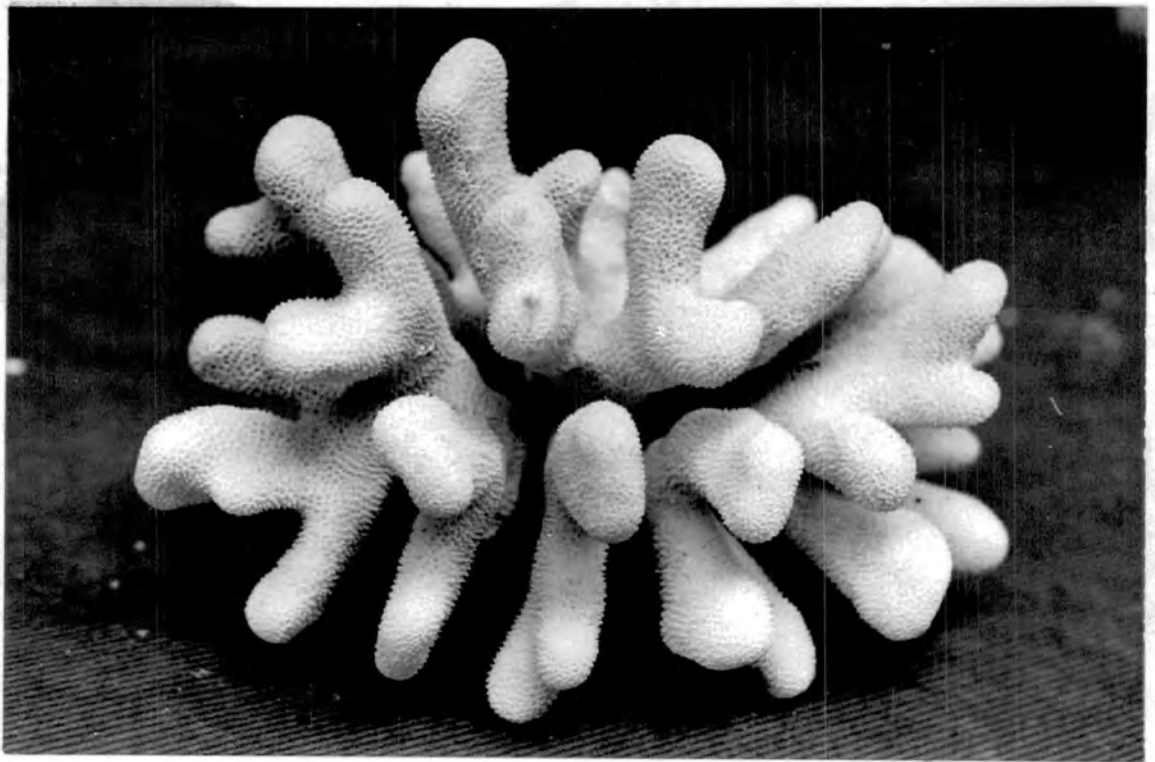
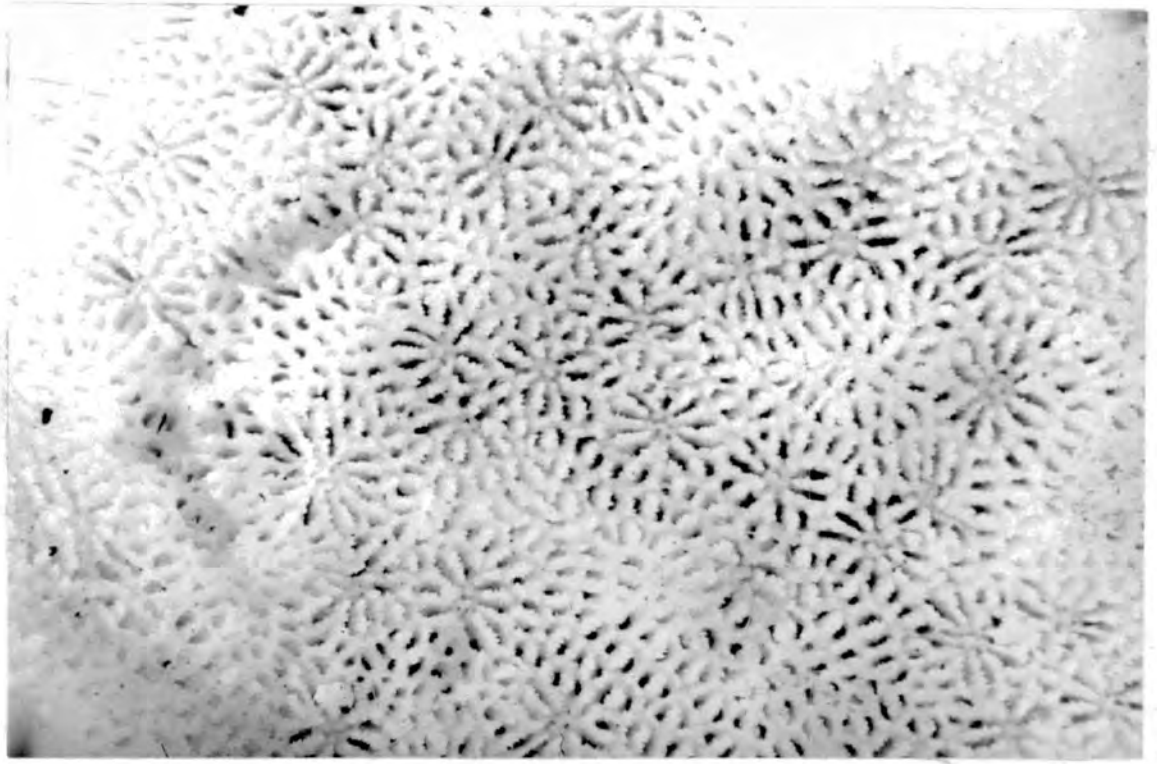
Finally, the author has reason to believe that the subgenus *Pavona* (*Polyastra*) may be a form of *Pavona varians* Verrill. While this systematic question remains unsolved, the author has retained *P.* (*Polyastra*), but with some reservations as to its validity.

PHOTOGRAPHS

The photographs which follow cover only a small range of the many genera found at Egmont and Chagos Bank. It was not possible to include more photographs, and unfortunately many interesting genera have not been represented.

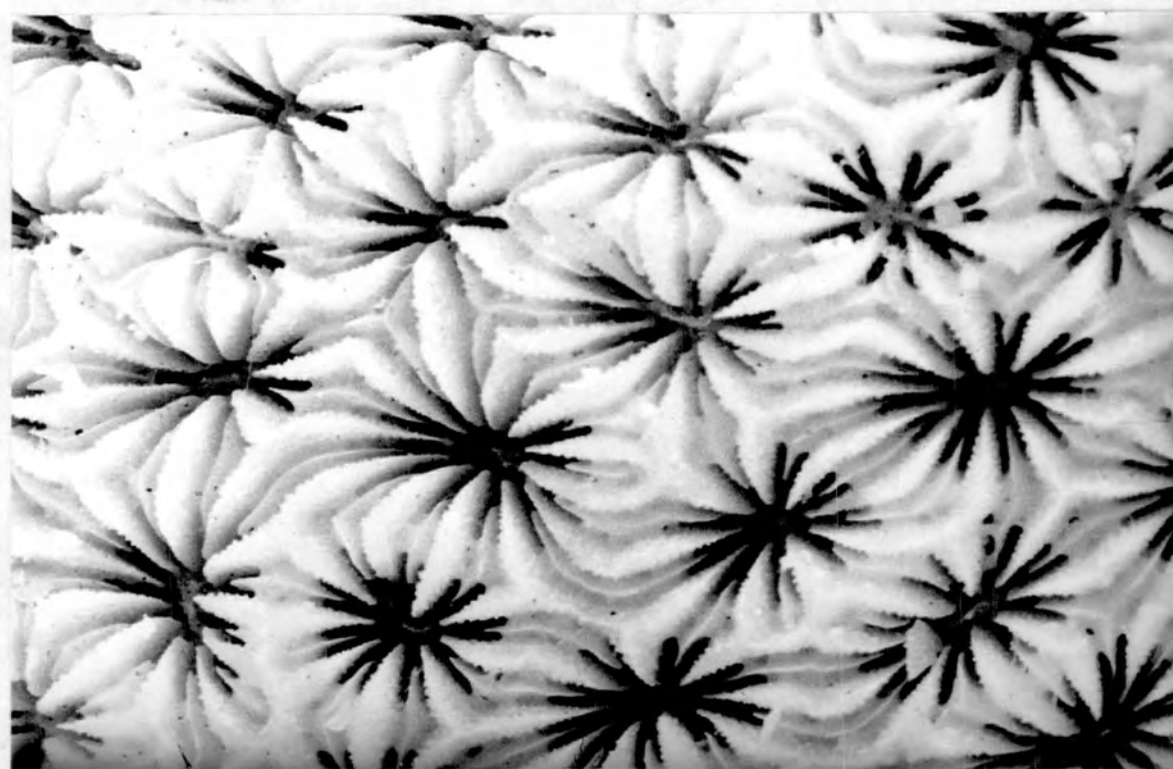
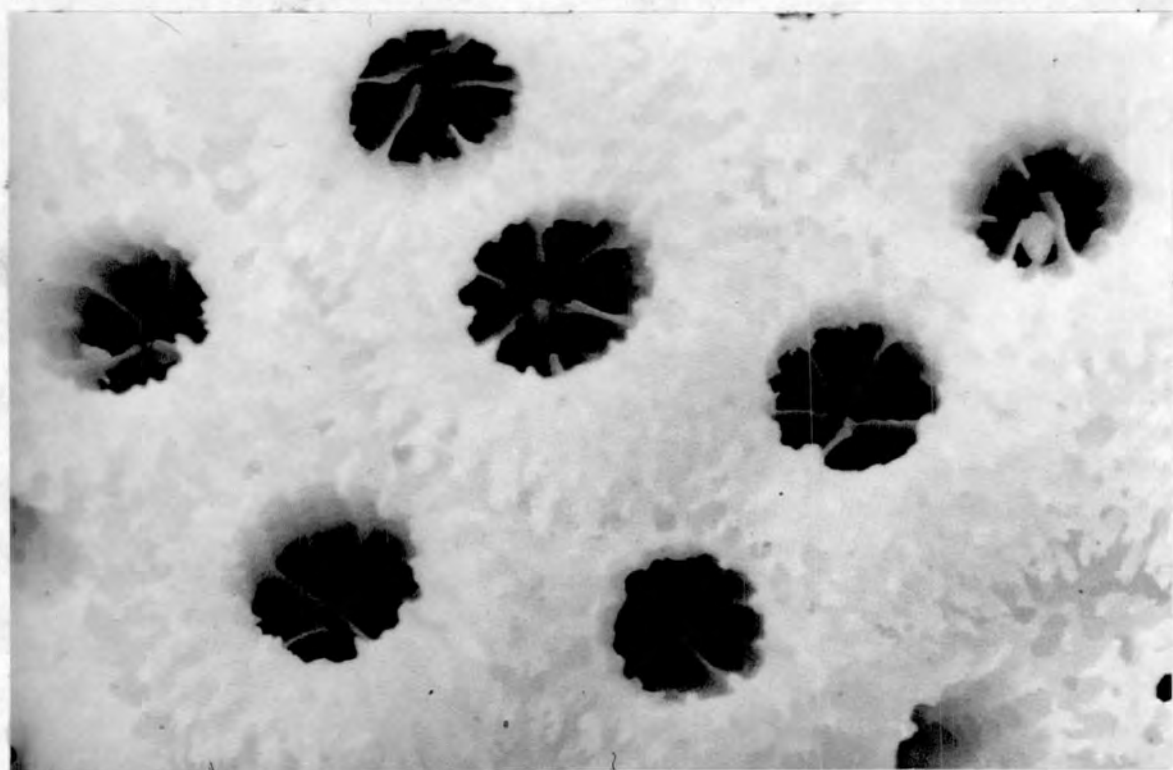
Some of the photographs were taken using a Zeiss "Tessovar" and the magnifications are indicated as appropriate.

I should like to thank Mr. Ted Hinton-Clifton for providing this photographic equipment and for assisting me with this work.



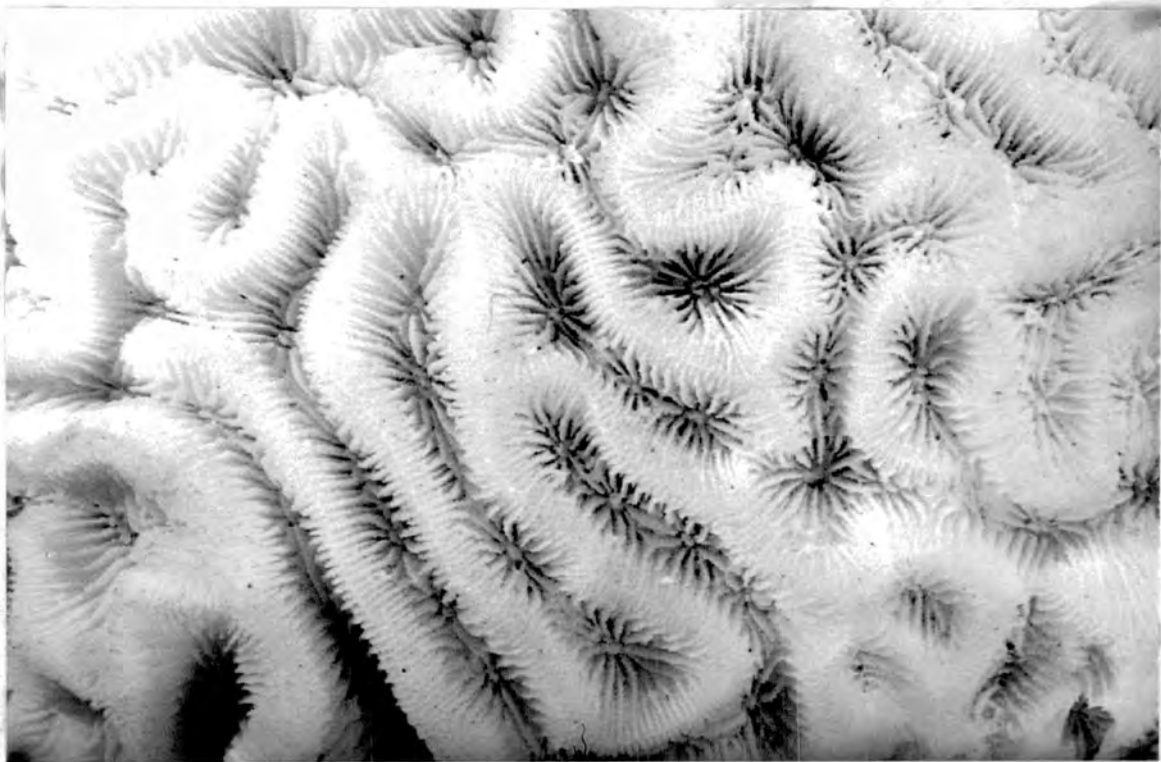
Above : *Psammocora* (*Psammocora*) x 11.25

Below : *Stylophora* cf. *mordax*



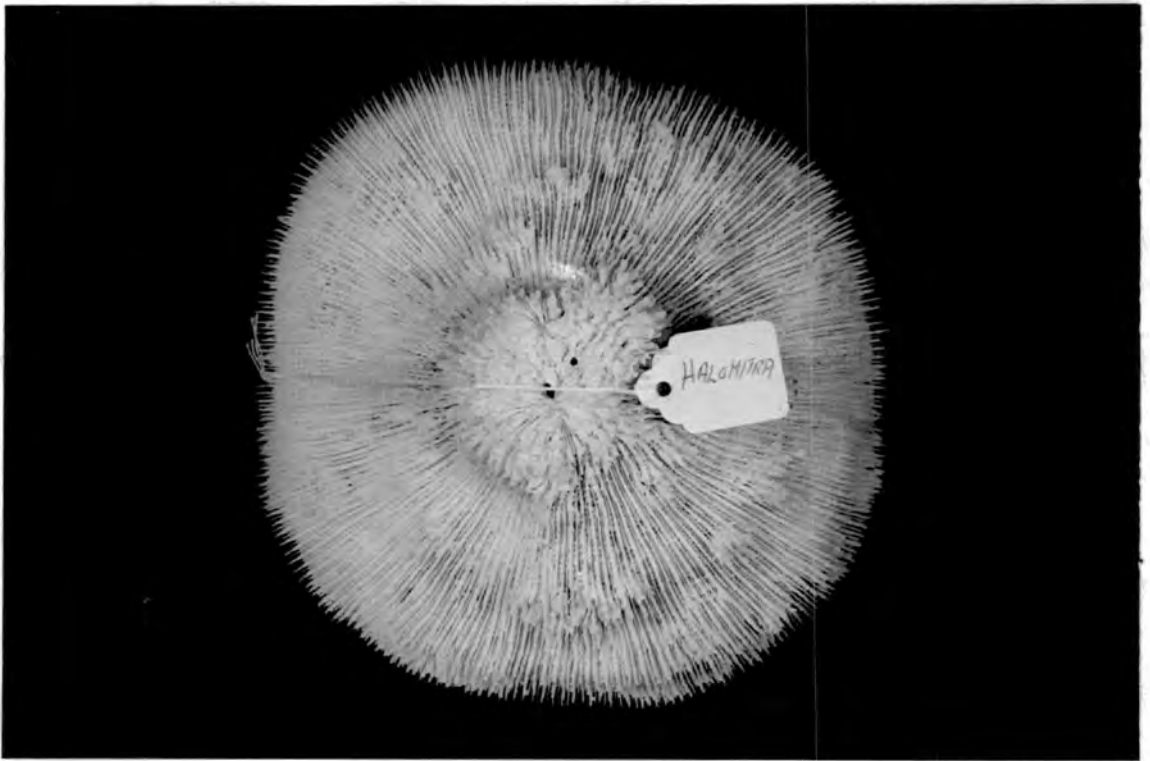
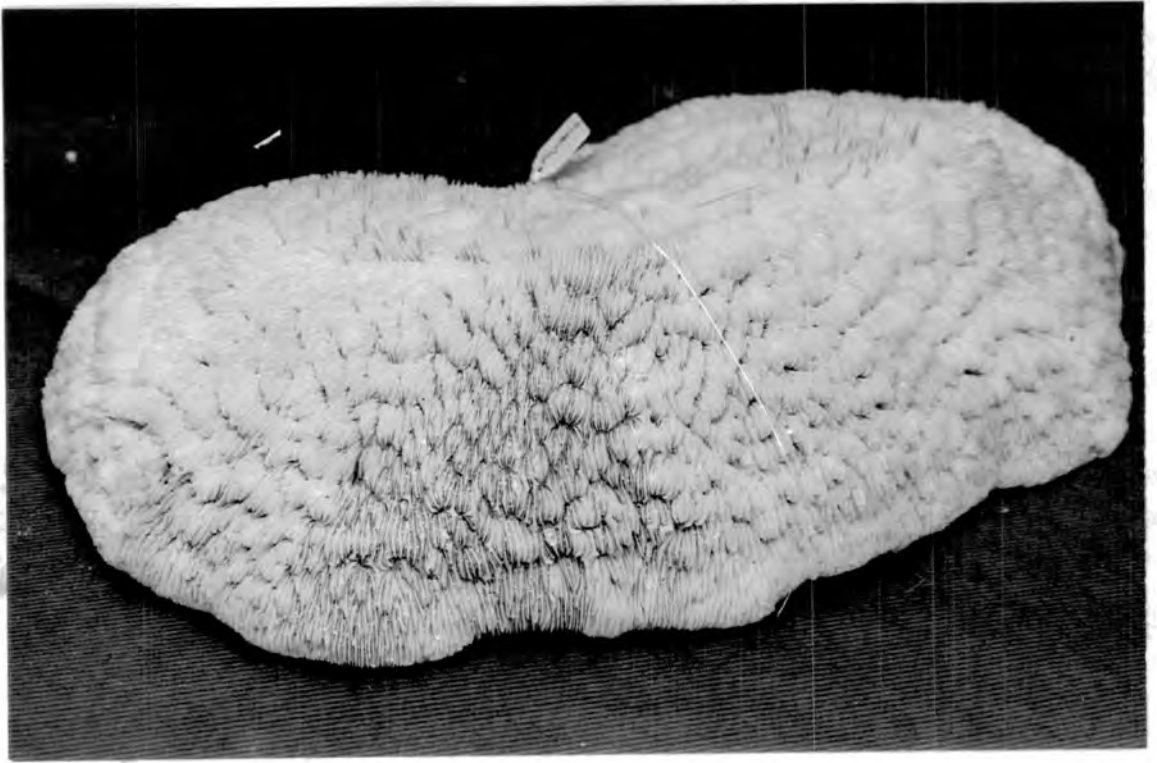
Above : *Astreopora* x 10

Below : *Pavona clavus* group x 9



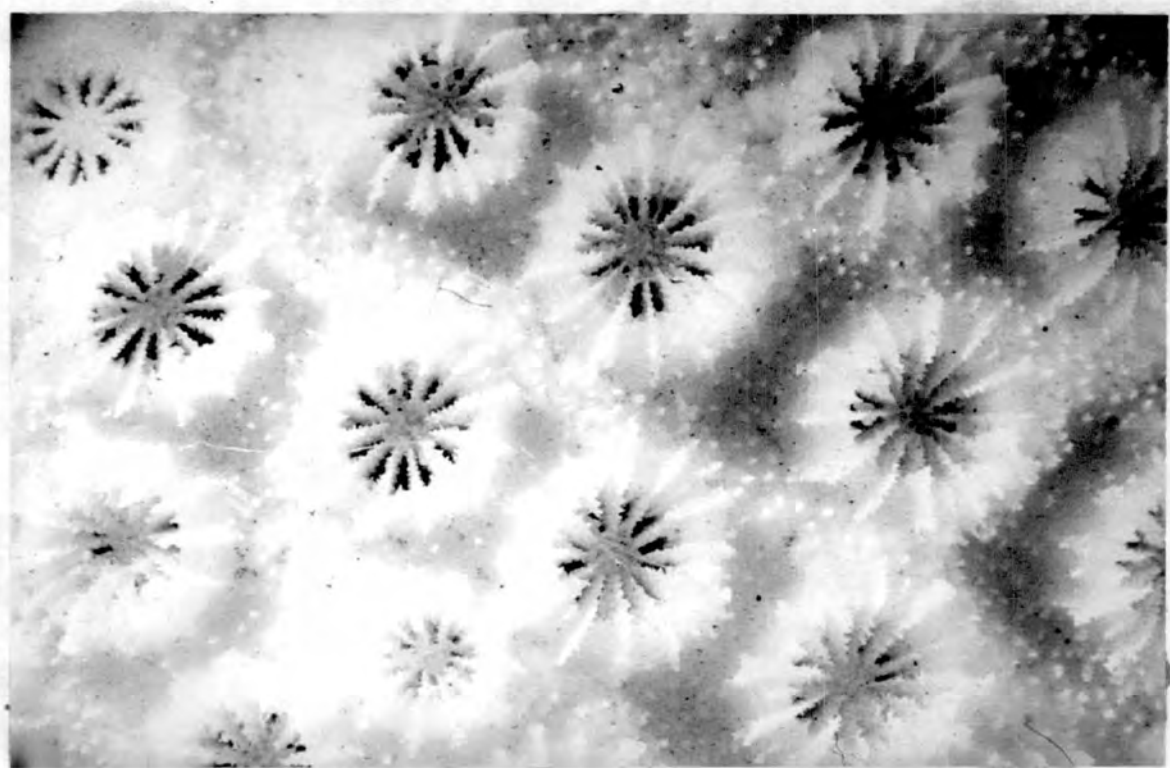
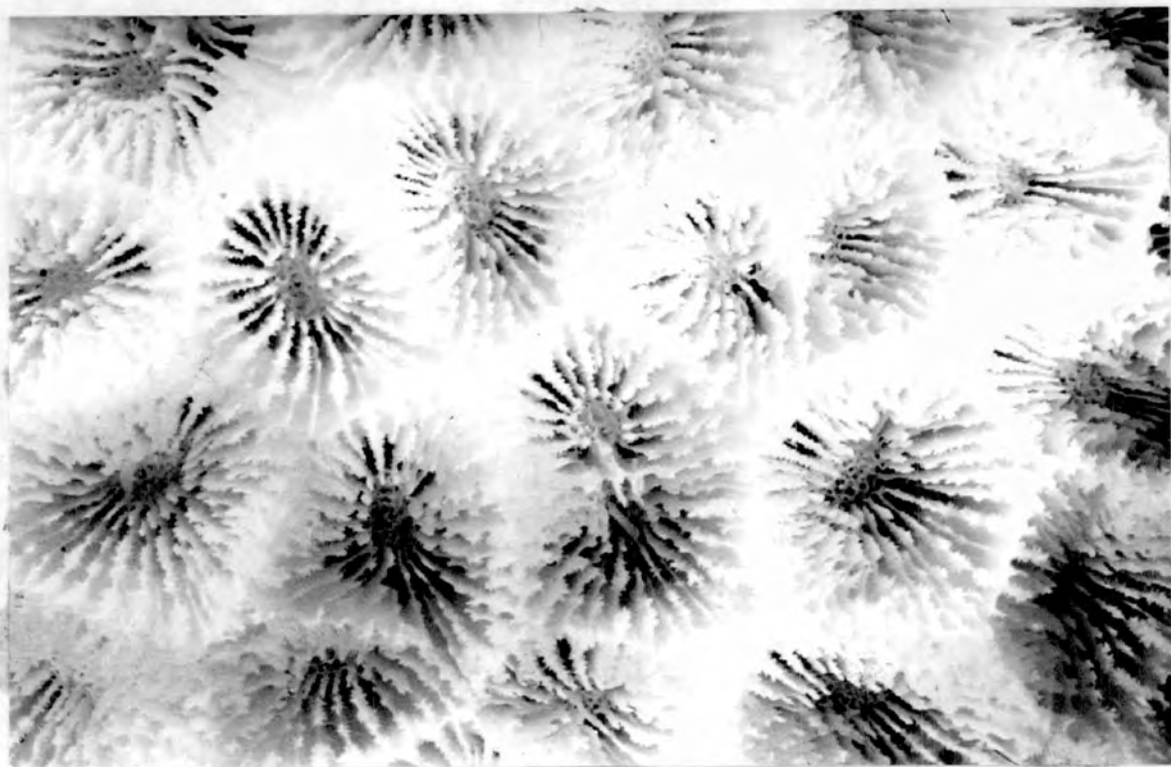
Above : *Favona (Polyastra)* × 5.6

Below : *Pachyseris*



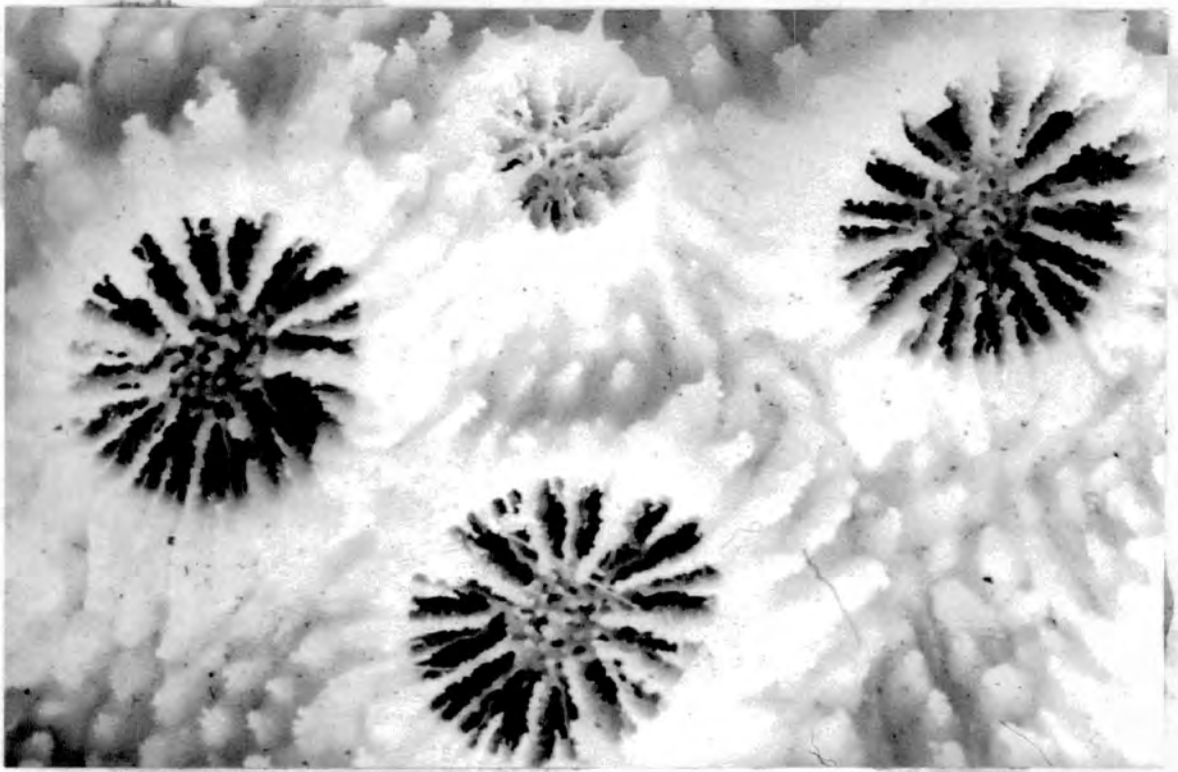
Above : *Herpolitha*

Below : *Halomitra*



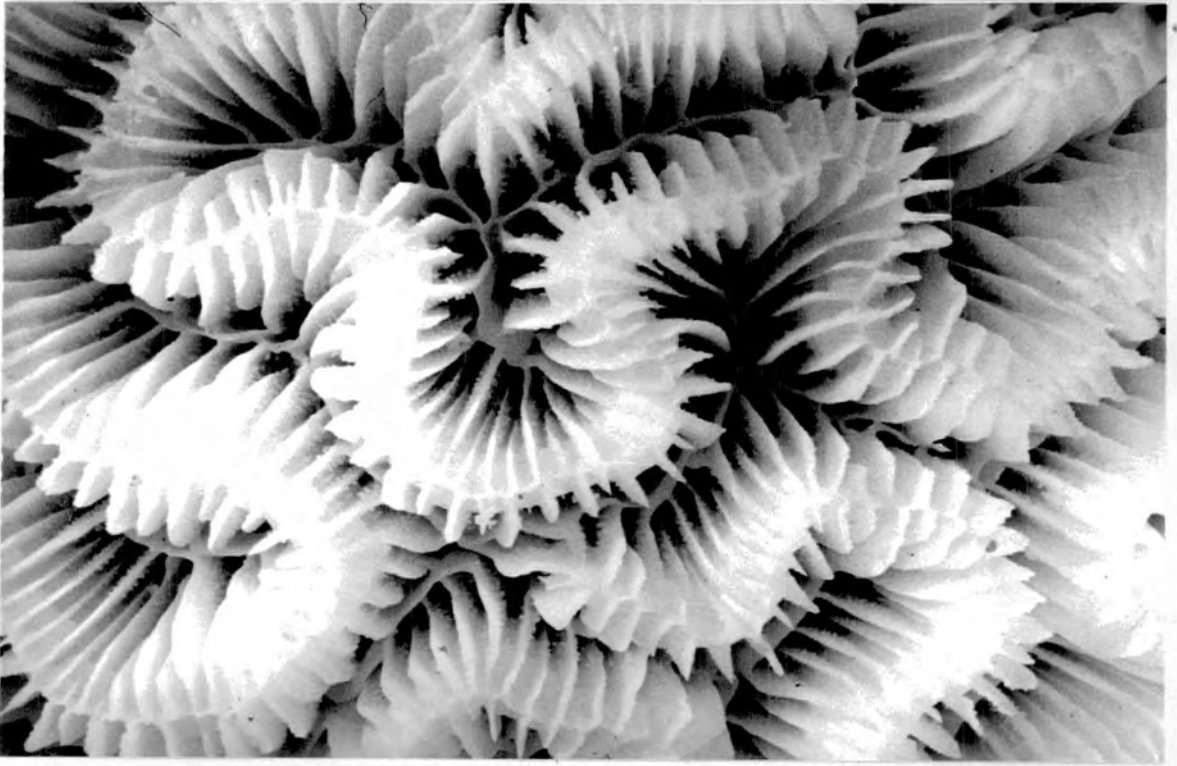
Above : *Goniastrea* cf. *palauensis* × 3.6

Below : *Cyphastrea* × 9

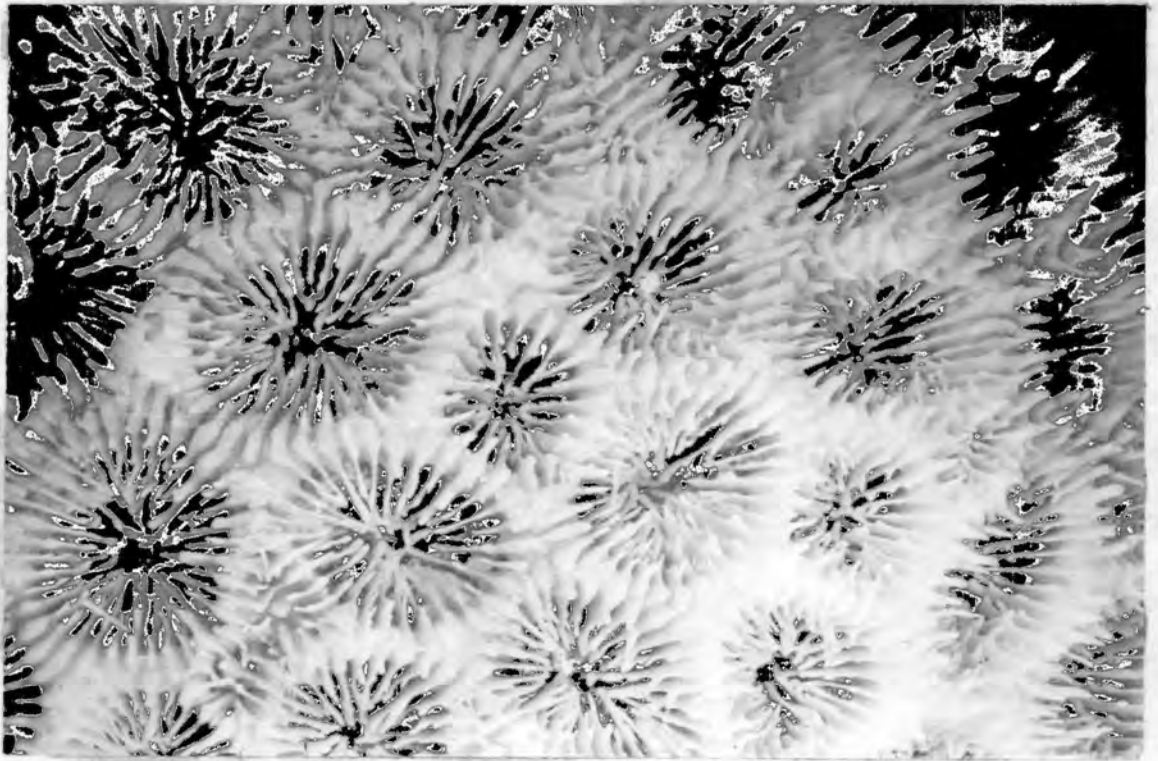
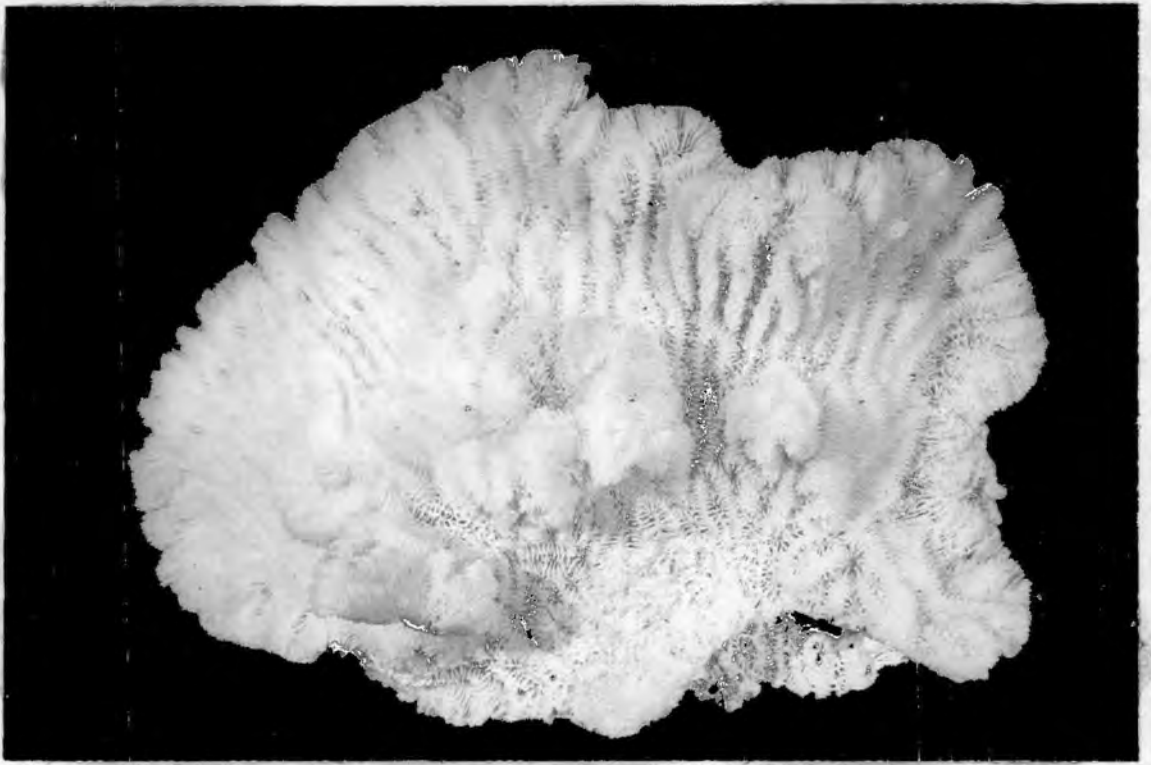


Above : *Echinopora* cf. *germacea* x 9

Below : *Ctenella*

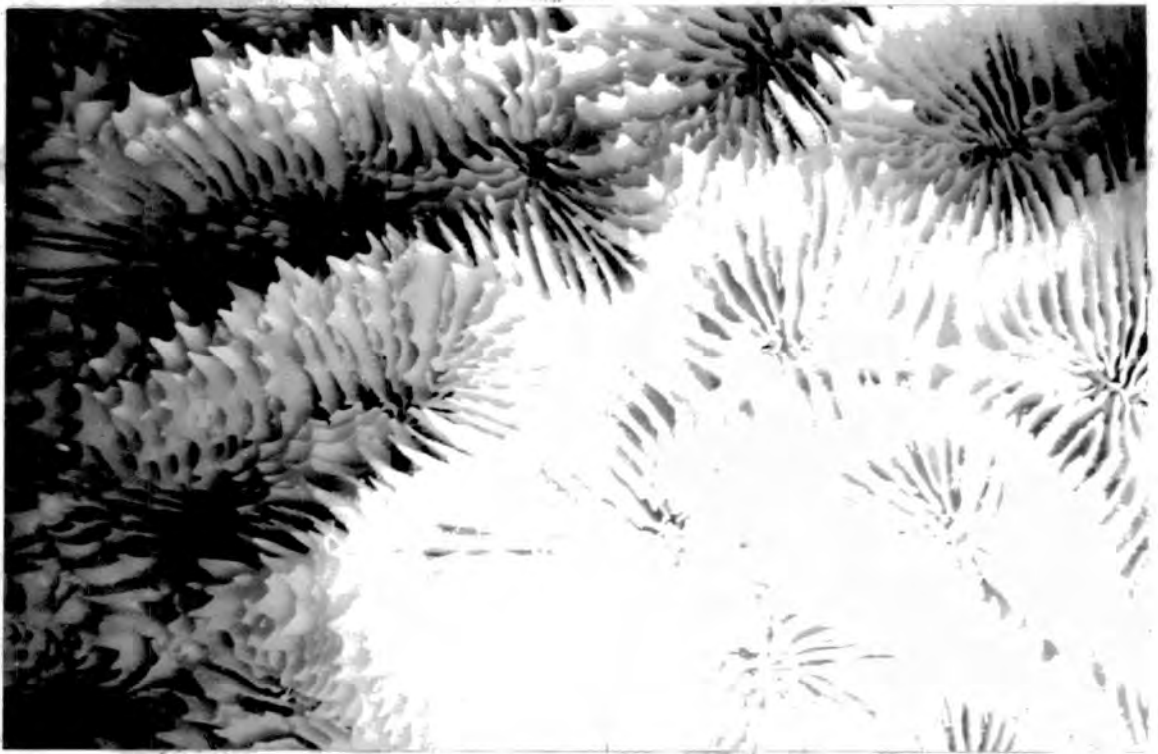
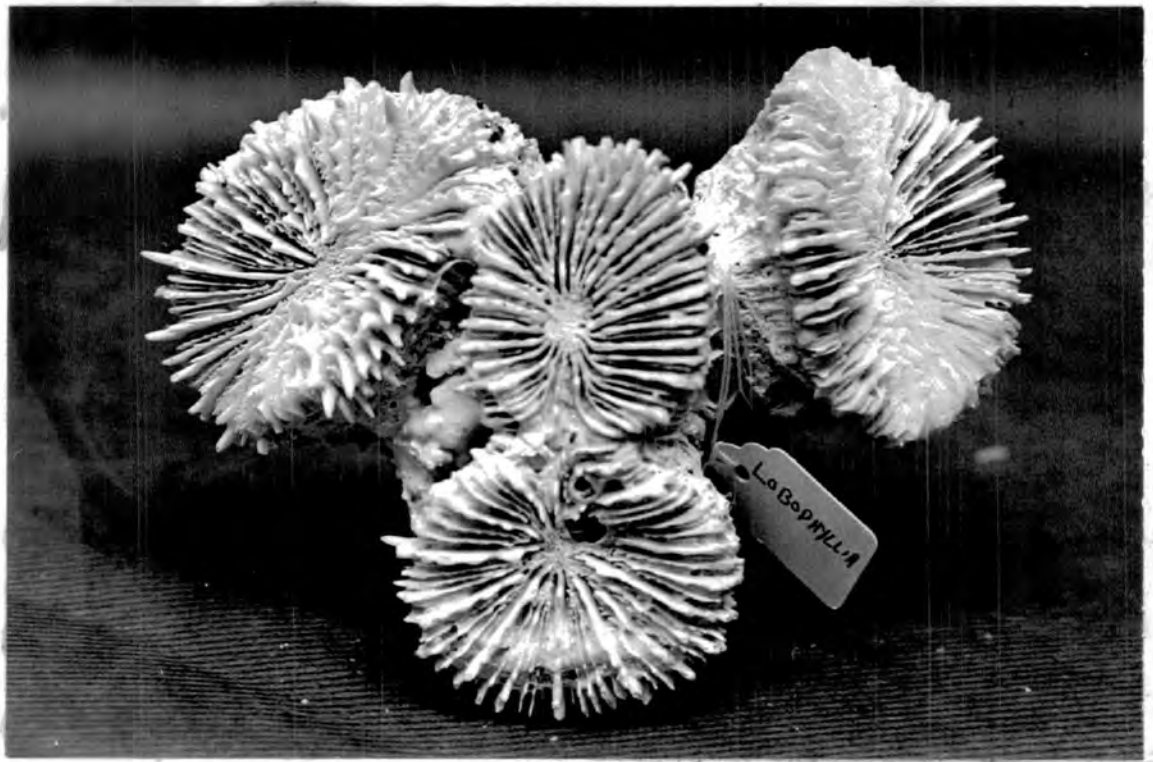


Ctenella x 4.5



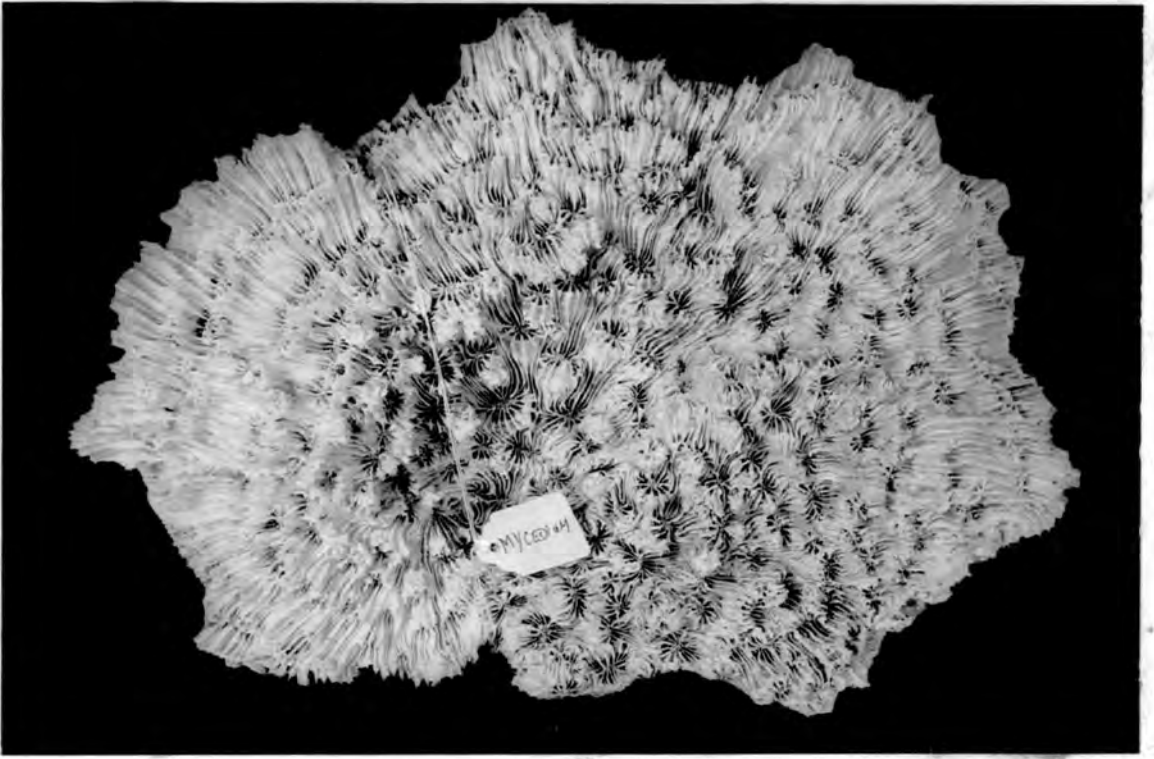
Above : *Merulina*

Below : *Acanthastrea* x 1.8



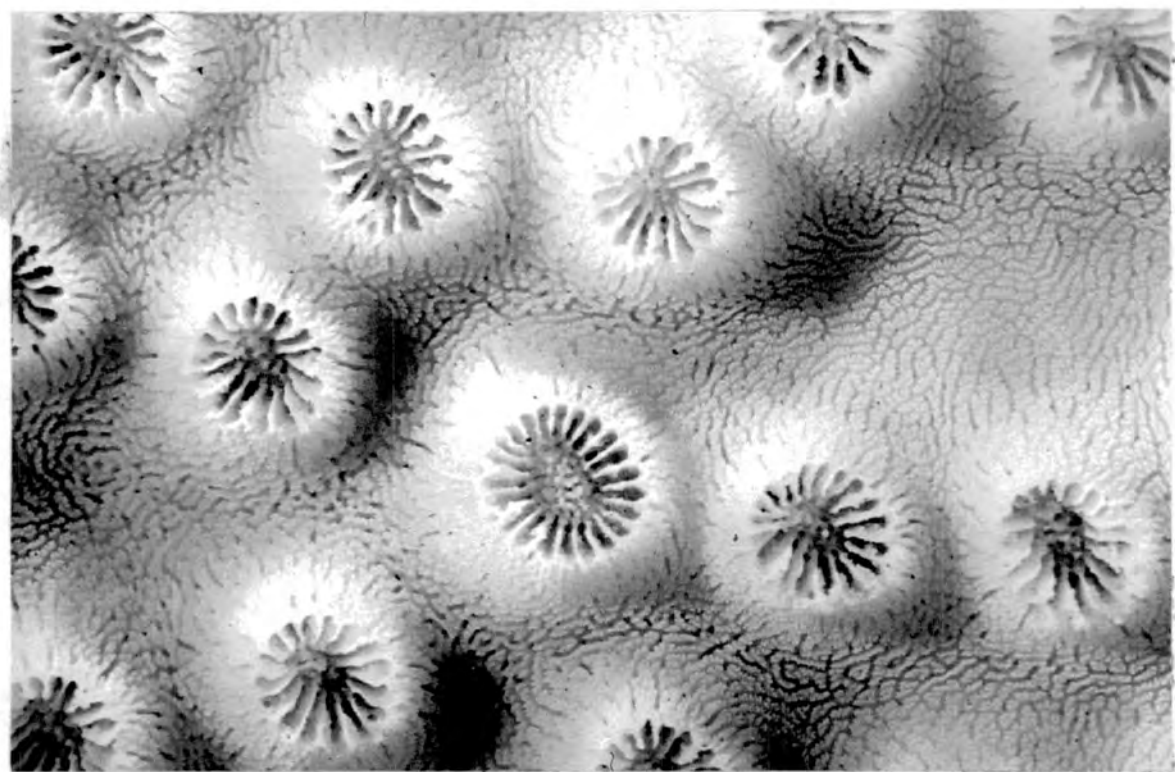
Above : *Lobophyllia*

Below : *Symphyllia* x 1.8



Above : *Mycedium*

Below : *Tubastrea*



Turbinaria x 7.9

APPENDIX B

SECTION I **Species similarity coefficients for Chagos Bank
coral data**

SECTION II **Specimens collected at Egmont Atoll on Transects 2 to 10.**

SECTION III **A SHUFFLE showing specimens collected in the 222 quadrat
and random samples from Chagos Bank which were used for
subsequent analysis of data.**

SECTION I Species Similarity coefficients for Chagos Bank coral data

Species similarity coefficients were calculated, pairing 42 of the most common genera and species, using data from 222 quadrat and random samples. The coefficients were computed using programs in the CLUSTAN IA package, according to the following general formula :-

$$\frac{a}{a + b + c}$$

<u>Species 1</u>	+	<u>Species 2</u>
	-	
	+	+
	-	-
	+	a
	-	b
	+	c
	-	d

where a = the number of occurrences of both genera/species in the same sample

b = the number of occurrences of the first genus/species without the second

c = the number of occurrences of the second genus/species in the absence of the first.

The results are given in Table 8, showing coefficients for the ten nearest neighbours in each case. A key to the species number (e.g. S₁, S₂) is given below. It was hoped that the coefficients might show similarity between certain pairs of genera or species, especially for corals showing some zonation with depth and being most common at about the same depth. The lack of any conclusive results is probably due to insufficient data.

Table 8 Species similarity coefficients

		PAIR RELATIONS													
10 K-LISTAGE LISTS (I.E. THE 10 NEAREST NEIGHBOURS OF EACH CASE SPECIFIED IN THE LEFT HAND MARGIN, GIVEN IN ORDER AND PRECEDED BY THE SIMILARITY COEFFICIENT.)															
S 1	S ₁ 0.375 9 0.262 24 0.296 29 0.175 29	0.354 30	0.344 42	0.314 10	0.309 15	0.296 22	0.290 13	0.277 4	0.263 11						
S 2	S ₂ 0.296 5 0.175 29	0.278 24	0.275 41	0.255 4	0.257 9	0.253 33	0.216 25	0.206 34	0.197 24						
S 3	S ₃ 0.240 14 0.118 11	0.235 28	0.182 7	0.154 10	0.148 29	0.143 32	0.136 23	0.125 8	0.125 20						
S 4	S ₄ 0.327 5 0.224 29	0.309 9	0.294 42	0.282 25	0.281 30	0.277 1	0.247 23	0.245 6	0.245 2						
S 5	S ₅ 0.327 4 0.230 24	0.305 9	0.296 2	0.296 33	0.289 42	0.278 23	0.261 24	0.261 25	0.250 10						
S 6	S ₆ 0.275 29 0.160 24	0.270 30	0.245 4	0.208 9	0.209 25	0.187 22	0.174 35	0.167 23	0.167 33						
S 7	S ₇ 0.275 10 0.163 35	0.228 27	0.197 23	0.190 11	0.192 3	0.172 36	0.171 30	0.164 42	0.164 4						
S 8	S ₈ 0.255 29 0.184 1	0.237 38	0.211 24	0.209 13	0.206 9	0.200 26	0.197 23	0.197 30	0.192 4						
S 9	S ₉ 0.450 25 0.290 10	0.410 29	0.396 42	0.388 23	0.375 1	0.309 4	0.307 22	0.306 30	0.305 5						
S 10	S ₁₀ 0.341 11 0.240 35	0.334 1	0.315 23	0.305 34	0.290 9	0.289 42	0.280 29	0.275 7	0.260 5						
S 11	S ₁₁ 0.341 10 0.215 15	0.280 13	0.263 1	0.250 29	0.235 9	0.233 36	0.233 35	0.225 22	0.218 30						
S 12	S ₁₂ 0.334 13 0.130 42	0.250 40	0.225 15	0.193 16	0.179 1	0.150 23	0.138 17	0.138 37	0.135 30						
S 13	S ₁₃ 0.382 15 0.209 8	0.334 12	0.298 38	0.268 1	0.260 11	0.256 9	0.237 16	0.235 22	0.230 30						
S 14	S ₁₄ 0.250 24 0.193 9	0.244 38	0.240 3	0.238 29	0.231 35	0.219 23	0.207 1	0.207 32	0.197 15						
S 15	S ₁₅ 0.382 13 0.209 42	0.309 1	0.275 38	0.260 23	0.260 25	0.239 22	0.225 12	0.218 9	0.215 11						
S 16	S ₁₆ 0.237 13 0.084 42	0.193 12	0.134 15	0.104 14	0.100 8	0.091 1	0.091 31	0.091 37	0.091 38						
S 17	S ₁₇ 0.223 39 0.112 21	0.211 40	0.187 25	0.153 15	0.152 38	0.140 13	0.138 12	0.130 23	0.120 22						
S 18	S ₁₈ 0.194 38 0.091 13	0.132 15	0.177 20	0.137 31	0.130 1	0.112 11	0.100 22	0.096 4	0.094 5						
S 19	S ₁₉ 0.197 29 0.148 23	0.178 9	0.177 34	0.172 26	0.171 4	0.167 1	0.167 5	0.167 14	0.150 36						
S 20	S ₂₀ 0.188 28 0.091 29	0.179 38	0.177 18	0.167 31	0.162 11	0.125 3	0.109 22	0.100 13	0.100 32						
S 21	S ₂₁ 0.194 39 0.122 23	0.142 10	0.167 27	0.155 9	0.153 13	0.149 32	0.143 30	0.138 1	0.138 42						
S 22	S ₂₂ 0.358 29 0.235 13	0.316 25	0.307 9	0.302 30	0.296 1	0.293 23	0.260 36	0.239 15	0.238 26						
S 23	S ₂₃ 0.435 29 0.257 42	0.408 25	0.398 9	0.315 10	0.283 22	0.278 5	0.266 24	0.262 1	0.260 15						
S 24	S ₂₄ 0.278 2 0.209 4	0.265 23	0.250 14	0.247 9	0.246 29	0.230 5	0.226 32	0.211 8	0.211 33						
S 25	S ₂₅ 0.450 30 0.247 30	0.408 23	0.380 29	0.316 22	0.290 42	0.282 4	0.273 35	0.261 5	0.260 15						
S 26	S ₂₆ 0.286 36 0.172 19	0.236 22	0.204 23	0.200 8	0.200 11	0.200 29	0.196 10	0.190 24	0.175 35						
S 27	S ₂₇ 0.242 34 0.125 32	0.224 7	0.211 10	0.177 1	0.167 21	0.156 42	0.148 11	0.137 9	0.134 15						
S 28	S ₂₈ 0.250 32 0.146 29	0.236 3	0.188 20	0.186 14	0.182 11	0.177 1	0.162 36	0.162 38	0.147 13						
S 29	S ₂₉ 0.435 23 0.261 5	0.410 9	0.390 25	0.358 22	0.296 35	0.292 42	0.280 19	0.275 6	0.263 35						
S 30	S ₃₀ 0.354 1 0.231 23	0.312 43	0.306 9	0.302 22	0.281 4	0.279 6	0.247 25	0.245 33	0.234 10						
S 31	S ₃₁ 0.167 30 0.108 1	0.137 13	0.134 14	0.128 15	0.121 29	0.120 41	0.118 38	0.117 5	0.114 13						
S 32	S ₃₂ 0.250 28 0.143 3	0.226 24	0.207 14	0.200 33	0.179 34	0.179 9	0.167 11	0.149 21	0.148 36						
S 33	S ₃₃ 0.296 5 0.194 41	0.257 35	0.245 30	0.223 2	0.216 25	0.211 24	0.204 22	0.200 32	0.194 29						
S 34	S ₃₄ 0.228 5 0.135 23	0.206 2	0.179 32	0.177 17	0.170 22	0.163 24	0.152 25	0.148 26	0.139 33						
S 35	S ₃₅ 0.296 29 0.215 42	0.273 25	0.257 33	0.246 10	0.237 5	0.231 14	0.220 4	0.218 23	0.216 5						
S 36	S ₃₆ 0.305 19 0.200 5	0.266 26	0.263 29	0.260 9	0.260 22	0.255 1	0.242 27	0.233 11	0.205 4						
S 37	S ₃₇ 0.178 15 0.130 23	0.173 14	0.152 35	0.150 40	0.149 42	0.149 1	0.148 25	0.140 13	0.138 12						
S 38	S ₃₈ 0.248 13 0.194 19	0.275 15	0.244 14	0.237 8	0.233 11	0.223 29	0.198 9	0.196 24	0.194 1						
S 39	S ₃₉ 0.223 17 0.122 4	0.209 15	0.194 21	0.192 13	0.189 30	0.154 40	0.143 11	0.133 25	0.123 10						
S 40	S ₄₀ 0.296 12 0.091 32	0.211 17	0.194 35	0.190 17	0.112 15	0.108 14	0.104 27	0.099 23	0.095 13						
S 41	S ₄₁ 0.276 2 0.112 10	0.194 24	0.184 5	0.148 24	0.144 36	0.139 9	0.125 25	0.120 31	0.117 24						
S 42	S ₄₂ 0.354 3 0.215 5	0.354 1	0.312 49	0.294 4	0.292 29	0.290 25	0.289 5	0.288 10	0.267 24						

Key to numbering in Species Similarity Coefficients

- S₁ *Psammopora* (*Plesioseris*) spp.
 S₂ *Stylophora* cf. *mordax* + *Stylophora* spp.
 S₃ *Stylophora* cf. *pistillata*
 S₄ *Pocillopora* cf. *eydourii*
 S₅ *Acropora* spp. type 1
 S₆ *Acropora* spp. type 2
 S₇ *Acropora* spp. type 3
 S₈ *Astreopora* spp.
 S₉ *Montipora* spp.
 S₁₀ *Favona clavus* group
 S₁₁ *Favona varians* group
 S₁₂ *Leptoseris* spp.
 S₁₃ *Leptoseris?* *mycetoseroides* group
 S₁₄ "*Agariciella*" spp.
 S₁₅ *Pachyseris* spp.
 S₁₆ *Coscinaraea* spp.
 S₁₇ *Horastrea* spp.
 S₁₈ *Cyathoseris* spp.
 S₁₉ *Fungia* (*Pleuractis*) spp.
 S₂₀ *Fungia* (*Fungia*) *fungites*
 S₂₁ *Goniopora* spp.
 S₂₂ *Porites* massive group
 S₂₃ *Favia pallida/favus* group
 S₂₄ *Favia stelligera*
 S₂₅ *Favites pentagona* group
 S₂₆ *Favites virens/abdita* group

- S₂₇ *Goniastrea* cf. *palauensis*
S₂₈ *Goniastrea* *pectinata/planulata* group
S₂₉ *Platygyra* spp.
S₃₀ *Leptastrea* spp.
S₃₁ *Cyphastrea* spp.
S₃₂ *Echinopora* cf. *gemmacea*
S₃₃ *Galaxea* cf. *fascicularis*
S₃₄ *Ctenella* spp.
S₃₅ *Acanthastrea* spp.
S₃₆ *Symphyllia* spp.
S₃₇ *Lobophyllia* spp. + Mussid fragments
S₃₈ Pectiniids
S₃₉ *Dendrophyllia* + Dendrophylliids (fragments)
S₄₀ *Favites* spp.
S₄₁ *Heliopora* *coerulea*
S₄₂ *Porites* massive/encrusting group

SECTION 11 Samples collected at Egmont from Transects 2 to 10

Specimens were collected below 24m and to a maximum depth of 45m; there are also samples from Transect 6 above 9m. In all cases data from the reef flat collections are insufficient. (Unknown specimens are those which were recorded in the field log but the identifications could not be traced.)

TRANSECT 1 Insufficient data

TRANSECT 2 *Stylophora mordax*
Acropora humilis
Montipora tuberculata group
Leptoseris? mycetoseroides group
Favia
Favia stelligera
Favia pallida/favus group
Favites virens/abdita group
Favites pentagona group
Oulophyllia
Platygyra
Echinopora gemmacea
Galaxea fascicularis
Symphyllia (specimens unknown = about 6)

TRANSECT 3 *Psammopora (Plesioseris)*
Pocillopora eydouxi
Acropora hyacinthus group
Montipora tuberculata group
Pavona clavus group
Porites massive/encrusting group
Favites pentagona group
Echinopora gemmacea
Dendrophyllia
Heliopora coerulea (specimens unknown = about 3)

TRANSECT 4

Stylophora mordax
Stylophora sp.
Acropora cf. *variabilis*
Acropora cf. *abrotanoides*
Acropora sp.
Astreopora
Montipora foveolate group
Montipora tuberculate group
Fungia (*Pleuractis*)
Herpolitha limax
Porites massive/encrusting group
Favia stelligera
Favia
Favites virens/abditata group
Favites pentagona group
Favites
Goniastrea cf. *palauensis*
Hydnophora
Galaxea fascicularis
 ?*Dendrophyllia*
Turbinaria

(specimens unknown = about 6)

TRANSECT 5

Psammocora (*Plesioseris*)
Stylophora mordax
Acropora humilis
Acropora
Astreopora
Montipora tuberculate group
Montipora non-tuberculate group
Pavona clavus group
 "Agariciella"
 ?*Cycloseris*
Porites lichen
Favites pentagona group
Favites
Hydnophora
Echinopora gemmacea
Galaxea fascicularis
Ctenella
Symphyllia
Dendrophyllia
 ?*Dendrophyllia*
Turbinaria

(specimens unknown = about 14)

TRANSECT 6

(below 24m)

Pocillopora eydouxi
Acropora
Pavona clavus group

(specimens unknown = 1)

(above 9m)

Psammocora (*Plesioseris*)
Stylophora mordax
Acropora palifera
Acropora

TRANSECT 6

(above 9m) (Contd.)

Pavona clavus group
Fungia
Favia stelligera
Favites pentagona group
Favites
Goniastrea cf. *palauensis* (specimens unknown = about 1)

TRANSECT 7

Psammocora (*Plesioseris*)
Stylophora mordax
Pocillopora eydouxi
Pocillopora
Acropora
Astreopora
Montipora foveolate group
Montipora non-tuberculate group
Pavona clavus group
Leptoseris
Porites massive/encrusting group
Favites virens/abditata group
Favites
Goniastrea cf. *palauensis*
Cyphastrea
Galaxea fascicularis
 ?*Dendrophyllia*
Heliopora coerulea (specimens unknown = about 1)

TRANSECT 8

Pocillopora eydouxi
Acropora humilis
Montipora tuberculate group
Pavona clavus group
Fungia (*Pleuraetis*)
Favia stelligera
Favites pentagona group
Platygyra
Symphylia (specimens unknown = about 3)

TRANSECT 9

Psammocora (*Plesioseris*)
Pocillopora eydouxi
Acropora
Montipora tuberculate group
Pavona clavus group
Leptoseris
Porites cf. massive/encrusting group
Favites pentagona group
Platygyra
Leptastrea
Symphylia
Mycidium (specimens unknown = about 1)

TRANSECT 10*Acropora cf. variabilis**Acropora**Montipora* non-tuberculate group*Pavona clavus* group*Leptoseris? mycetoseroides* group*Pachyseris**Favia**Favites virens/abditata* group*Favites pentagona* group*Leptoria**Galaxea fascicularis**Mycidium*

(specimens unknown = about 3)

SECTION IIISpecimens collected in quadrat and random samplesat Chagos Bank, which were used for analysis of data

As previously stated, about one-third of the data from the Chagos Bank had to be discarded, and only 222 of the 317 quadrat and random collections could be used for further analysis of the data. Table 9 is a SHUFFLE to show which genera and species were contained in the 222 samples; this is intended for reference purposes only.

The species code used in the computer print-out may not in some cases be clear to the reader, and therefore a key is given below, showing the full names of the genera and species. In addition there is a key to the sample numbers, indicating the location and depth of each sample and whether the collection was random or from a quadrat.

KEY TO GENERA AND SPECIES IN COMPUTER OUTPUT

<u>No.</u>	<u>Code</u>	<u>Genus or species</u>
102	?PSA EXSE	? <i>Psammocora</i> spp.
002	PLES SPP	<i>Psammocora</i> (<i>Plesioseris</i>) spp.
003	STYL MORD	<i>Stylophora</i> cf. <i>mordax</i>
004	STYL PIST	<i>Stylophora</i> cf. <i>pistillata</i>
005	STYL ONE	<i>Stylophora</i> spp. type 1
006	STYL DEEP	<i>Stylophora</i> spp. deep water forms
007	STYL SPP	<i>Stylophora</i> spp.
008	SERI SPP	<i>Seriatopora</i> spp.
009	POCI DAMI	<i>Pocillopora</i> cf. <i>damicornis</i>
010	POCI DANA	<i>Pocillopora</i> <i>danae/verrucosa</i>
011	POCI EYDO	<i>Pocillopora</i> cf. <i>eydouxi</i>
012	POCI SPP	<i>Pocillopora</i> spp.
013	ACRO PALI	<i>Acropora</i> <i>palifera</i>
014	ACRO ONE	<i>Acropora</i> spp. type 1
015	ACRO TWO	<i>Acropora</i> spp. type 2
016	ACRO THRE	<i>Acropora</i> spp. type 2
017	ACRO SPP	<i>Acropora</i> spp.
018	ASTR SPP	<i>Astreopora</i> spp.
019	MONT SPP	<i>Montipora</i> spp.
020	PAVO CLAV	<i>Pavona</i> <i>clavus</i> group
022	PAVO VARI	<i>Pavona</i> <i>varians</i> group
023	POLY SPP	<i>Pavona</i> (<i>Polyastra</i>) spp.
024	PSEU SPP	<i>Pavona</i> (<i>Pseudocolumnastrea</i>) spp.
025	PAVO SPP	<i>Pavona</i> spp.
026	LEPT SPP	<i>Leptoseris</i> spp.
027	LEPT ONE	<i>Leptoseris</i> spp. type 1
028	LEPT MYCE	<i>Leptoseris?</i> <i>mycetoseroides</i> group
029	CF L MYCE	cf. <i>Leptoseris?</i> <i>mycetoseroides</i> group
020	AGAR SPP	" <i>Agariotiella</i> " spp.
030	PACH SPP	<i>Pachyseris</i> spp.
031	COSC SPP	<i>Coscinaraea</i> spp.
032	CF C SPP	cf. <i>Coscinaraea</i> spp.
033	CF C CONV	cf. <i>Coscinaraea</i> spp. convoluted
034	HORA SPP	<i>Horastrea</i> spp.
035	CF H SPP	cf. <i>Horastrea</i> spp. <i>cerioid</i>
036	CYCL SPP	<i>Cycloseris</i> spp.
037	PLEU SPP	<i>Fungia</i> (<i>Pleuraetis</i>) spp.
038	VERR SPP	<i>F.</i> (<i>Verrillofungia</i>) spp.
109	?VER SPP	<i>F.</i> (? <i>Verrillofungia</i>) spp.
041	FUNG FUNG	<i>F.</i> (<i>Fungia</i>) <i>fungites</i>
110	?FUN FUNG	<i>F.</i> (? <i>Fungia</i>) <i>fungites</i>
042	FUNG YOUN	Young <i>Fungia</i>
047	PODA SPP	<i>Podabacia</i> spp.
048	GONI SPP	<i>Goniopora</i> spp.
049	GONI X TY	<i>Goniopora</i> spp. type 1
050	PORI MASS	<i>Porites</i> massive group
051	PORI M/EN	<i>Porites</i> massive/encrusting group
052	PORI LICH	<i>Porites</i> <i>lichen</i>
053	PORI BRAN	<i>Porites</i> spp. branching
108	SYNA SPP	<i>Porites</i> (<i>Synaraea</i>) spp.

<u>No.</u>	<u>Code</u>	<u>Genus or species</u>
054	AI VE SPP	<i>Alveopora</i> spp.
055	FAVI PALL	<i>Favia pallida/favus</i> group
056	FAVI STEL	<i>Favia stelligera</i>
057	FAVI CF S	<i>Favia</i> cf. <i>stelligera</i>
058	FAVI SPP	<i>Favia</i> spp.
059	FVIT PENT	<i>Favites pentagona</i> group
060	FVIT VIRE	<i>Favites virens/abdita</i> group
061	FVIT SPP	<i>Favites</i> spp.
062	OULO SPP	<i>Oulophyllia</i> spp.
063	GONA PALA	<i>Goniastrea</i> cf. <i>palauensis</i>
064	GONA PECT	<i>Goniastrea pectinata/planulata</i> group
066	GONA SPP	<i>Goniastrea</i> spp.
067	PLAT SPP	<i>Platygyra</i> spp.
068	LTOR SPP	<i>Leptoria</i> spp.
070	HYDN SPP	<i>Hydnophora</i> spp.
071	LSTR SPP	<i>Leptastrea</i> spp.
072	CYPH SPP	<i>Cyphastrea</i> spp.
073	ECHI GEMM	<i>Echinopora</i> cf. <i>gemmacea</i>
074	ECHI LAME	<i>Echinopora</i> cf. <i>lamellosa</i>
076	GALA FASC	<i>Galaxea</i> cf. <i>fascicularis</i>
077	GALA SMAL	<i>Galaxea</i> spp. type 1
078	CTEN SP.	<i>Ctenella</i> sp.
080	ACAN SPP	<i>Acanthastrea</i> spp.
081	LOBO SPP	<i>Lobophyllia</i> spp.
082	?LOB SPP	? <i>Lobophyllia</i> spp.
083	SYMP SPP	<i>Symphyllia</i> spp.
084	?SYM SPP	? <i>Symphyllia</i> spp.
085	MUSS FRAG	Mussid fragments
086	EPHY SPP	<i>Echinophyllia</i> spp.
087	?EPH SPP	? <i>Echinophyllia</i> spp.
088	OXYP SPP	<i>Oxypora</i> spp.
089	MYCE SPP	<i>Mycedium</i> spp.
090	?MYC SPP	? <i>Mycedium</i> spp.
091	PECT SPP	<i>Pectinia</i> spp.
092	PECT FRAG	Pectinid fragments
098	DEND SPP	<i>Dendrophyllia</i> spp.
099	TUBA SPP	<i>Tubastrea</i> spp.
100	TURB SPP	<i>Turbinaria</i> spp.
101	DEND YOUN	Dendrophylliids
103	TUBI MUSI	<i>Tubipora musica</i>
104	HELI COER	<i>Helipora coerulea</i>
105	HYDR VARI	Hydrozoans

KEY TO SAMPLE NUMBERS IN COMPUTER OUTPUT

<u>Sample Number</u>	<u>Transect and location</u>	<u>Depth (m)</u>
001	3 North Brother	18 Q
002	3	18 R
003	3	24 Q
004	3	24 R
006	4 North Brother	27 R
008	5 Middle Brother	6 Q
009	5	6 R
010	5	18 Q
011	5	18 R
012	5	33 Q
013	5	24 Q
014	5	24 R
015	6 Middle Brother	45 R
016	6	18 R
017	6	18 Q
018	6	30 R
019	7 Middle Brother	6 Q
020	7	6 R
021	7	12 Q
022	7	12 R
023	8 Middle Brother	6 Q
024	8	6 R
025	8	18 Q
026	8	18 R
027	9 South Brother	30 Q
028	10 South Brother	24 Q
029	10	24 R
030	11 South Brother	38 R
031	11	12 Q
032	11	24 Q
033	11	38 Q
034	11	38 R
035	14 Grande Passe Mounds	10 Q
036	14	18 Q
037	14	10 R
038	14	18 R
039	15 Grande Passe Mounds	9 Q
040	15	9 R
041	15	19 Q
042	15	19 R
043	15	27 Q
044	15	27 R
045	16 Grande Passe Mounds	12 Q
046	16	12 R
047	16	18 Q
048	16	21 Q
049	16	21 R
050	17 Eagle Island	12 Q
051	17	12 R
052	17	18 Q
053	17	18 R

<u>Sample number</u>	<u>Transect and location</u>	<u>Depth</u>
054	17	24 Q
055	17	24 R
056	17	30 Q
057	17	30 R
058	17	38 Q
059	17	38 R
060	18 Eagle Island	38 Q
061	18	38 R
062	18	45 Q
063	11	6 Q
064	18	6 R
065	18	3 Q
066	18	3 R
067	18	30 Q
068	18	30 R
069	18	12 R
070	18	24 Q
071	18	24 R
072	19 Eagle Island	12 Q
073	19	6 Q
074	19	18 R
075	19	18 Q
076	19	30 Q
077	19	30 R
078	19	24 Q
079	19	24 R
080	19	3 Q
081	19	3R
082	20 Sea Cow	36 Q
083	20	36 R
084	20	41 R
085	20	41 Q
086	20	6 Q
087	20	6 R
088	20	3 Q
089	20	3 R
090	20	24 Q
091	20	24 R
092	20	18 Q
093	20	18 R
094	20	12 Q
095	20	12 R
096	21 Sea Cow	3 Q
097	21	6 Q
098	21	6 R
099	21	18 Q
100	21	24 Q
101	21	24 R
102	21	30 Q
103	24 Passe Jacques	21 Q
104	24	21 R
105	24	15 Q
106	24	15 R
107	24	30 Q
108	24	30 R

<u>Sample Number</u>	<u>Transect and location</u>	<u>Depth</u>
109	27 Danger Island	21 Q
110	27	21 R
111	28 Danger Island	12 R
112	28	18 R
113	28	30 Q
114	28	32 Q
115	28	32 R
116	28	3 Q
117	28	6 Q
118	28	6 R
119	32 Resurgent	18 Q
120	32	18 R
121	32	9 Q
122	32	9 R
123	33 Resurgent	15 R
124	34 Resurgent	15 Q
125	34	24 R
126	35 Resurgent	3 Q
127	35	33 R
128	36 Eagle Island	30 Q
129	37 Between Eagle and Sea Cow	38 Q
130	37	38 R
131	37	30 Q
132	37	30 R
133	37	45 Q
134	37	45 R
135	37	18 Q
136	37	18 R
137	37	12 Q
138	37	12 R
139	38 Between Eagle and Sea Cow	18 Q
140	38	18 R
141	38	12 Q
142	38	12 R
143	38	30 Q
144	38	30 R
145	38	24 Q
146	38	24 R
147	39 East of Eagle	33 Q
148	39	18 R
149	39	45 R
150	39	12 Q
151	39	12 R
152	40 Sea Mound east of Eagle	38 Q
153	40	38 R
154	40	30 Q
155	40	30 R
156	40	24 Q
157	40	24 R
158	40	12 Q
159	40	12 R
160	41 Eagle Island	24 Q
161	41	24 R
162	41	30 Q
163	41	30 R
164	41	18 Q

<u>Sample Number</u>	<u>Transect and location</u>	<u>Depth</u>
165	41	18 R
166	41	38 Q
167	41	38 R
168	41	6 Q
169	41	6 R
170	41	12 Q
171	41	12 R
172	41	45 Q
173	41	45 R
174	41	3 R
175	42 Danger Island	25 Q
176	42	18 R
177	42	9 Q
178	42	9 R
179	42	3 Q
180	42	3 R
181	43 Grande Passe	24 Q
182	43	24 R
183	43	42 R
184	43	18 R
185	43	30 Q
186	99 Diego Garcia	21 Q
187	99	21 R
188	1 North Brother	18 Q
189	1	6 Q
190	2 North Brother	18 Q
191	6 Middle Brother	6 Q
192	6	30 Q
193	10 South Brother	12 Q
194	2 North Brother	18 R
195	11 South Brother	45 Q
196	11	45 R
197	17 Eagle Island	6 Q
198	17	3 Q
199	17	3 R
200	17	45 Q
201	17	45 R
202	19 Eagle Island	6 R
203	27 Danger Island	24 Q
204	27	24 R
205	27	30 R
206	27	38 Q
207	27	38 R
208	27	30 Q
209	28 Danger Island	39 Q
210	34 Resurgent	15 R
211	35 Resurgent	24 Q
212	36 Eagle Island	30 R
213	36	3 Q
214	36	3 R
215	39 East of Eagle	33 R
216	39	18 Q

<u>Sample Number</u>	<u>Transect and location</u>	<u>Depth</u>
217	40 Sea Mound east of Eagle	18 Q
218	40	18 R
219	42 Danger Island	25 R
220	42	18 Q
221	43 Grande Passe	42 Q
222	12 South Brother	32 Q
223	12	6 R
224	12	18 Q

TABLE 5 Genera and species ordered in depth classes from 3m to 45m

Data from quadrat samples only. See text for explanation.

	3-6 m	9- 12m	15- 19m	21- 25m	27- 32m	33- 45m
<i>Acropora</i> spp. type 1	○ ○ ○					
<i>Leptoria</i> spp.	○ ○ ○					
<i>Heliopora coerulea</i>	▨	○ ○ ○				
<i>S.cf.mordax</i> + <i>Stylophora</i> spp.	■	○ ○ ○	○ ○ ○			
<i>Galaxea cf. fascicularis</i>	▨	▨	○ ○ ○	○ ○ ○		
<i>Pocillopora cf. eydouxi</i>	▨		▨	▨		
<i>Favia stelligera</i>	▨		○ ○ ○			
<i>Platygyra</i> spp.	■		▨	■	▨	○ ○ ○
<i>Favites pentagona</i> group	■		▨		▨	○ ○ ○
<i>Favia pallida/favus</i> group	■				▨	○ ○ ○
<i>Montipora</i> spp.	■				■	○ ○ ○
<i>Acropora</i> spp. type 2	▨		▨	○ ○ ○		
<i>Leptastrea</i> spp.	▨	■		▨	▨	
<i>Favites virens/abditata</i> group	○ ○ ○		▨	○ ○ ○		
<i>Echinopora cf. gemmacea</i>		▨		○ ○ ○		
<i>Acanthastrea</i> spp.	○ ○ ○	▨	▨	▨		
<i>Acropora</i> spp. type 3		▨		○ ○ ○		
<i>Astreopora</i> spp.		■	▨	▨	○ ○ ○	○ ○ ○
<i>Ctenella</i> spp.	○ ○ ○	○ ○ ○	▨	○ ○ ○	○ ○ ○	
<i>Fungia (Pleuraetis)</i> spp.	○ ○ ○	○ ○ ○	▨	○ ○ ○	○ ○ ○	
<i>Porites</i> massive group	▨	■	▨	■	○ ○ ○	○ ○ ○
<i>Acropora</i> spp. (incl. <i>A. palifera</i>)	▨	▨	■	▨	○ ○ ○	○ ○ ○
<i>Porites</i> massive/encrusting group	▨	▨	■	▨	○ ○ ○	○ ○ ○
<i>Favona clavus</i> group		▨	▨	▨		
<i>Favona varians</i> group		▨	▨			○ ○ ○
<i>Psammocora (Plesioseris)</i> spp.		▨	■	▨	■	▨
" <i>Agariciella</i> " spp.			▨	▨	○ ○ ○	
<i>Goniopora</i> spp.			▨	▨	○ ○ ○	
<i>Goniastrea cf. palauensis</i>			▨	▨	○ ○ ○	○ ○ ○
<i>Symphyllia</i> spp. + Mussid fragments			■	▨	▨	○ ○ ○
<i>Stylophora cf. pistillata</i>				○ ○ ○		
<i>Seriatopora</i> spp.				○ ○ ○		
<i>Cyphastrea</i> spp.				○ ○ ○		
<i>Oulophyllia</i> spp.				○ ○ ○		
? <i>Psammocora</i> spp.				○ ○ ○		
<i>Goniastrea pectinata/planulata</i> group				▨		
<i>Horastrea</i> spp.				▨	▨	○ ○ ○
<i>Dendrophyllia</i> + <i>Dendrophylliid</i> fragments				▨	▨	○ ○ ○
<i>Tubastrea</i> spp.					○ ○ ○	
<i>Fungia (Fungia) fungites</i>					▨	
<i>Cycloseris</i> spp.					▨	
Pectiniids (all genera)					■	▨
<i>Pachyseris</i> spp.					■	■
<i>Leptoseris? mycetoseroides</i> group		○ ○ ○	○ ○ ○	▨	▨	■
<i>Leptoseris</i> spp.					▨	■
<i>Coscinaraea</i> spp.						▨

No. of quadrats in depth class

21 16 24 20 18 19

Present in % of quadrats

< 15%



15-24%



in depth class

25-50%



> 50%



Table with 102 rows of codes (e.g., PPSA EXSE, PLES SPP) and 100 columns of binary data (0s and 1s).

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